

Changes in otter diet in South Wales 1984-2016

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Crynodeb gweithredol

Mae afonydd wedi wynebu effeithiau sylweddol oherwydd gweithgaredd dynol, yn enwedig yn ystod y degawdau diwethaf, ac mae hyn wedi effeithio ar oroesiad rhywogaethau afonol. Gan eu bod yn ysglyfaethwyr apig, mae dyfrgwn yn dibynnu ar amrywiol rywogaethau o ysglyfaeth, a gall newidiadau yn y we fwyd ddyfrol effeithio ar eu poblogaeth. Bu'r prosiect hwn yn astudio newidiadau yn neiet dyfrgwn ar draws chwe dalgylch yn Ne Cymru gyda'r nod o ddeall y goblygiadau ar bresenoldeb dyfrgwn.

Roedd yr astudiaeth yn cynnwys casglu a dadansoddi baw dyfrgwn i geisio darganfod gweddillion eu hysglyfaeth. Casglwyd y baw yn ystod yr ail, y trydydd a'r chweched arolwg cenedlaethol o Gymru (1984-85, 1991, a 2015-16) o 517 o safleoedd ar draws chwe dalgylch afon: Teifi, Tywi, Cleddau, Wysg uchaf, Gwy uchaf, a Hafren uchaf. Penderfynwyd beth oedd cynnwys deiet dyfrgwn drwy adnabod rhannau caled yr ysglyfaeth yn weledol (esgyrn, cennau pysgod, plu, ffwr).

Gwelwyd newidiadau sylweddol yn neiet dyfrgwn dros gyfnod yr astudiaeth, gyda gostyngiad nodedig yn nifer y llyswennod oedd yn cael eu bwyta a chynnydd yn y nifer o rywogaethau pysgod llai fel crethyll a phennau lletwad, ac ysglyfaeth nad ydynt yn bysgod (amffibiaid, cimychiaid, mamaliaid, adar).

Drwy archwilio deiet dyfrgwn ar raddfa'r dalgylch, roedd yn bosibl disgrifio rhai gwahaniaethau lleol e.e. mewn dalgylchoedd yng ngorllewin Cymru, roedd eogiaid yn ffurfio cyfran debyg o ddeiet dyfrgwn ar draws y cyfnodau astudio, tra bo gweddillion eogiaid yn neiet dyfrgwn wedi gostwng yn rhan uchaf Afon Gwy. Fodd bynnag, mae'n bwysig nodi'r cyfyngiadau yn nosbarthiad y samplau ar draws y dalgylch oherwydd y ffin weinyddol (Cymru a Lloegr) wrth ddehongli'r canlyniadau.

Nid yw'n hawdd cael gafeael ar ddata ysglyfaeth a biomas, neu mae'n brin ar gyfer y rhan fwyaf o rywogaethau. Felly nid oedd bob amser yn bosibl asesu a oedd newidiadau yn neiet dyfrgwn yn adlewyrchu argaeledd ysglyfaeth. Mae cymariaethau bras â thueddiadau sy'n hysbys yn achos llyswennod a salmonidau yn dangos nad ydynt bob amser yn gysylltiedig. Ar ben hynny, mae'r canlyniadau yma'n awgrymu nad yw poblogaethau dyfrgwn yn ddibynnol ar yr hyn a elwir yn "hoff ysglyfaeth". Mae'r boblogaeth sefydlog o ddyfrgwn yn rhan uchaf Hafren yn dangos ei bod hi'n bosibl cynnal poblogaethau o ddyfrgwn (yn y tymor byr o leiaf) ar ddeietau nad ydynt yn cynnwys llawer o llyswennod na salmonidau.

Fodd bynnag, nid yw'r goblygiadau yn glir ar gyfer poblogaethau dyfrgwn yn achos gostyngiadau parhaus a ragwelir mewn salmonidau mewn dalgylchoedd lle mae dyfrgwn yn bwyta cyfran uwch o salmonidau. Mae angen rhagor o waith monitro ac ymchwilio i ddeall y goblygiadau hyn ac yn bwysicach hefyd y goblygiadau ar gyfer rhywogaethau ysglyfaethus, yn enwedig rhywogaethau gwarchodedig eraill e.e. pennau lletwad.

Executive summary

Rivers have faced significant impacts from human activity, especially in recent decades, affecting the survival of riverine species. The Eurasian otter (*Lutra lutra*), being an apex predator, depends on various prey species, and changes in the aquatic food web may impact their population. This project studied changes in otter diet across six catchments in South Wales with the aim of understanding the implications on otter presence.

The study involved the collection and analysis of otter spraints (faeces) to identify prey remains. The spraints were collected during the second, third, and sixth national surveys of Wales (1984-85, 1991, and 2015-16) from 517 sites across six river catchments: Teifi, Tywi, Cleddau, upper-Usk, upper-Wye, and upper-Severn. Otter diet was determined through the visual identification of hard parts of prey (bones, fish scales, feathers, fur).

Significant changes in otter diet were observed over the study period, with a notable decline in the consumption of eels and an increase in the consumption of smaller fish species like stickleback and bullhead, and non-fish prey (amphibians, crayfish, mammals, birds).

Through examination of otter diet at the catchment scale, it was possible to describe some localised differences e.g. in west Wales catchments, salmonids made up a similar proportion of otter diet across the study periods, whilst in the upper-Wye salmonid remains in otter diet declined. However, limitations in sample distribution across the catchment due to administrative boundary (Wales and England) are important to note when interpreting the results.

Data on prey availability and biomass are either not easily accessible, or are lacking for most species. Therefore it was not always possible to assess if changes in otter diet reflect prey availability. Broad comparisons with known trends of eel and salmonids indicate that they are not always associated. Furthermore, results here suggest that otter populations are not dependent on so called “favoured prey”. The stable otter population in the upper-Severn indicates that it is possible for otter populations to be sustained (at least in the short term) on diets that are not high in eels or salmonids.

However, the implications for otter populations of the predicted continued salmonid declines in catchments where otters consume a higher proportion of salmonids are unclear. Further monitoring and research is needed to understand these implications and importantly also the implications for prey species, particularly other protected species e.g. bullhead.

Introduction

River ecosystems have been heavily impacted by human activity, especially in recent decades. The range of pressures exerted on rivers have significantly impacted the health and survival of riverine species (WWF, 2024). As a consequence, aquatic food webs have undergone substantial and rapid changes in their composition, evident across all trophic levels (Moi, et al., 2024). As an apex predator in UK riverine ecosystems, these dramatic changes in food webs could pose a risk to Eurasian otters. However the trophic flexibility of the species, allowing it to exploit a wide variety of aquatic and some terrestrial prey (e.g. Drake, 2023), may enable adaptation to changes in prey communities.

Wales wide monitoring of otters in the form of ecological surveys have been conducted six times between 1977 and 2018. Whilst initially these surveys tracked an increase in otter distribution across Wales (from 20% of sites surveyed having signs of otters in 1977-78, to 90% in 2009-10), the most recent survey provided the first evidence of a potential downturn of that recovery to 70% detection rate in 2015-18 (Kean and Chadwick, 2021). Changes vary between hydrometric areas, with some showing substantial declines, while others remain apparently stable. Reasons for this are unclear, and a number of possibilities are under consideration; changes in prey availability (e.g. declining eel and salmonid populations, ICES, 2023, Milner and Garcia de Leaniz., 2023) could be a factor.

Where otters have recovered from historical declines, prey biomass was thought to be the determining factor of the carrying capacity of a waterbody (Chanin, 2003). Additionally, changes in the prey species consumed might reduce total energy acquisition. Anecdotal, as well as more scientifically rigorous investigations, indicate otters favour large, nutrient rich prey species such as eels and salmonids (Jenkins and Harper, 1980, Britton et al., 2006). Increased energetic costs of capturing multiple smaller prey compared with large prey such as salmonids or eel have been hypothesised (Moorhouse Gann et al., 2020). Some changes in diet can also result in nutrient deficiencies e.g. thiamine deficiency has been recorded in captive otters (*Lontra Canadensis*, Aulerich, 1995) and is a potential driver of wildlife population declines (Sutherland et al, 2017).

The recovery and morphological identification of prey remains from spraint – otter droppings (Grant and Harrington, 2015, Britton et al., 2017, Clavero et al., 2005 Jedrzejewska et al., 2001) and stomach contents (Moorhouse-Gann et al., 2020) provides a wide body of evidence describing spatial, temporal and biotic variation in otter diet. More recent advances in molecular techniques has generated further insight, providing greater taxonomic resolution (particularly for more cryptic prey which are fully digested and do not allow recovery of prey bones) (Drake et al., 2023). Recent analyses indicate that otter diet has changed across recent decades in England and Wales (1994-2010 Moorhouse Gann et al., 2020, Almeida et al., 2012), with less frequent predation on eels *Anguilla anguilla*, and more frequent predation on stickleback species (family *Gasterosteidae*) and bullhead *Cottus gobio*. Another UK study combining DNA metabarcoding with morphological analysis of prey remains, but over a shorter and more recent time period (2007-2016) found no significant temporal change (Drake, 2023). This more recent diet research demonstrated some broad spatial scale associations of otter diet with known prey distributions (e.g. greater consumption of marine prey near the coast and greater consumption of bullhead inland).

Here, we build on this body of evidence of otter dietary changes by examining changes at a finer spatial resolution. We describe differences in otter diet between six catchments in south Wales, evaluate the evidence for change over time in each catchment, and compare those findings with changes in otter presence as identified by comparison of data from the sixth national Otter Survey Wales (Kean and Chadwick, 2021).

Methods

The diet of the otter was determined through the visual identification of prey remains (hard parts – bones, fish scales, feathers, and fur) within otter spraints (faeces). This method allows for ease of sample collection over large spatial and temporal scales. The method is widely used to describe otter diet, and its employment in this study ensures comparability with other studies. They give only a good indication of what otters have eaten, but due to the variation in the quantity of hard parts in each prey type, and differences in the digestibility of those hard parts (Carss and Parkinson, 1996) some detail of diet is not captured well i.e. some prey may not be identifiable following digestion in the otter.

Spraint collection

Spraints were collected during the second, third and sixth national surveys of Wales (1984-85, 1991, and 2015-16) from 517 sites across six river catchments; Teifi, Tywi, Cleddau, Usk, Wye, Severn. No spraints were collected on the Cleddau and the Severn in the 1984-1985 survey period, nor on the Wye and the Usk in the 1991 survey period (Table 1). One spraint was collected from each site and sampling event (occasionally two). Spraints collected during the second (1984-85) and third (1991) surveys were stored in a freezer at the Cardiff University Llysdyman Field Centre, Newbridge on Wye (no longer operational). Spraints collected during the sixth survey were stored at Cardiff University School of Bioscience, Cardiff.

