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# Top-down effects of Eurasian otter (*Lutra lutra*) diet on the trophic functionality of freshwater systems in the UK & Ireland

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MRes thesis by

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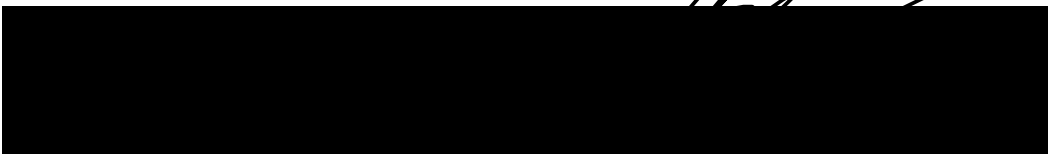
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## Abstract

The Eurasian otter (*Lutra lutra*) has been described as both a generalist and specialist predator, but there is little literature on the trophic effects of otter diet on a freshwater system. We analysed otter dietary data from across the UK and Ireland to identify any potential patterns in the trophic functionality and characteristics of predated freshwater fish species across sites, in order to deduce any possible trophic effects of top-down control. These were inferred by comparing our results with previous research on otter feeding ecology, prey characteristics and the cascading trophic effects of more studied carnivore species. We also tested whether prey trophic level patterns were consistent between sites. Five functional/morphological categories were selected for cross-comparison analysis between prey types (trophic level, resilience, mean adult length, body form, and aquatic zone). Each prey type identified was assigned a value/group within each category and the mean RFO% of each species across sites was used as a proxy occurrence value, with overlapping values added together.

The results showed that freshwater fish prey followed a consistent trophic pattern across sites. Otters primarily predated on species between trophic levels 3.2-3.6, with the latter representing 30.3% of all freshwater fish predated upon. Trophic levels of prey types also remained consistent between sites indicating a trophic niche that otters repeatedly prioritised. We determined that otter diet mostly consisted of small-medium (10-25cm) fish, primarily demersal and benthopelagic species with resilience levels ranging from medium-low. We also theorised a potential range of otter prey selection based on locomotion specialisation and net energy gain.

Upon review of the diet and trophic effects of prey species, we believe that otters may increase primary production at the demersal zone through top-down control of secondary consumers. We presented arguments for potential increases to biodiversity; population increases of small invertebrates; potential reduction in helminth populations; and possible control of invasive species. We also identified possible areas of disturbance risk to otter's primary foraging grounds, which could alter the theorised trophic effects imparted by their diet. We argued that there is sufficient evidence to show that otter feeding ecology is more specialist than generalist in the UK and Ireland and discussed some inherent issues with these classifications.

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Lastly, we identified some key issues with the methodologies and reporting of data in some of the reviewed studies on otter diet. We argued that standardisation of methods and data transparency could prevent limitations on the speed at which we advance our understanding within this field.

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## 1.0 Introduction

It is currently estimated that 30% of species have become threatened or gone extinct due to human activities since the 1500s (Isbell et al., 2022), with carnivores being traditionally one of the most challenging and controversial groups to be issued protection due to a long-standing history of human-carnivore conflict (Sillero-Zubiri & Laurenson, 2001; Chapron et al., 2014). Predation of livestock (Karanth & Sunquist, 1995; Zimmermann et al., 2010), competition over game species (Reynolds & Tapper, 1996; Klenke et al., 2013) and perceived threats to human wellbeing (Penteriani et al., 2016) are some of the factors that have traditionally portrayed both large and small carnivores in a negative light, causing most populations to have decreased dramatically in abundance and range (Di Marco et al., 2014; Marneweck et al., 2021). However, our understanding of the ecological roles and trophic functions of carnivores has increased significantly, allowing us to demonstrate the instrumental role predators have in promoting ecosystem health through top-down management of prey species (Hoeks et al., 2020; Davoli et al., 2022). Research on the feeding ecology of carnivores is of vital importance to conservation efforts (Carrs, 1995; Roemer et al., 2009; Monterroso et al., 2019), and so there is a call to fill gaps in our knowledge on the trophic effects of lesser studied species (Ripple et al., 2014).

Carnivore foraging strategies are governed by a combination of intrinsic and extrinsic factors. Intrinsic factors are those specific to the predator itself and can include age, sex, health and hunting experience (Heggberget & Moseid, 1994; Araújo et al., 2014), while extrinsic factors are those relating to prey species and environment, i.e. predator/prey densities, prey activity patterns and distribution (Svanbäck & Bolnick, 2005; Rosenblatt et al., 2015). The combination of these factors dictates the optimal foraging strategy for a predatory species (MacArthur & Pianka, 1966), where the energetic costs and benefits of predating upon a prey species are weighed against each other in order to maximise net energy gain. This allows us to classify carnivores into two broad feeding categories: generalists and specialists. Generalist feeding strategies exploit a wide range of prey types, suggest that diet composition reflects prey availability, and infer more opportunistic/less selective feeding behaviours (Andersson & Erlinge, 1977). Specialist feeding strategies usually require greater time and energy spent to locate specific prey items (Stephens & Krebs, 1986), and infer a process of selection (Andersson & Erlinge, 1977).

The Eurasian otter (*Lutra lutra*), henceforth referred to as “otter”, has often been described as a generalist predator (Remonti et al., 2010; Almeida et al., 2012; Krawczyk et al., 2016). This hunting plasticity allows otters to occupy a variety of systems and adapt their diet to fluctuating environments and prey densities (Ruiz-Olmo & Jiménez, 2009). However, otters have also been described as specialists (McCarthy & Hassett, 1993; Clavero et al., 2003), due to their highly piscivorous diet and physiological/morphological adaptations to hunt prey in the water (Kruuk, 2006). While otters are known to predate on multiple prey types across various taxonomic families, they demonstrate a clear preference towards fish (Erlinge, 1968). This will generally represent the bulk of their diet, except where seasonal or location-specific restrictions make other prey types more reliable (Beja, 1996; Clavero et al., 2003; de la Hey, 2008). While these two strategies seem diametrically opposed to one another, it may be better to consider them as a continuum rather than absolutes and that otters lie somewhere in-between both categorisations.

Previous studies into otter diet tend to focus primarily on the individual size, population density or assemblage of prey species taken (Lanszki et al., 2001; Miranda et al., 2008; Sittenthaler et al. 2013), but there is little literature on the trophic effects otter diet has on a system. By focusing on the species assemblage taken at different sites, rather than trophic functionality of prey, we may misinterpret patterns in otter feeding ecology as simply opportunistic/generalist, rather than selective/specialised. For this study we have collated previously reported otter dietary lists recorded across the UK and Ireland, and supplemented these with our own recorded data collected on the Gower Peninsula, Wales.

We wish to test whether prey trophic levels and functionality differs across sites, or whether these follow consistent patterns. In doing so we can determine whether otters found in the UK and Ireland follow more generalist or specialist feeding strategies, thus allowing us to better predict how the reintroduction and/or management of these animals might affect prey species present. We also wish to analyse the trophic functionality of prey species identified in order to predict the cascading effects that otter diet might impart upon these freshwater systems through disruption of their populations. In doing so we hope to contribute towards building a framework on how to better understand and predict the trophic implications of reintroducing otters into an unoccupied water body and how to better manage existing populations, regardless of geographic location within the UK and Ireland.



## 2.0 Methods

### 2.1 UK and Ireland Dietary Data Selection

We reviewed the findings of many otter dietary lists reported by studies carried out across the UK and Ireland since the 1970s. While studies reported their findings using a variety of metrics and methods, in this study we focused on using the percentage relative frequency of occurrence (RFO%) as a measure of prey taken using the methods described by Watson (1978):

$$RFO\% = \frac{\text{Number of occurrences of a prey type}}{\text{Total number of occurrences for all prey types}} \times 100$$

As such only papers reporting their results as RFO% using this methodology, or those that provided the necessary information to allow for translation using this calculation, were selected. The final list included 11 studies that covered sites across England, Ireland, Scotland, and Wales (Appendix 2). While this study only compares freshwater fish species and has excluded all other occurrences, the RFO% for each species is reflective of the total catchment data of each study.

### 2.2 Supplementary Gower Data

The Gower Peninsula is an area of roughly 180 km<sup>2</sup> located in south-west Wales, containing various freshwater systems. Four freshwater sites known to be occupied by otters were chosen across the peninsula to collect spraint samples: Clyne Valley (river mouth – 1000m inland), Pwff Du (river mouth – 650m inland), Three-Cliffs Bay (river mouth – 1500m inland) and Hillend (river mouth – 235m inland). Both sides of the riverbanks, and any protruding features within the water were thoroughly searched at these sites for otter spraints. Each site was revisited a minimum of five times, although only dates where samples were taken have been recorded.