The survey sites selected in the first national survey of Wales (1977-78) have been revisited in each subsequent national survey, with the exception of a small number of sites that had changes in accessibility, either physical or landowner permission (see sixth survey for details). In the Usk catchment spraint collection was limited to the upper catchment (Figure 1). It is important to note that the surveys were restricted to Wales, so the lower, English, sections of the rivers Wye and Severn were not surveyed.

For further analysis, we selected only spraints that were collected in summer (from May to September), in order to avoid variability resulting for seasonal patterns in otter diet (25 spraints excluded). In order to reduce spatial autocorrelation, when two spraints had been collected at the same site (or within <2.5km on the same catchment) during the same survey, just one was selected randomly for inclusion in further analysis. Finally, those spraints suspected of not belonging to otters (i.e. identification failures of the surveyor) or from which no information on diet composition (i.e. no identifiable hard prey remains) could be extracted were also excluded from the analyses. The application of these filtering criteria resulted in a total of 701 spraints.

Table 1 Number of spraints analysed across six catchments and three survey periods

Catchment	No. of survey sites	Spraints analysed 1984-85	Spraints analysed 1991	Spraints analysed 2015-16
Cleddau	67	<i>None collected</i>	60	31
Severn	101	<i>None collected</i>	67	82
Teifi	75	38	49	26
Tywi	90	86	73	48
Usk	62	15	<i>None collected</i>	11
Wye	122	43	<i>None collected</i>	72
TOTAL	517	184	249	270

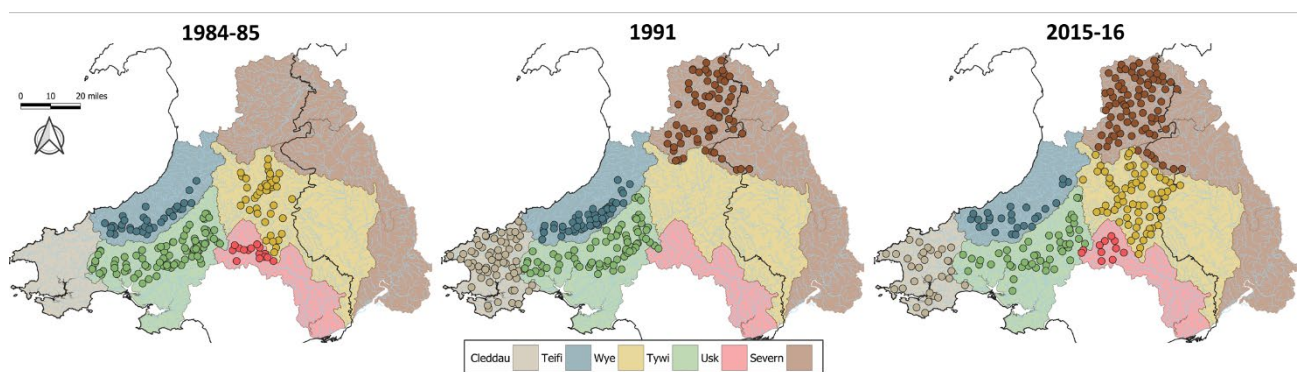


Figure 1 Locations of otter spraints included in this study from across three survey time periods (total n=701).

Microscopy and Prey identification

Spraints were thawed and then placed in petri dishes and immersed in a solution of water and commercial biological detergent (10:1) for 12-24 hr to aid the removal of digested matter. They were then gently rinsed under running tap water through a 0.5 mm mesh, to remove digested matter, soil or detergent residue (i.e. only hard parts remained). The undigested remains were removed from the sieve and placed on filter paper, and air dried.

Undigested prey remains were examined using a binocular microscope and identified and recorded with the aid of published references (Conroy, Watt, Webb, & Jones, 2005; Day, 1966; Libois, Hallet-Libois, & Rosoux, 1987; Miranda & Escala, 2002; Teerink, 1991), online resources (<http://fishbone.nottingham.ac.uk/> and <https://osteobase.mnhn.fr/>) and our own reference collection of prey remains.

Prey remains were identified by Sergio Bedmar, who is experienced in this procedure. Prey remains were identified to the lowest possible taxonomic level. However, the taxonomic resolution was not the same for all samples or species, due to different extent of deterioration of remains, or to a lack of diagnostic structures. Therefore, some prey species were pooled into prey types. For example, to reliably differentiate salmon and trout, recovery of the atlas bone or jaw parts was required. As there were poor recovery rates for these bones, salmon and trout were pooled in the “salmonid” category. Similarly,

some structures allowed the identification of some cyprinids to species level: minnows (*Phoxinus phoxinus*) and stone loaches (*Barbatula barbatula*), however a lack of distinguishing structures meant it was necessary to create a broad category of “other cyprinid” to include prey species belonging to the Leuciscidae (chub and roach) and the Cyprinidae (carp and barbel) families.

Each prey type was recorded as present or absent from every spraint. Fourteen different prey types were identified: nine of which were included in statistical models (Table 2). Two of those nine groups (mammal and bird) were infrequently found (n=18, 27 respectively) overall, but commonly enough in some catchments to be included in some statistical analyses. Four groups; marine fish, other fish, cyprinid, and crayfish, were also recorded occasionally but were not included in statistical models due to low sample size. Invertebrate remains (excluding crayfish) were commonly found (n=343) but were not included in statistical analysis because it is not possible to ascertain if consumption is direct or the result of secondary predation.

Table 2 Prey remains identified from otter spraints. N = number of spraints in which that prey type occurred. * = insufficient data so excluded from further analysis.

Prey type	Detail	N	Species names/other taxonomic subgroupings identified	Included in further analysis
Fish	Bullhead	354	<i>Cottus gobio</i> (354)	PCA+GLM
Fish	Salmonid	386	Salmonidae - species not identified (338), <i>Salmo trutta</i> (trout, 48)	PCA+GLM
Fish	Eel	279	<i>Anguilla anguilla</i> (279)	PCA+GLM
Fish	Stone Loach	223	<i>Barbatula barbatula</i> (223)	PCA+GLM
Fish	Minnow	170	<i>Phoxinus phoxinus</i> (170)	PCA+GLM
Fish	Stickleback	45	Gasterosteidae, species not identified (45)	PCA+GLM
Fish	*Other fish	*23	*Percidae (13), Petromyzontidae (lampreys; 9), <i>Exos lucius</i> (pike; 1)	*None
Fish	Other cyprinids	20	Other Cyprinidae and Leuciscidae (excluding <i>Phoxinus Phoxinus</i> and <i>Barbatula barbatula</i>)	PCA
Fish	*Marine fish	*9	*Pleuronectiformes (flatfish and sole; 5), Gobiidae (goby; 3), Blenniidae (blenny; 2), and <i>Syngnathus acus</i> (pipefish; 1)	*None
Non-fish	Amphibians	116	Anura (frogs and toads; 105) and Caudata (newts; 16)	PCA+GLM
Non-fish	Avian/Birds	27	Species not identified	PCA+GLM
Non-fish	Crayfish	20	Astacidae – species not identified	PCA
Non-fish	Mammal	18	Soricidae (shrew; 2), <i>Neomys fodiens</i> (water shrew; 1), Cricetidae (vole; 1), not identified mammals (14)	PCA+GLM
Non-fish	*Invertebrates (excluding crayfish)	*343	*Including insects, molluscs, and others	*None

Calculation of diet composition

There are a variety of ways in which animal diet can be described. The terms used to describe these calculations are not universally agreed and so for clarity we have detailed in full the calculations made for this study.

‘Occurrence’: There is no correlation between the number of bones counted in a spraint and the number of fish eaten; some fishes have more bones than others, and some bones are more prone to breakage that prevents identification (Conroy et al., 2005). Therefore each prey type identified in a spraint was considered as *one occurrence* regardless of how many items (bones, scales etc) of each prey type that spraint contained.

‘Frequency of occurrence’: Diet composition was expressed in terms of the percentage of spraints in which each prey type occurred, also known as “percentage occurrence”, or frequency of occurrence (FO). FO was calculated as:

(Number of spraints containing a given prey type/Total number of spraints in a sample) x100

‘Relative frequency of occurrence’ gives a measure of how frequent a prey type occurred relative to other prey types. Relative frequency of occurrence (RFO) was also calculated to facilitate comparison across survey years and catchments surveyed. RFO was calculated as:

(Number of occurrences of a prey type/total number of occurrences of all prey types) x100

N.B. there is no universal calculation of RFO, some studies calculate it based on prey type occurrences (as we have), others to each prey item.

Data visualisation

In order to visualise the overall temporal and spatial trends in otter diets we employed a principal components analysis (PCA). PCA summarises the variation contained within many variables into just a few new variables, known as Principal Components, which can then be plotted to visualise trends.

PCA was applied to the frequency of occurrence values for 11 prey types (Bullhead, Eel, Salmonid, Cyprinid, Minnow, Stone Loach, Stickleback, Amphibian, Mammal, Avian, Crayfish), across the six catchments and three sampling periods. PCA was performed using the ‘dudi.pca’ function in the ade4 package (version 1.7-22) in R (version 4.3.0) with rescaling applied.

Statistical analysis

In order to simultaneously test for change over time and spatial differences, we modelled presence / absence of each prey type, using a series of generalised linear models (GLMs). In each model, presence / absence of the prey type was the dependent variable, fitted with binomial error distributions and logit link function, i.e. the models described the probability of occurrence of each prey type. Models were fitted to the nine most common prey types

when there was sufficient data (see Table 2). For other prey types there was insufficient data to permit multivariate modelling.

Survey year and catchment were fitted to all models as independent (predictor) variables, to test for differences in probability of occurrence between survey years, and between catchments. The interaction term 'year: catchment' was also fitted, to test whether change over time differed between catchments / whether the nature of spatial differences differed between survey years. Model fit was evaluated by visualisation of the extracted deviance residuals, to check that their distribution met model assumptions. Model simplification was carried out using a process of stepwise deletion, to assess the significance of variables in the model based on the p-value of the chi-squared test.

Because sampling effort differed between catchments, it was necessary to repeat the models for each prey type with different year / catchment combinations as follows:

- Across all survey years (1984-85, 1991, 2015-16): data from Teifi and Tywi only for 7 prey types
- Between 1984-5, and 2015-16: data from Teifi, Tywi, Wye and Usk catchments for 9 prey types
- Between 1991, and 2015-16: data from Teifi, Tywi, Cleddau and Severn catchments only for 7 prey types

Results

Otter diet was varied, with fish prey dominant across all six river catchments and all three survey periods (Table 2). Full FO and RFO results are given in Appendix 1.

Overall diet

There were some significant differences in otter diet both between survey periods and between catchments, and for some types of prey the pattern in change over time differed between catchments (statistical model result details in Appendix 2). When all data were collated across the six river catchments, overall, there was a shift away from eels and salmonids, with multiple other prey types (bullheads, stickleback, mammals, birds, amphibians, crayfish, cyprinids, stone loach and minnow) explaining more of the variation in otter diet in recent years (Figure 2). Even when eel and salmonids dominated, otter diet in south Wales across all time periods (1984-2016) has always been diverse, each survey (single time period, single catchment) recorded between eight and thirteen prey types across a catchment.