Fig. 1: Map of the UK and Ireland. Purple rectangular area highlights the Gower Peninsula. Map created using Digimap online ordinance survey tool (<http://edina.ac.uk/digimap>).

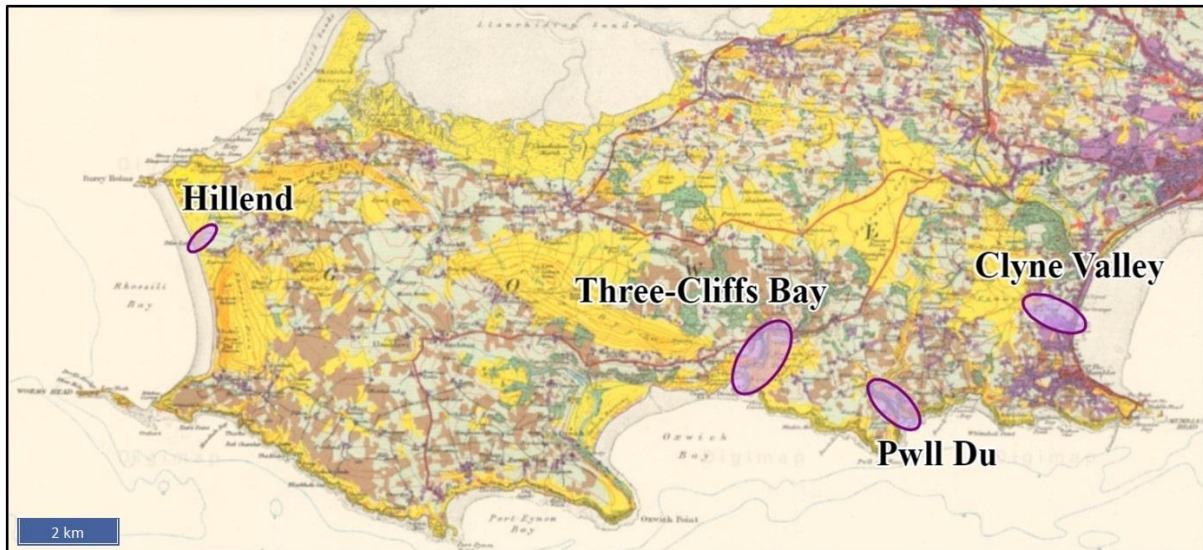


Fig. 2: Map of the Gower Peninsula, South Wales. Circled areas represent all four sampling sites used for otter spraint collection. Map created using Digimap online ordinance survey tool (<http://edina.ac.uk/digimap>).

A total of 44 spraints were collected between 31/05/2021 and 14/01/2022. Due to freedom-of-movement restrictions in place during the COVID-19 global pandemic, sample collection dates could not be scheduled reliably and so no attempt was made to differentiate between seasonality.

### *2.3 Gower Spraint Analysis & Prey ID*

Samples were left in individual solutions of warm water and ~1 tbsp of washing detergent for a period of 24 hours to dissolve the spraints. Once dissolved, the samples were sifted using a 5mm sieve under warm running water to separate out the hard tissue. These were then left to dry in paper towels for a further 24 hours at room temperature. Once dry, the samples were analysed using a microscope between x10-x40 magnification.

Fish, mammalia and amphibia vertebrae and jawbones, henceforth referred to as “occurrences”, were noted as present/absent in each sample. Individual occurrences were also counted. Occurrences of crustacea, insecta and mollusca were only marked as present/absent, even where multiple occurrences appeared in a single sample. This was due to the difficult nature of identifying individual occurrences from these families as separate specimens, as carapaces were crushed into small fragments. While insecta and mollusca represented a very small percentage of overall occurrences, crustacea made up a relatively large part of the biomass

found across samples (Appendix 1) and should be taken into consideration when reviewing these results.

Occurrences were identified to family-level using “Otter Spraint Analysis” (J.B. Webb, 1979) and supplementary ID guides provided by project supervisor, then further identified to species-level where possible. We used the FishBase<sup>TM</sup> online tool (Froese & Pauly, 2022) to exclude potential species from the list based on distribution and depth-range (excluding those typically found at >15m). Marine species were also excluded. It is important to note that the family leuciscidae has been incorporated into cyprinidae for the purpose of this study. This was done as, prior to 2018, leuciscidae was considered a subfamily of cyprinidae and most of the dietary lists used for this analysis pre-date this new classification.

#### *2.4 Statistical Analysis*

Five functional and/or morphological categories were selected for use in the cross-comparison analysis between species. These included trophic level, resilience, mean adult length, body form and aquatic zone (Table 1). All information for these categories was collated using the FishBase<sup>TM</sup> online database (Froese & Pauly, 2022). Each identified species was then assigned a value/group within each of the five selected categories, with family-level groups given a combined mean or grouped value. The species RFO% from each dietary list was used as a proxy occurrence value for each of these categories, with overlapping groups added together.

Table 1: Functional and/or morphological categories selected for analysis of otter freshwater fish prey types identified across collected Gower data and collated UK and Ireland studies.

<b>Category</b>	<b>Description</b>
Trophic Level (TL)	A species position in the food chain. TL2 represents herbivorous/detritivorous diets, while TL 4.5 represents a top predator. Also refers to interactions between species.
Mean Adult Length	Estimated average length (cm) once an individual reaches maturity. Occurrences identified to family level were estimated by averaging the mean adult length of all species within said family present within UK and Ireland freshwater systems.
Resilience	Categorical representation of species minimum doubling time (Low = 4.5-14 years; Medium = 1.4-4.4 years; High = less than 15 months). Occurrences not identified to species level were labelled as “uncategorised”.
Body Form	Body shape of fish species (fusiform, elongated, eel-like, flat, short and/or deep, or compressiform).
Aquatic Zone	The aquatic zone represents the space a prey species primarily occupies within the water column (Benthopelagic, demersal, pelagic, or pelagic-neritic). Occurrences not identified to species level were labelled as “uncategorised”.

We then performed a Kruskal-Wallis one-way ANOVA on each category to test the means between inter-categorical groups and discern whether otters were favouring specific groups or taking prey evenly across them. We also performed a Pearson’s correlation test to measure the relationship between mean adult length of prey (explanatory variable) and RFO% (response variable) to see if prey size was an influencing factor in selection/catchment success. Finally, we performed a Kruskal-Wallis one-way ANOVA test on the trophic levels of prey species between sites to discern whether these varied or were similar across the different sites and assemblages. All statistical tests were performed using GraphPad Prism (version 9.4.0. for Windows, GraphPad Software, San Diego, California USA, [www.graphpad.com](http://www.graphpad.com))