Due to the limitations of this dataset the interpretation of trends is difficult and should be done with an awareness of those limitations. Those limitations were missing data (not all

catchments had spraint collected in all survey years) and low sampling frequency (only three time points over 32 years).

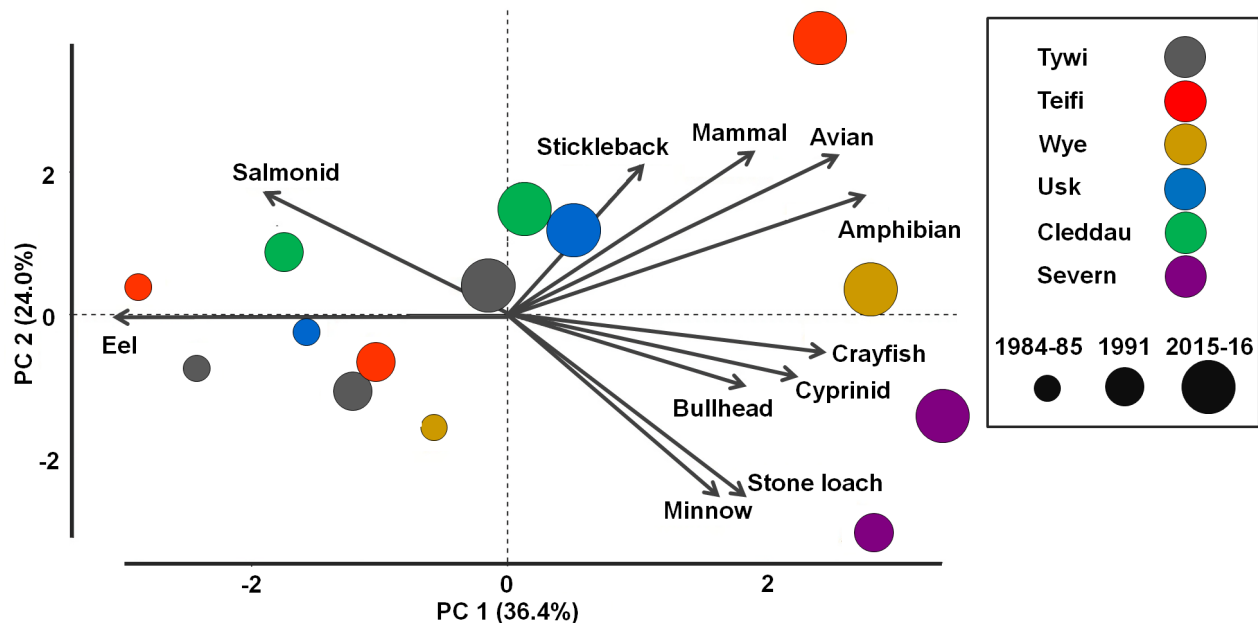


Figure 2 Otter diet Principal Components Analysis (PCA) plot of the first two principal components. Arrows = the loadings: how the original variables correlate with the principal components. Each symbol plotted represents the otter diet across a river catchment in a sampling period. Note that Cyprinid prey type excludes minnows (*Phoxinus phoxinus*) because they can be reliably differentiated.

Differences between catchments

When looking across the river catchments, the composition of otter diet in the Wye and Severn was somewhat different from the other rivers (Figure 3). The spatial distribution of samples collected in the Wye and Severn were restricted to the upper sections of these catchments because the lower areas are in England. Diet in the six catchments were characterised by:

Teifi (1984-85, 1991 and 2015-16)

- In 1984-5 survey otter diet was dominated by eels and salmonids (87%).
- Salmonids were the biggest proportion of diet in all survey periods.
- Eel decline
- Bullheads and non-fish prey have increased.

Tywi (1984-85, 1991 and 2015-16)

- In 1984-85 survey, salmonids were the most common prey type.
- Eel, bullhead and salmonid were the three most common prey types in all surveys.
- Eel decline

- Similar proportion of salmonids in all survey periods.
- Bullhead and amphibian increase

Cleddau (1991 and 2015-16)

- Eel and salmonids were the most common in 1991 and 2015-16.
- Eel and salmonid decline.
- Increase in bullhead, amphibians and marine fish
- Fewer stone loach in 2015-16 than in 1991.

Severn (1991 and 2015-16)

- Unusual in that stone loach and minnow were the most common prey types in 1991.
- Stone loach and minnow decrease.
- Eel rare in 1990 and absent in 2015-16
- Bullhead, amphibian, crayfish more common in 2015-16 than previously

Wye (1984-85 and 2015-16)

- In 1984-85 survey, salmonids were most common prey type.
- Salmonid decrease
- Bullhead and amphibian increase
- Eels uncommon in 1984-85 and absent in 2015-16
- In 1984-85 stone loach and minnow were a bigger proportion than in other catchments, and both small decrease
- Crayfish present in 2015-16 survey only

Usk (1984-85 and 2015-16)

- In 1984-85 survey, salmonids were most common prey type.
- Similar proportion of salmonids in both survey periods.
- Eel decrease, and eels not recorded in 2015-16
- Large increase in bullhead

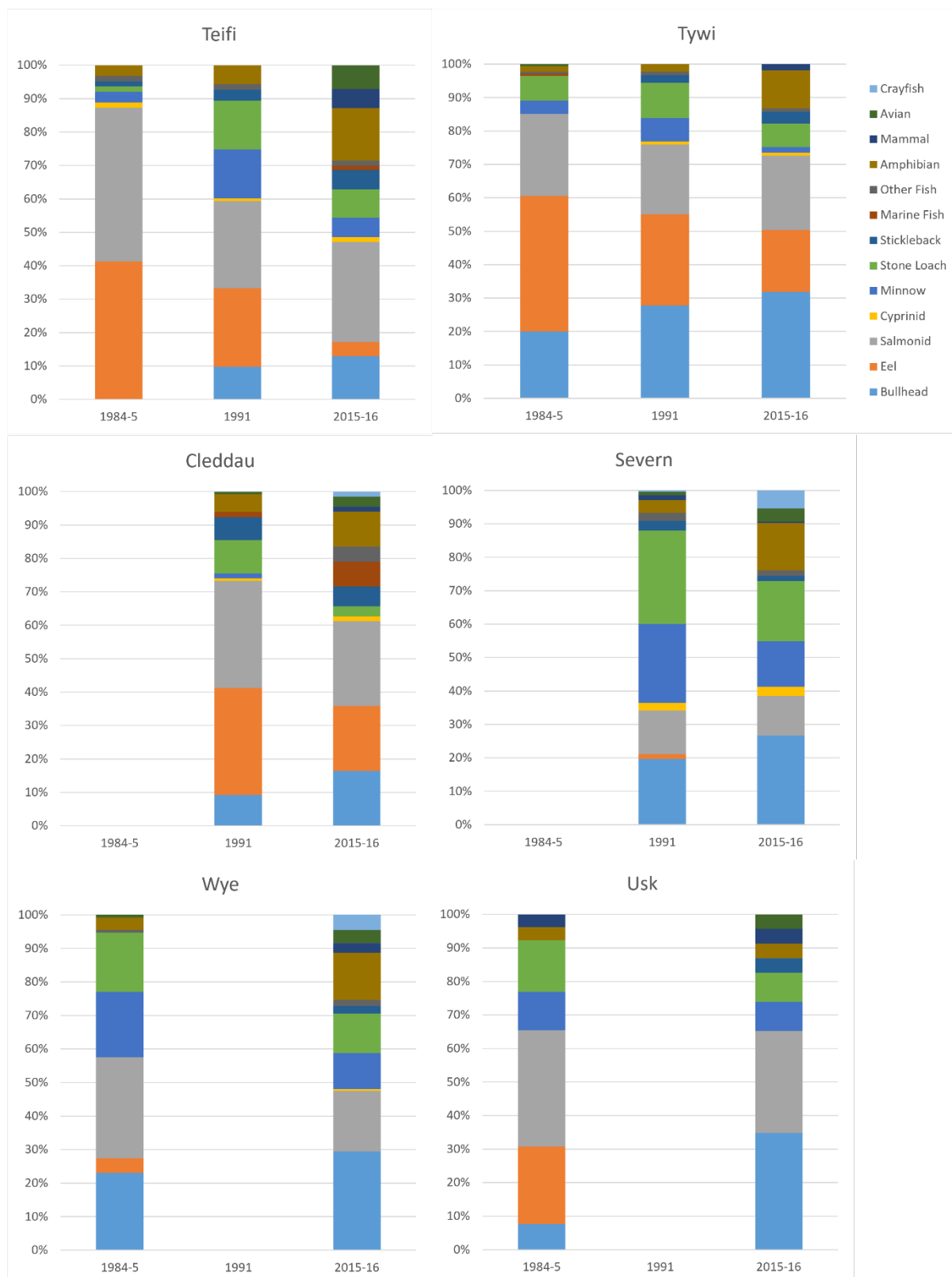


Figure 3 Composition of otter diet (using relative frequency of occurrence data)

Changes in individual prey types in otter diet

This section describes how the individual prey species/type categories have increased or decreased over time. Fish prey are described first in order from most frequently recorded to the least, followed by non-fish prey in the same order. Finally, the frequency of occurrence of prey types not included in statistical analyses are described.

Fish

Salmonids (*Salmonidae*)

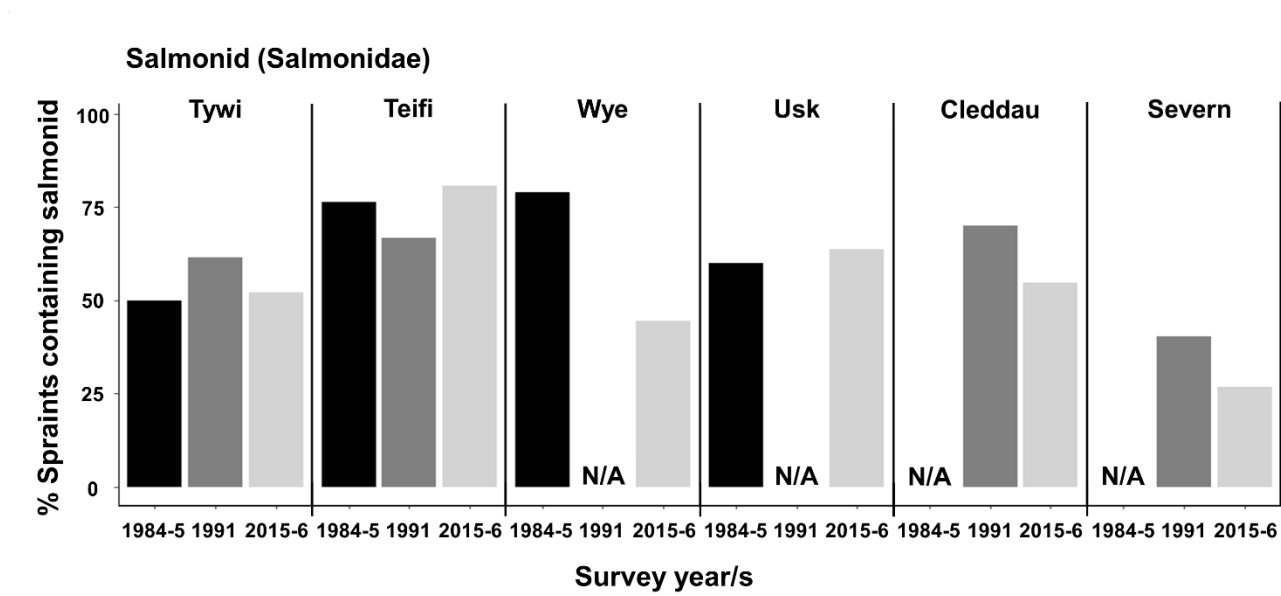


Figure 4 Frequency of occurrence of salmonid remains in otter spraint. N/A= spraints were not collected during this survey.

Salmonid remains were present in otter spraint in all time periods and in all survey catchments (where surveyed). The river catchment frequency of occurrence of salmonids ranged from 27-81% across the three survey periods, occurring in 59% of spraints overall. There were significantly fewer salmonid remains found in Twyi spraint than Teifi spraint, and the Severn had the fewest salmonid remains of all the catchments.

On the Wye, salmonids occurred significantly less frequently in 2015-16 than in 1984-5. Between year differences in the occurrence of salmonids were not significant in any of the other catchments.

Bullhead (*Cottus gobio*)

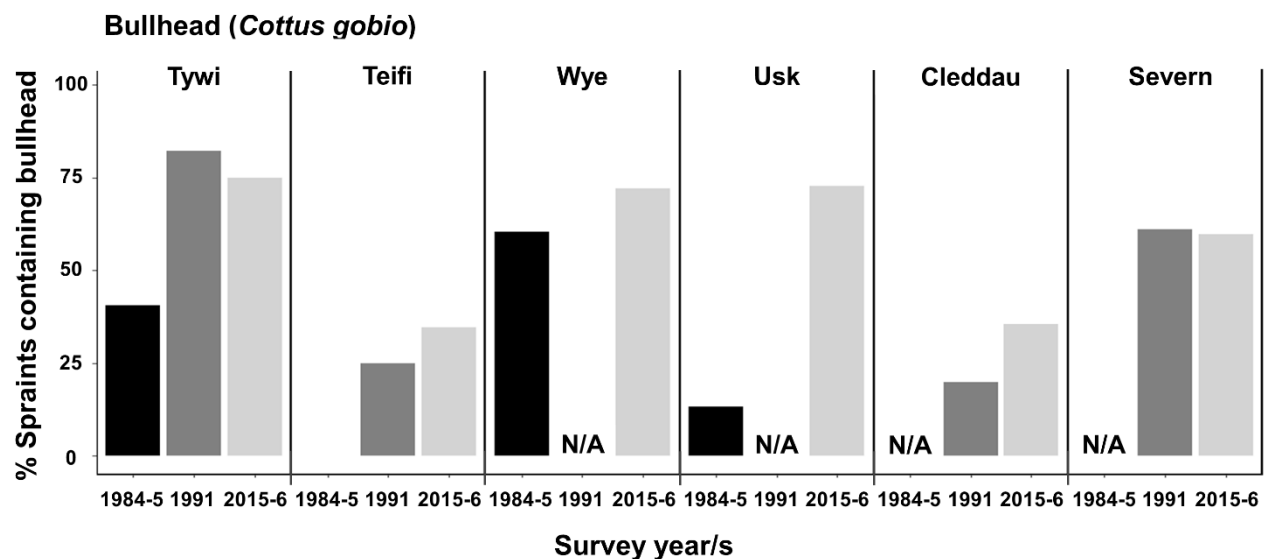


Figure 5 Frequency of occurrence of bullhead remains in otter spraint. N/A= spraints were not collected during this survey.

The river catchment frequency of occurrence of bullhead ranged from 0-82% across the three survey periods, occurring in 47% of spraints overall. For bullhead, the interaction term in the models was significant indicating that the time trends were significantly different between catchments. In most catchments there was a general trend to an increase in frequency of occurrence of bullhead remains, with the exception of the Tywi and Severn catchment surveys where similar frequencies of bullhead were recorded in 2015-16 and 1991.

There was a significant difference in the occurrence of bullhead between the Teifi, Tywi, Severn and Cleddau catchments, with fewer remains recorded in the Teifi and Cleddau.

European Eel (*Anguilla anguilla*)

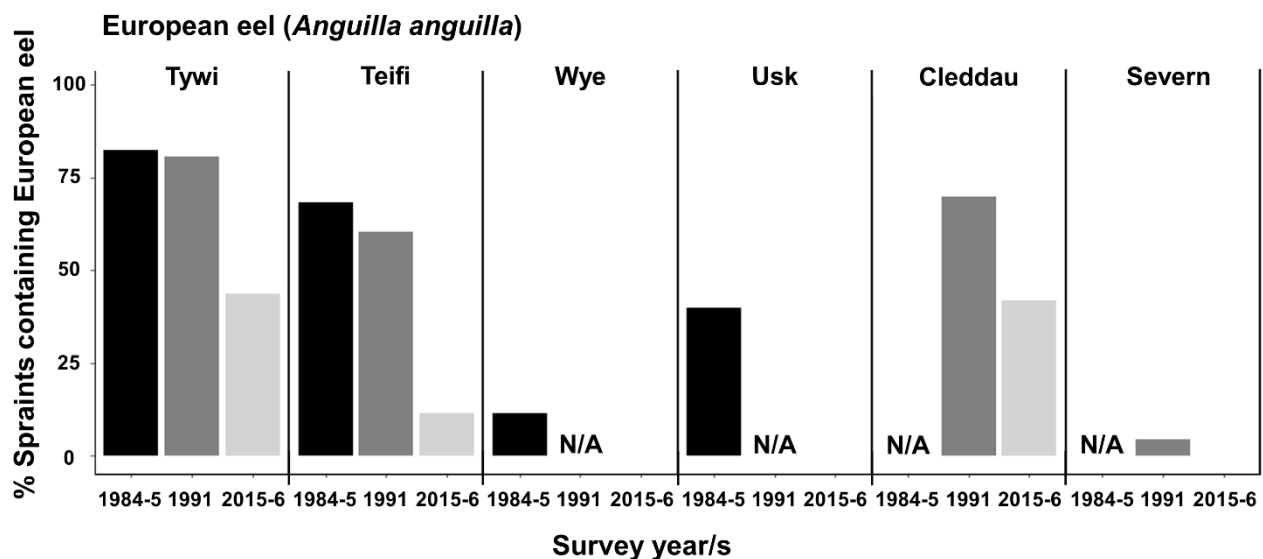


Figure 6 Frequency of occurrence of European eel remains in otter spraint. N/A= spraints were not collected during this survey.

The river catchment frequency of occurrence of eel ranged from 0-83% across the three survey periods, occurring in 40% of spraints overall. There were significant differences in frequency of occurrence between catchments, with eel being far more common in the west Wales river catchments (Teifi, Tywi, Cleddau) than the east Wales catchments (Wye, Usk, Severn). In the most recent survey (2015-16), eels contributed far less to otter diet in the Teifi catchment (12% occurrence) than in the Tywi, and the Cleddau catchments (42% and 44% occurrence).

There was a significant decline in the occurrence of eels in otter diet in all catchments. In the Tywi and Teifi, the two catchments where there were samples collected in all 3 surveys, this decrease in the occurrence of eels became significant between 1991 and 2015-16 surveys. In the Wye, Usk and Severn, no eels were recorded in the most recent survey (2015-16).

Stone Loach (*Barbatula barbatula*)

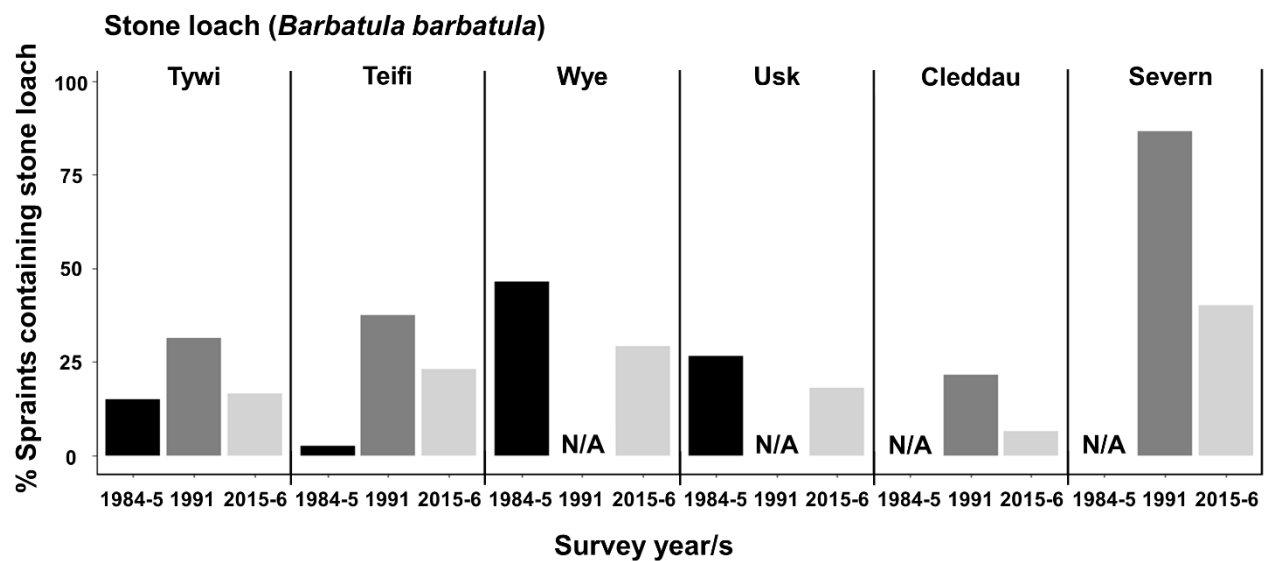


Figure 7 Frequency of occurrence stone loach remains in otter spraint. N/A= spraints were not collected during this survey.

Stone loach were recorded in 29% of spraint overall but was variable between different catchments and survey periods (3% to 87%). There were significant differences between survey years and between some catchments. The 1991 survey of the Severn had an unusually high frequency of occurrence of stone loach remains. For the catchments where data are available, there was higher frequency of occurrence of stone loach in 1991 than the other surveys.