## 2.5 Body Form and Locomotion Type

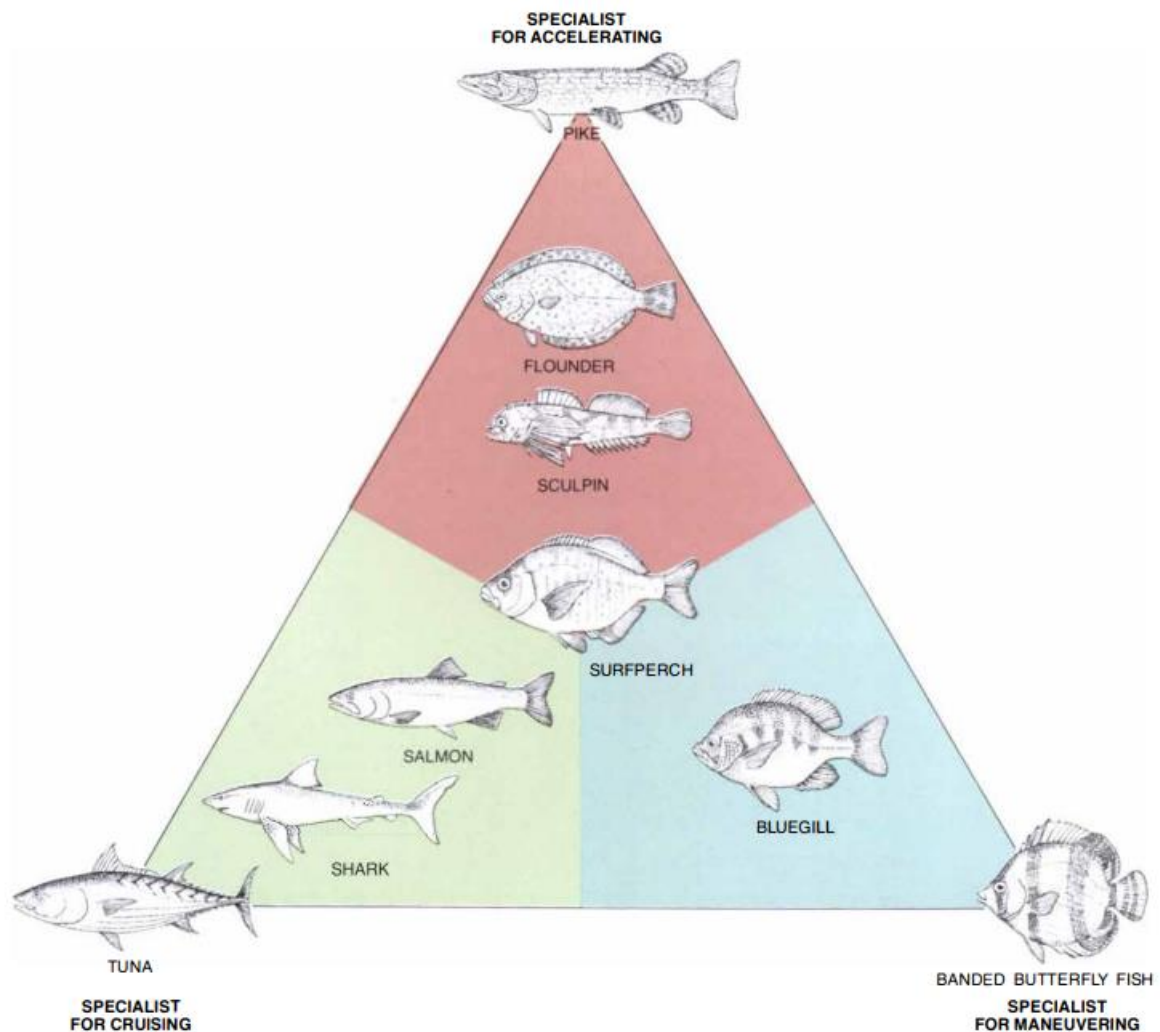


Fig. 3: Illustration of the changes in functional morphology for locomotion in fish. Species located at the corners of the triangle represent locomotion specialists in one of three categories: acceleration, cruising, and manoeuvring. Specialists excel within their category but perform poorly in others. Species in the central region are considered locomotion generalists and may pull slightly towards one of the three specialisations. Graph and data collated from Webb (1984<sub>b</sub>).

To further analyse the potential effects of prey body form on any selection process by otters, we used previous work performed by Webb (1984<sub>b</sub>) describing how body form is linked to locomotion type in fish. We theorised that the shape and locomotion type of prey may also be an influencing factor in possible prey selection by otters and compared the data from our combined dietary lists to the different locomotion types described in this paper in order to form a potential range of preferred prey. Prey catchment success of these different locomotion

categories was also used to infer how disruption to their populations may influence other species.

Table 2: Prey catchment success rates and trade-offs of different locomotion specialities across theorised range of otter prey species, as reported by Webb (1984<sub>b</sub>).

<b>Locomotion Specialisation</b>	<b>Catchment Success</b>	<b>Strategy Trade-offs</b>
Peak Acceleration	70-80%	Relies on prey to come within range to strike quickly, lowering the total number of prey encountered.
Peak Cruising	10-15%	Cruising wide distances at high speeds allows for more opportunities to encounter prey.
Generalist	40-50%	Intermediate form allows for exploitation of niches not occupied by specialists.