Minnow (*Phoxinus phoxinus*)

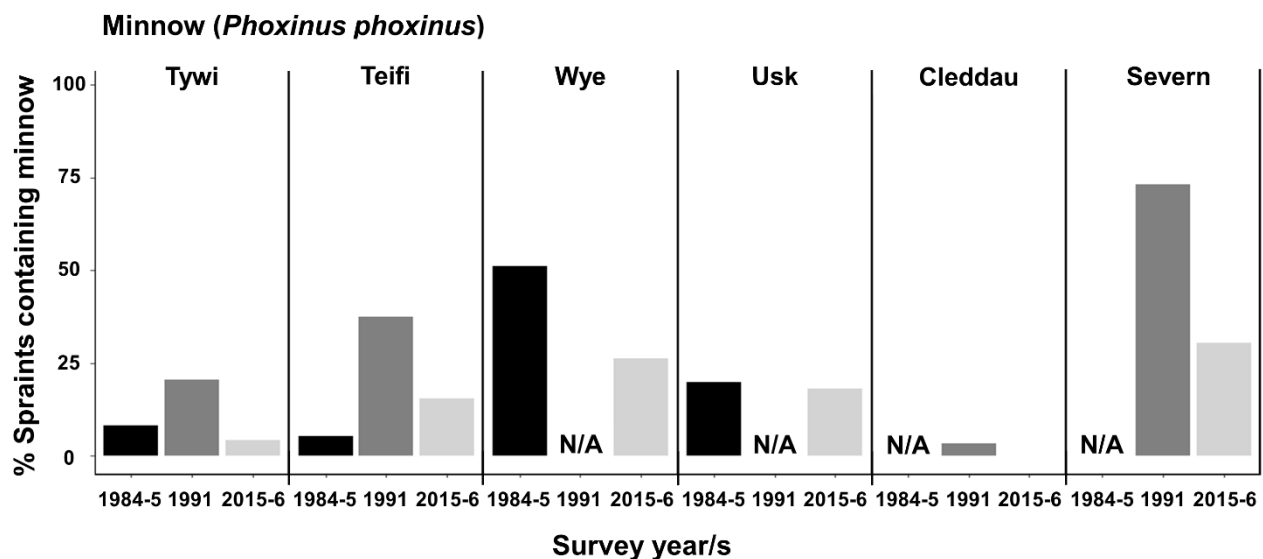


Figure 8 Frequency of occurrence minnow remains in otter spraint. N/A= spraints were not collected during this survey.

Minnow occurred in 22% of spraint overall, but was highly variable between different catchments and survey periods (0%-73%). At one extreme, minnow were very commonly recorded in the Severn (up to 73% in 1991). In contrast, minnow remains were rarely found in otter spraint collected in the Cleddau.

Significantly fewer minnow remains were recorded in 2015-16 compared to 1984-5, and this is very clear in the Wye catchment. For catchments where there were data from 1991 (Tywi, Teifi, Cleddau and Severn), the highest occurrences of minnows were in that survey time period, and indeed there were significantly more minnows in 1991 than in 2015-16.

Stickleback (*Gasterosteidae*)

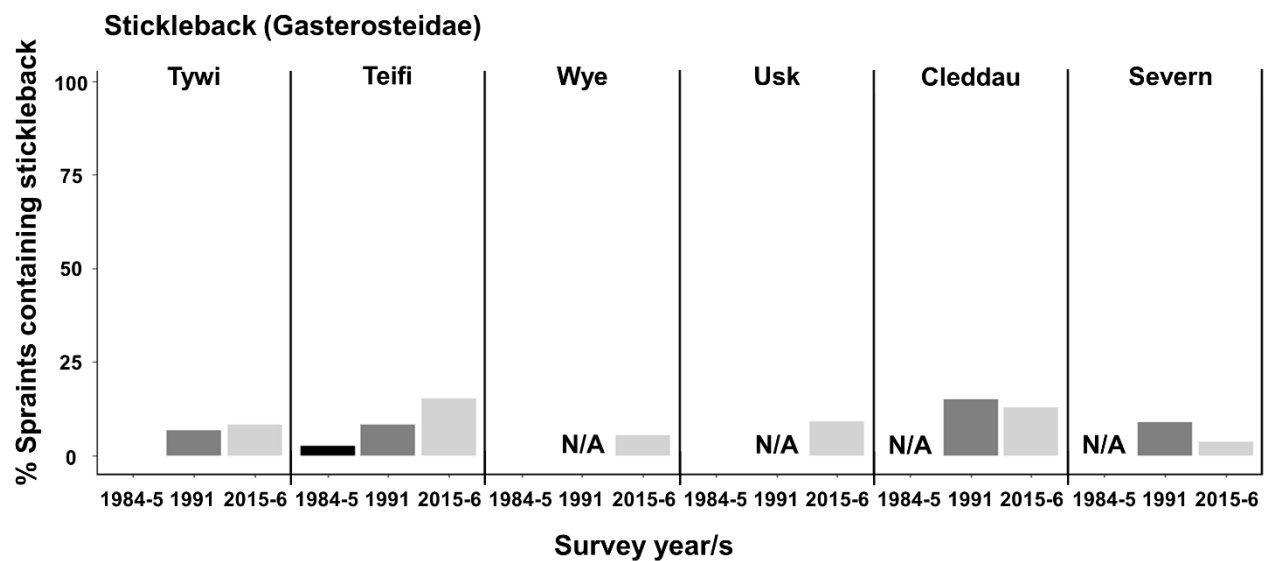


Figure 9 Frequency of occurrence stickleback remains in otter spraint. N/A= spraints were not collected during this survey.

Stickleback were infrequently recorded: in just 7% of spraints overall, ranging from 0-15% in the different catchments and survey years. There were significantly more stickleback recorded in the 2015-16 surveys in the Tywi, Teifi, Wye and Usk than in the 1984-5 surveys in the same catchments. In the Teifi and Tywi catchments where there was data from all three survey periods there were significantly more stickleback remains found in later surveys than in earlier surveys.

Non-fish prey

Amphibians (frog, toad and newt)

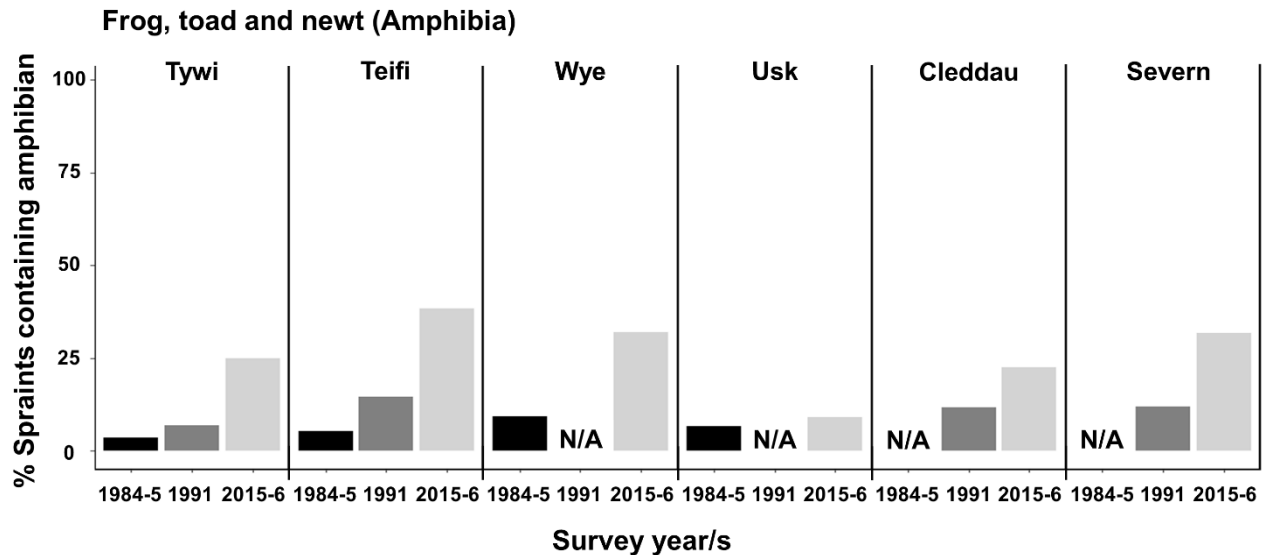


Figure 10 Frequency of occurrence amphibian remains in otter spraint. N/A= spraints were not collected during this survey.

Amphibians were recorded in 16% of spraints overall, ranging from 3-38% in the different catchments and survey years. There were significantly more amphibian remains in recent years in all catchments.

Birds

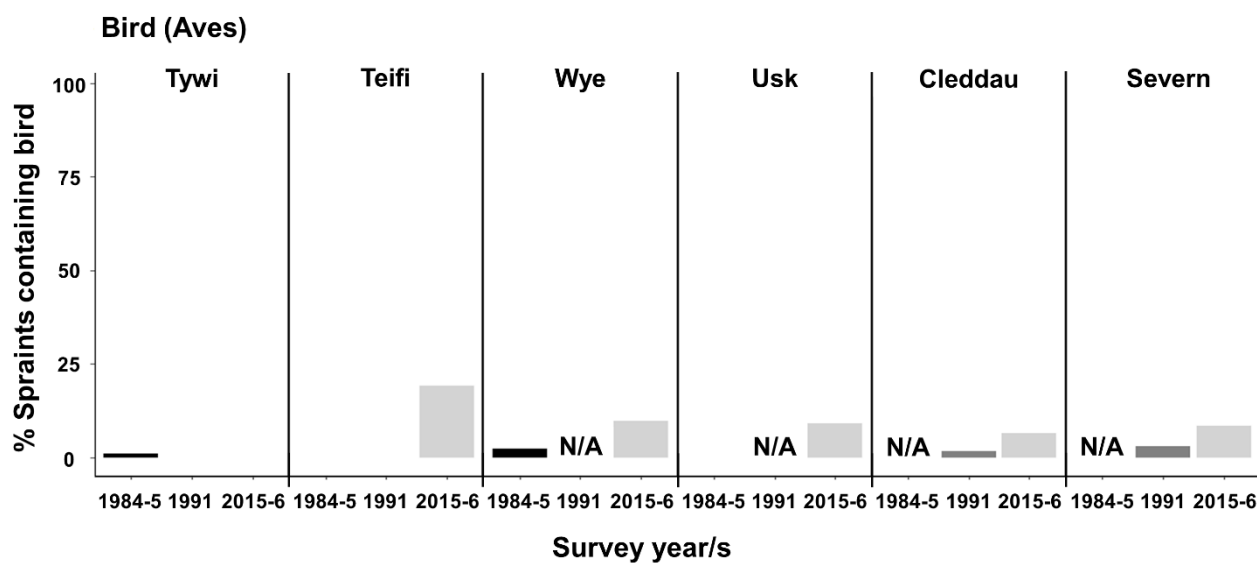


Figure 11 Frequency of occurrence of bird remains in otter spraint. N/A= spraints were not collected during this survey.

Bird remains were very infrequently recorded: overall in only 4% of spraint, ranging from 0 to 19% in the different catchments and survey years. There were only sufficient data to statistically test for differences in the model that compared the Teifi, Tywi, Wye and Usk catchments in 1984-5 and 2015-16: there was significantly more bird remains found in 2015-16 than 1984-5 in those catchments.

Mammals

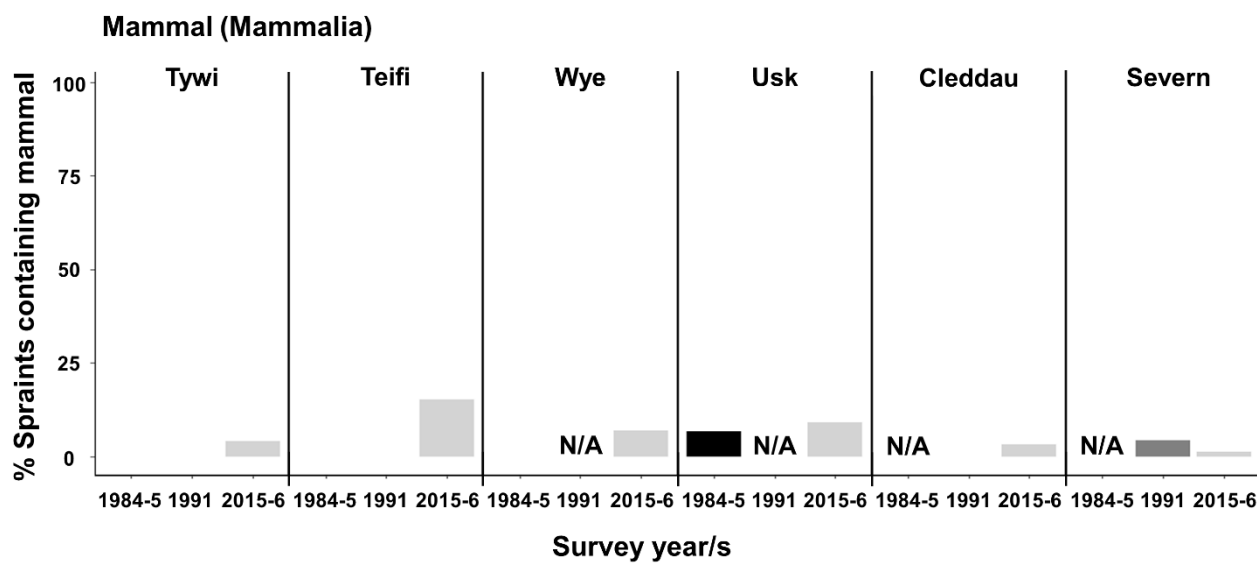


Figure 12 Frequency of occurrence of mammal remains in otter spraint. N/A= spraints were not collected during this survey.

Mammal remains were very infrequently recorded: overall in only 4% of spraint, ranging from 0 to 15% in the different catchments and survey years. There was only sufficient data to test for differences in the model that compared the Teifi, Tywi, Wye and Usk catchments in 1984-5 and 2015-16. There were significantly more mammal remains recorded in 2015-16 than in 1984-5.

Other prey types not included in statistical testing

Three prey types; other cyprinids (excluding minnows), marine fish, and crayfish, were all infrequently found in otter diet, so it was not possible to statistically test for patterns in occurrence. The grouping “other fish” was also not included – see below for explanation. Therefore only a description of the frequency of occurrence data for these four prey groups are given below.

Crayfish (*Astacidae*)

Crayfish were not recorded in any spraint collected in 1984-5, and only in 1% of samples in 1991, all in the Severn catchment. In the 2015-16 surveys they were recorded in the Wye (11% of spraint), Cleddau (3% of spraint) and Severn (12% of spraint). The author (Eleanor Kean) notes that in recent surveys (2022/23) of the England section of the upper Severn, crayfish remains were also common in spraint there.

Other cyprinids (excluding *Phoxinus phoxinus*)

Other cyprinids, refers to those remains identified as from the family Cyprinidae, but which were not identified as minnow (*Phoxinus phoxinus*). This group was rarely recorded in otter spraint (n=3%) ranging between 0-7% between catchments and survey periods. This group was never recorded in spraints from the Usk (although note smaller sample size overall in the Usk). It appears to be becoming a more commonly recorded group: in 1984-5 it was recorded in 1 out of 4 catchments, in 1991 in all four catchments, in 2015/16 in five out of six catchments.

Marine fish

Over all survey areas and time periods, marine fish remains were very infrequently recorded: in only 2% of spraint. They were most commonly recorded in spraint collected in the Cleddau catchment in 2015-16%, here they were found in 16% of spraint. Marine fish remains were never recorded in spraint collected in the Wye, Usk or Severn catchments.

Other fish

This category constitutes remains that can be identified as originating from fish, but no further identification is possible. Therefore it is unknown how broad a taxonomic grouping this is, and therefore it bears very little biological relevance. This category was recorded in 3% of spraint overall (range= 0-10%). This category was most commonly recorded in the Cleddau in 2015-16, where it was recorded in 10% of spraints. In contrast, it was never

recorded in spraints from the Usk, although note smaller sample size and distribution overall in the Usk.

Otter diet and otter population survey results

A national scale survey of otter populations is conducted in Wales approximately every 7-10 years, and in five out of the six diet study catchments, a reduction in otter signs was recorded in the most recent survey (Figure 13). To examine the question *are otters more common in areas where they can consume supposed 'preferred prey' i.e. eels and salmonids?* we have presented plots of the percentage of spraint containing eel, salmonids or bullhead against the results of the most recent survey of 2015-16 (most recent survey only to prevent conflation with recovery from persistent organic pollutants). Whilst there is not enough data to test these associations, the plots (Figure 14) give an indication that the higher occurrence (RFO) of the three most common prey types is not associated with a higher percentage of survey sites where otter signs were observed. In contrast, these preliminary observations suggest that higher salmonid consumption by otters may correspond to reduced evidence of otter presence.

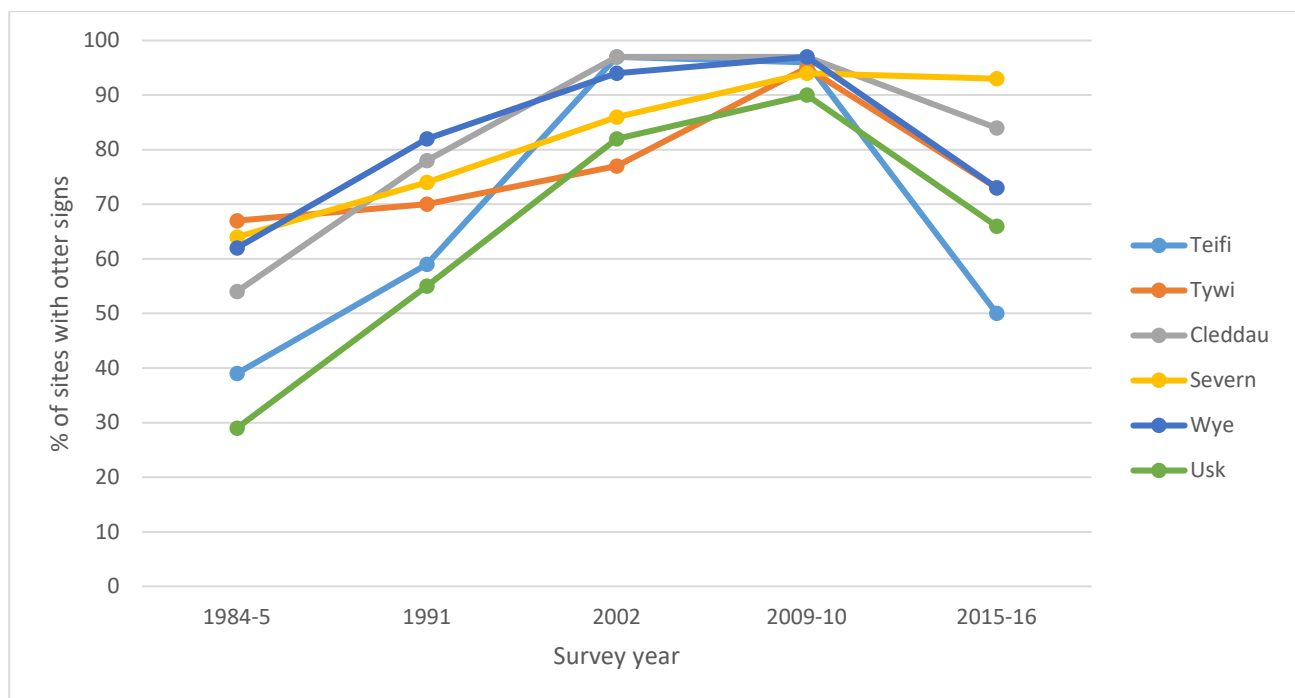
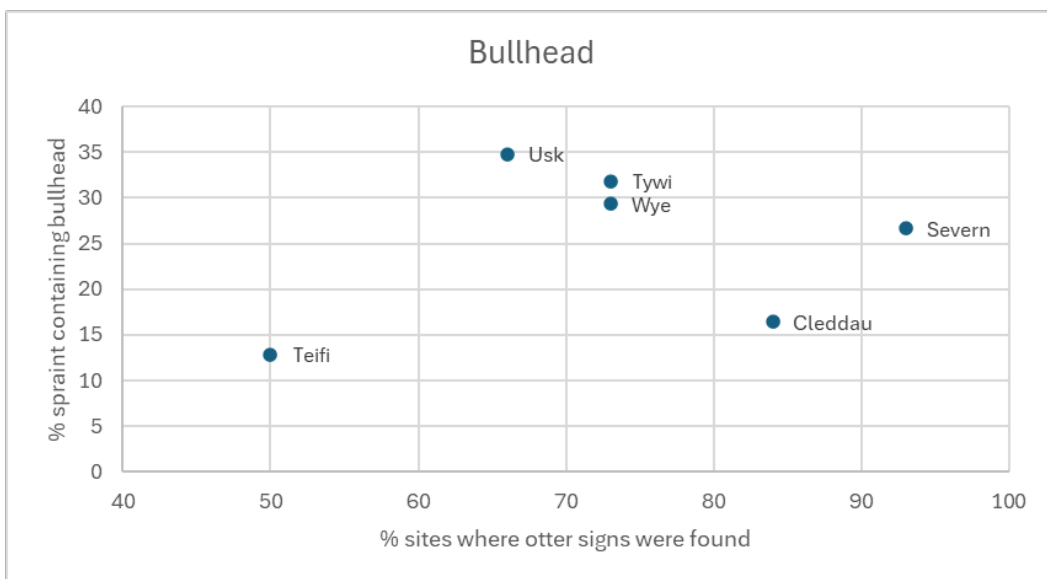
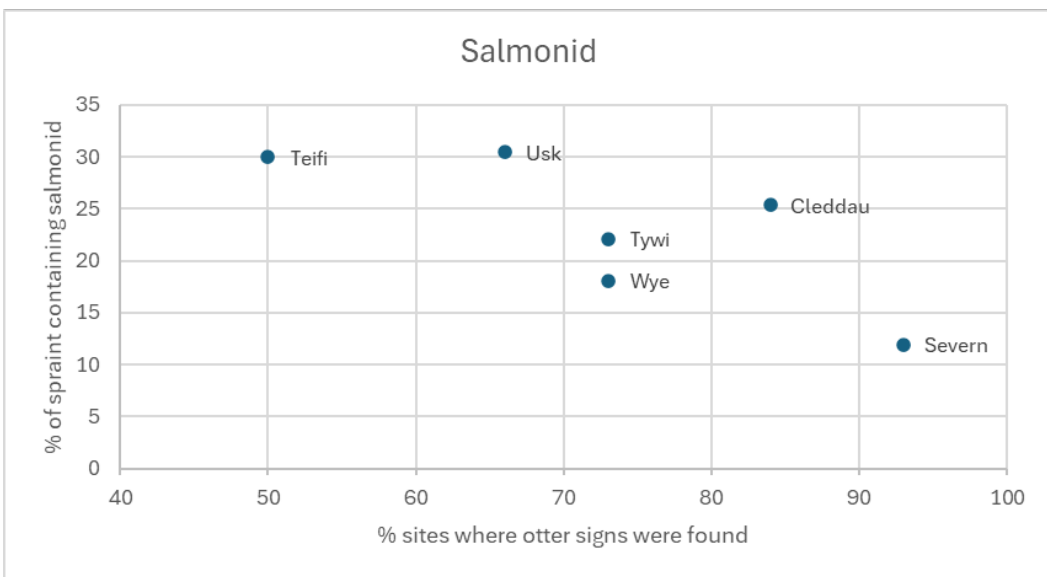
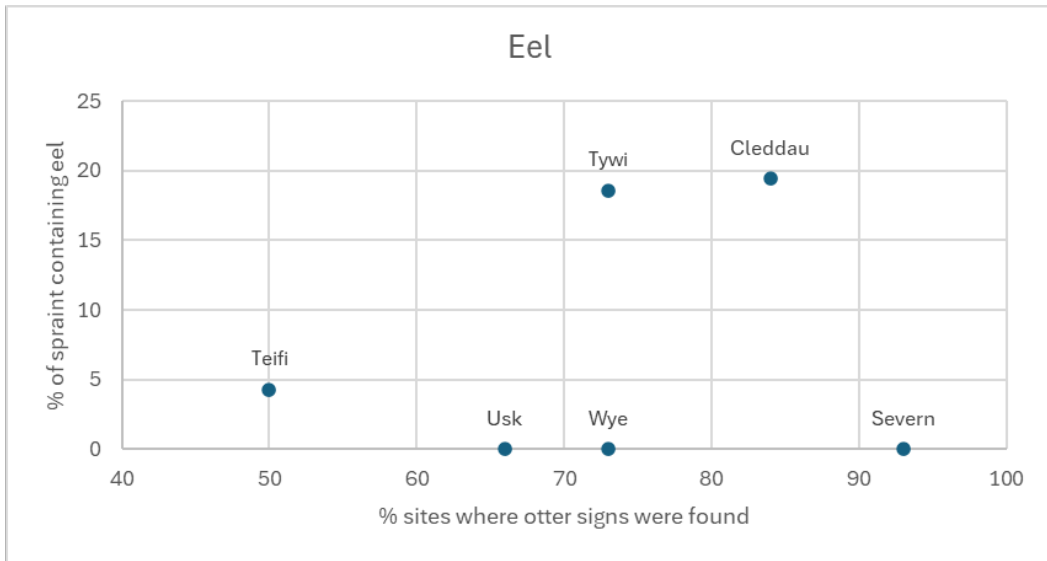


Figure 13 Otter Survey Wales results for the six diet study catchments



Discussion

The diet of the otter in south Wales has undergone a profound change over the last few decades, in common with other otter diet studies in UK (Almeida et al., 2012; Moorhouse-Gann, 2000). This may reflect the wider changes in river ecosystems. Whilst previous studies have shown similar trends with an overall decrease in eels and salmonids and an increase in other prey types (e.g. Moorhouse-Gann, 2000), this study allowed the examination of trends on a catchment scale and revealed localised differences between catchments. In some instances these localised differences were strong enough to skew the overall trend, for example, the apparent decline in salmonids in otter diet was only significant for the upper-Wye.

Spatial differences in otter diet

Similar otter dietary patterns were recorded amongst the west Wales catchments (Teifi, Tywi, Cleddau): characterised by previous high proportions of eel and replaced by either bullhead, amphibians, marine fish or other prey. The otters on the Tywi and Cleddau have maintained similar proportions of salmonids over each three surveys time periods. The samples collected for the mid and east Wales catchments (Usk, Wye and Severn) were limited to upper catchment only, and this might explain some of the differences observed e.g. otter diet in the Severn was characterised by low to zero eel, much lower salmonids and much greater minnow and stone loach than in other catchments.

Whilst the study design allowed for matching of catchments over time, because there have been changes in otter populations, it was not possible to match samples to specific sites. Therefore there were some changes in distribution of samples between sampling periods (surveys). For example, in the Wye catchment there was a wider distribution in the 2025-26 survey than in the 1984-5 survey. Changes in distribution of available spraint will likely be associated with some change in habitat and therefore prey.

All of the river catchments studied, with the exception of the Severn, are protected SAC rivers, all with notable issues of nutrient pollution. Further research could seek to investigate if there are any associations between changes in otter diet and changes in otter distribution within catchments associated with numerous variables including stream order, altitude, ecological condition (WFD status), riparian habitat, obstacles to fish passage etc.

Otter diet and prey availability

Diet diversity for some predators reflects the availability of different prey species, also known as the relative resource abundance. Specifically, predators that are generalists predate upon what is locally abundant. Conversely, specialists, have a more restricted range of prey regardless of what is available. For apex predators, it is possible to record population-level niche breadth even when there is individual level dietary specialisation. The otter is thought to be a generalist apex predator, and are known to have the capacity to switch to alternative prey as “preferred prey” decline. For example, when freshwater fish are less available, otters switch to alternative prey (e.g., Almeida et al., 2012; Britton et al.,

2006; Krawczyk et al., 2016; Remonti et al., 2010). Previously otters were thought to preferentially prey on salmonids and eels, although this assumption was largely based on anecdotal accounts rather than systematic recording of otter diet and prey availability. More recently, evidence suggests density-dependent predation by otters is likely (Drake et al., 2003, Almeida et al., 2012; Copp & Roche, 2003; Miranda et al., 2008) with the possible exception of the European eel (Drake et al., 2023).

Data on the availability of otter prey in Wales (e.g. survey and monitoring data/population trends) are lacking for most fish species, and other key prey types such as amphibians. There are however, good evidence reports that describe population trends for eels and some salmonids.

The clearest apparent relationship between prey availability evidence and the otter diet recorded in this study is for the **European eel**. The decline in European eel recruitment since the mid-1980s has been well documented across Europe (e.g. ICES, 2023) and locally (Henderson et al., 2012), and this broad decline in availability as a prey item is reflected in the otter diet recorded here.

There seems to be a disparity between the known distribution of eel in the upper Severn and Wye catchments in 1980s and 1990s (pers com. David Mee, NRW) compared to the low frequency occurrence of eel remains in otter spraints recorded here. Further investigation of eel records are beyond the scope of this report, particularly as reports are not available electronically. If eel were indeed widespread and numerous, it suggests that not all otters preferentially hunted eels, and that otters may exhibit individual or localised sub-population dietary specialisation. Metabarcoding of otter diet in 2007-2016 across England and Wales found that otters are still frequently consuming eels (Drake et al., 2023), whilst this is true for some catchments in this study, it was not for all. It is not clear if this reflects a disparity between the methodologies, (e.g. perhaps morphological identification as employed here only identifies larger eels), or localised sub-population specialisation in diet which was not investigated by Drake et al., 2023.

Salmon populations in Wales have been declining for two decades, with extirpation predicted in many Welsh rivers within the next few decades (e.g. Milner and Garcia de Leaniz., 2023). Population temporal trends for 22 salmon rivers have been published for 1990-2021 based on annual monitoring, and overall the trend is one of decline, but there is considerable variation within this. The lack of a clear temporal trend in salmonids in otter diet here, and in otter stomachs (Moorhouse Gann et al., 2020), may in part reflect variation in salmonid density between rivers. However, given the high frequency of occurrence of salmonid remains in otter spraint from rivers known to have had steep declines in at least some salmonid species, further research could be designed to investigate the possibility that otters selectively predate salmonids, and if so which species.

Whilst there is no established monitoring programme for **bullhead** in Wales, bullheads are recorded during routine electrofishing sampling conducted by NRW and others, and are a designated feature for many SAC rivers with associated requirements for statutory reporting. Based on the limited information available it is very unlikely that bullhead populations have increased. The conservation status of bullhead was classed as 'unknown' for 2002-7 and 2008-13 and 'unfavourable inadequate at Wales level' for 2014-

19 (NRW, 2021). More intensive monitoring of the Wye and Usk catchments in 2007 were conducted, which indicated bullheads were absent from some areas of the SACs, other sites had low densities and some had population structures indicating poor recruitment (Yeomans et al., 2008). As this appears to have been a one-off intensive study, it is not possible to assess change. It is not possible to explain the increase in bullhead in otter diet across all six catchments by increased availability of bullhead. It is however possible given the salmonid and eel declines that bullhead are now more relatively abundant than previously.

No population data are available for **stone loach** or **minnow**, which had very similar patterns in frequency of occurrence in otter diet. We have not been able to identify an explanation for the particularly high frequency of occurrence of both stone loach and minnow in the Severn in 1991.

Sticklebacks were infrequently recorded in this study which is in contrast to metabarcoding analysis of otter stomach contents where they were the most frequently detected taxa in the diet of otters (Drake et al., 2023). No population data are available for sticklebacks in Wales.

Amphibian remains increased in otter diet in all catchments, this is likely to represent selection for amphibians to replace other less available prey (e.g. eels) because during the time period 1984-2016 we are not aware of any reported increase in amphibian populations in Wales. Most amphibians (including *Triturus cristatus*) have been assessed as in the Least Concern IUCN category in Wales because there is no evidence for significant reduction in either population size or geographic range (Foster et al., 2021). Toads (*Bufo bufo*) have overall in England and Wales undergone a decline, but in Wales the population trend appears stable (Petrovan and Schmidt (2016). Whilst there is some evidence for seasonality to the consumption of amphibians by otters (e.g., Clavero et al., 2005; Moorhouse-Gann et al., 2020; Parry et al., 2015), it does not account for the differences recorded here, because all surveys were conducted at the same time of year (May-September, with 82% conducted May-July).

The distribution of **crayfish** remains in otter diet found here broadly reflects the known distribution of crayfish in Wales. The native white clawed crayfish has declined dramatically and the invasive signal crayfish has increased over a similar time period (James et al., 2015, Rogers and Watson, 2016). However data are not published at a sufficient resolution to ascertain if the increase in crayfish remains in otter spraint reflects an increase in availability or not.

Mammals and birds populations are not reported to have increased in the decades of this study, however as species were not identified it is not possible to assess if the increase in mammal and bird remains in otter spraint reflects an increase in availability or not.

It is notable that some fish species are absent in these diet analyses which are known to be present in some of these rivers e.g. **shad**. It is not known if this reflects dietary preference or a limitation in methods, although they were also not recorded in research using metabarcoding (Drake et al., 2023).

Otter diet and otter population trends

National distribution surveys undertaken approximately every eight years showed a steady increase in otter populations in the 1980s, 90s and 2000s in Wales, and elsewhere in the UK. There followed a small but significant decrease in percentage detection at survey sites between the fifth (2009-10) and sixth (2015-18) national surveys in Wales, and this was the case for five out of the six catchments investigated for otter diet here. Along with changes noted in prey availability (e.g. documented eels and salmonid population declines) this raised concerns by some working in the field that diet changes might be limiting otter populations.

The timing of prey and otter population declines and increases suggests this is not the case. Salmonid and eel population declines had started while the otter populations were still increasing. Most Atlantic salmon populations have been declining since approximately 2000 (Milner and Garcia de Leaniz., 2023), and indices of eel populations showed declining trends throughout the 1980s and 1990s (Defra, 2010). In contrast otter populations in Wales were consistently increasing during the 1980s, 90s, and 00s to at least 2010. Established ecological theory predicts a time lag in predator-prey dynamics, and although direct data for *Lutra lutra* are not available, the time lag observed here seem unfeasibly large to be a direct relationship.

In this study we did not find an association between higher predation of eels or salmonids and a higher otter detection rate (Figure 14). Furthermore, in the Severn catchment despite the often so-called “favoured prey” of otters (eels and salmonids) constituting a far lower proportion of otter diet than in other catchments (Figure 3), the otter population remained stable with a high percentage of sites with otter signs (93%) in the 2015-18 survey. Whilst this is only one catchment, it is clear that otter populations can be sustained (at least in the short term) on diets not high in eels or salmonids.

Recently published long-term research on sea otters (*Enhydra lutris*) traced diet shifts from larger to smaller prey as sea otter populations re-established after extirpation (Leach et al., 2024). This pattern somewhat parallels our observations of *Lutra lutra* in Wales, where otters have also exhibited an increased reliance on smaller prey species as populations have grown (although we do not have data on sizes of individuals consumed). While comparison between otter species may offer some insight to broader patterns, other local environmental and anthropogenic pressures on prey species may influence the specifics of the shifts.

Conclusion

There has been a drastic shift in otter diet in the last four decades and it is unclear if this may reflect wider changes in river ecosystems, or is a function of a population re-establishing. While fish still dominate, generally otter diet has become more diverse, with a larger reliance on smaller prey species. This study provides evidence of differences in otter diet between river catchments. The data presented here is the presence of prey in otter diet, it does not necessarily equate to biomass consumed of each prey type. Without adequate data on prey availability, and in particular the biomass available in the studied rivers it is not possible to determine if the shift in diet coincides with a loss of available prey

biomass. Further monitoring and research is needed to understand the potential implications for otters of dietary shifts and the predicted continued decline of key prey (salmonids), and importantly also the implications for prey species, particularly other protected species e.g. bullhead.

Recommendations

Further research should seek to;

- Investigate the association between prey availability and otter diet.
- Investigate the possibility that otters selectively favour salmonids, and if so which species.
- Investigate the implications of increased bullhead consumption on bullhead populations.
- Investigate if there is localised individual or sub-population specialisation in prey selection.
- Summarise eel population records for 1980-2016 for individual catchments to allow comparison to otter diet.
- Describe fish diversity in Welsh rivers.
- Investigate if there are any associations between changes in otter diet and changes in otter distribution within catchments associated with stream order, altitude, ecological condition (WFD status), riparian habitat, obstacles to fish passage etc.
- Continue to monitor otter populations.

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Appendix 1 Percentage Frequency of Occurrence (FO and Relative Frequency of Occurrence (RFO)

Prey occurrences across catchments and survey periods expressed as frequency of occurrence, and relative frequency of occurrence

River	Teifi	Teifi	Teifi	Teifi	Teifi	Teifi	Twyi	Twyi	Twyi	Twyi	Twyi	Twyi	Cleddau	Cleddau	Cleddau	Cleddau
Year	1980	1980	1990	1990	2010	2010	1980	1980	1990	1990	2010	2010	1990	1990	2010	2010
FO/RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO
FISH	97.36	96.83	100	94.31	92.31	71.43	98.84	97.71	100	97.69	97.87	86.73	100	93.89	96.77	83.58
Bullhead	0	0.00	25	9.76	34.62	12.86	40.7	20.00	82.19	27.78	75	31.86	20	9.16	35.48	16.42
Eel	68.42	41.27	60.42	23.58	11.54	4.29	82.56	40.57	80.82	27.31	43.75	18.58	70	32.06	41.94	19.40
Salmonid	76.32	46.03	66.67	26.02	80.77	30.00	50	24.57	61.64	20.83	52.08	22.12	70	32.06	54.84	25.37
Cyprinid	2.63	1.59	2.08	0.81	3.85	1.43	0	0.00	2.74	0.93	2.08	0.88	1.67	0.76	3.23	1.49
Minnow	5.26	3.17	37.5	14.63	15.38	5.71	8.14	4.00	20.55	6.94	4.17	1.77	3.33	1.53	0	0.00
Stone Loach	2.63	1.59	37.5	14.63	23.08	8.57	15.12	7.43	31.51	10.65	16.67	7.08	21.67	9.92	6.45	2.99
Stickleback	2.63	1.59	8.33	3.25	15.38	5.71	0	0.00	6.85	2.31	8.33	3.54	15	6.87	12.9	5.97
Marine Fish	0	0.00	0	0.00	3.85	1.43	1.16	0.57	0	0.00	0	0.00	3.33	1.53	16.13	7.46
Unidentified Fish	2.63	1.59	4.17	1.63	0	1.43	1.16	0.57	2.74	0.93	2.08	0.88	0	0.00	9.68	4.48
NON-FISH PREY	5.26	3.17	14.89	5.69	50	28.57	4.65	2.29	6.85	2.31	25.53	13.27	13.33	6.11	32.26	16.42
AMPHIBIAN	5.26	3.17	14.89	5.69	38.46	14.29	3.49	1.71	6.85	2.31	25	11.50	11.67	5.34	22.58	10.45
Anuran	5.26	3.17	14.89	5.69	30.77	11.43	3.49	1.71	6.85	2.31	12.5	5.31	11.67	5.34	22.58	10.45
Newt	0	0.00	0	0.00	11.54	4.29	0	0.00	0	0.00	14.58	6.19	0	0.00	0	0.00
Mammal	0	0.00	0	0.00	15.38	5.71	0	0.00	0	0.00	4.17	1.77	0	0.00	3.23	1.49
Avian	0	0.00	0	0.00	19.23	7.14	1.16	0.57	0	0.00	0	0.00	1.67	0.76	6.45	2.99
Crayfish	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	3.23	1.49

River	Severn	Severn	Severn	Severn	Wye	Wye	Wye	Wye	Usk	Usk	Usk	Usk
Year	1990	1990	2010	2010	1980	1980	2010	2010	1980	1980	2010	2010
FO/RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO
FISH	98.51	93.27	85.37	76.09	100	95.58	90.28	74.58	100	92.31	90.91	86.96
Bullhead	61.19	19.71	59.76	26.63	60.47	23.01	72.22	29.38	13.33	7.69	72.73	34.78
Eel	4.48	1.44	0	0.00	11.63	4.42	0	0.00	40	23.08	0	0.00
Salmonid	40.3	12.98	26.83	11.96	79.07	30.09	44.44	18.08	60	34.62	63.64	30.43
Cyprinid	7.46	2.40	6.1	2.72	0	0.00	1.39	0.56	0	0.00	0	0.00
Minnow	73.13	23.56	30.49	13.59	51.16	19.47	26.39	10.73	20	11.54	18.18	8.70
Stone Loach	86.57	27.88	40.24	17.93	46.51	17.70	29.17	11.86	26.67	15.38	18.18	8.70
Stickleback	8.96	2.88	3.66	1.63	0	0.00	5.56	2.26	0	0.00	9.09	4.35
Marine Fish	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Unidentified Fish	7.46	2.40	3.66	1.63	2.33	0.88	4.17	1.69	0	0.00	0	0.00
NON-FISH PREY	19.4	6.73	47.56	23.91	11.63	7.96	48.61	25.42	6.67	7.69	27.27	13.04
AMPHIBIAN	11.94	3.85	31.71	14.13	9.3	3.54	31.94	14.12	6.67	3.85	9.09	4.35
Anuran	11.94	3.85	30.49	13.59	9.3	3.54	29.17	11.86	6.67	3.85	9.09	4.35
Newt	0	0.00	1.22	0.54	0	0.00	5.56	2.26	0	0.00	0	0.00
Mammal	4.48	1.44	1.22	0.54	0	0.00	6.94	2.82	6.67	3.85	9.09	4.35
Avian	2.99	0.96	8.54	3.80	2.33	0.88	9.72	3.95	0	0.00	9.09	4.35
Crayfish	1.49	0.48	12.2	5.43	0	0.00	11.11	4.52	0	0.00	0	0.00

Appendix 2 Statistical model results table

	All survey years (Teifi, Tywi)			1984/85 and 2015/16 (Teifi, Tywi, Wye, Usk)			1991 and 2015/16 (Teifi, Tywi, Sev, Cle)		
Prey type	Year	Catchment	Year:catchment	Year	Catchment	Year:catchment	Year	Catchment	Year:catchment
Bullhead	-	-	*	-	-	**	NS	***	NS
Eel	***	***	NS	***	**	NS	***	**	NS
Salmonid	NS	**	NS	-	-	*	NS	***	NS
Minnow	NS	***	NS	*	***	NS	NS	***	NS
Stone Loach	***	NS	NS	-	-	*	***	**	NS
Stickleback	*	NS	NS	**	NS	NS	NS	NS	NS
Amphibian	*	***	NS	***	NS	NS	***	NS	NS
Mammal	data deficient			**	NS	NS	data deficient		
Bird	data deficient			**	NS	NS	data deficient		

Data Archive Appendix

No data outputs were produced as part of this project.