### 3.0 Results

#### 3.1 Gower Dietary Data

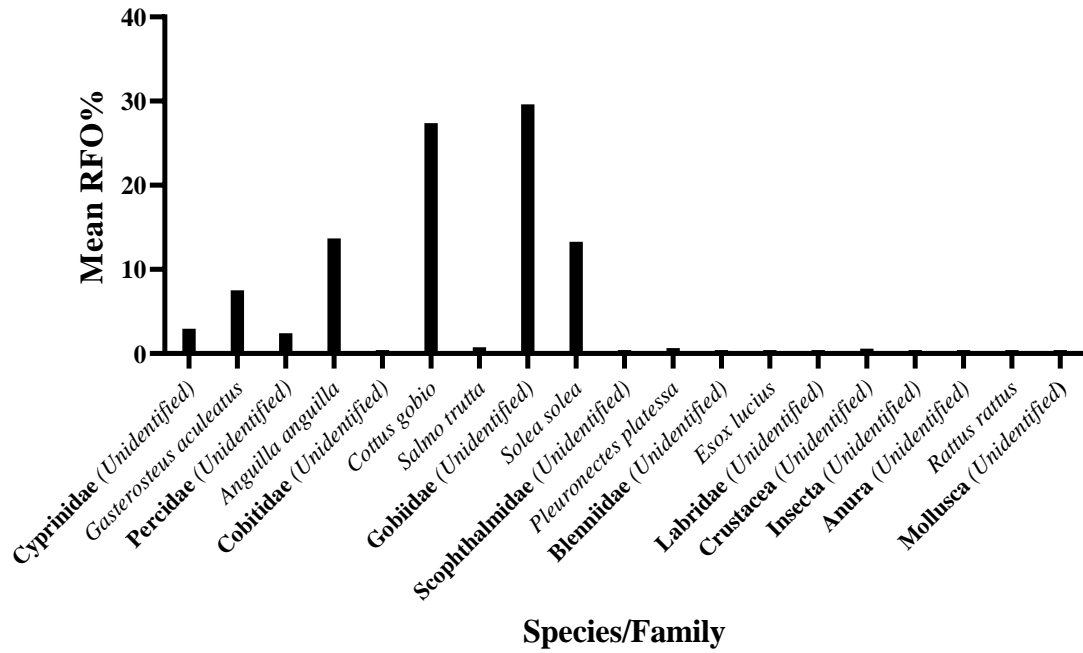


Fig. 4: Mean RFO% of all otter species/family prey groups identified during analysis of spraint samples collected on the Gower Peninsula between 31/05/2021 and 14/01/20.

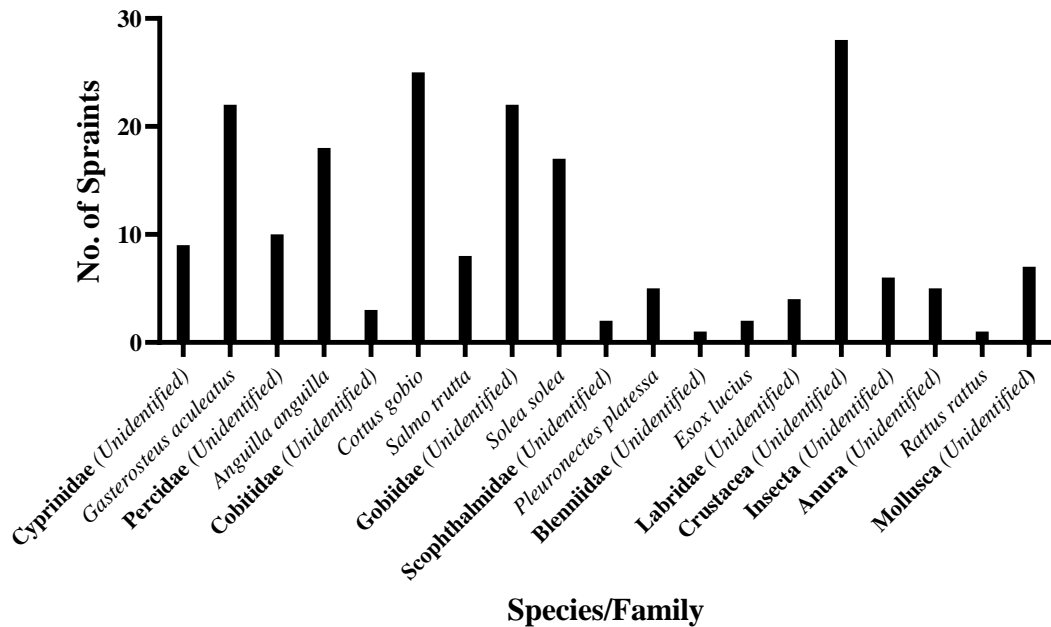


Fig. 5: Presence/absence data showing the number of spraints in which a species/family group was identified during analysis of samples collected on the Gower Peninsula between 31/05/2021 and 14/01/2022.



The analysis of spraint samples collected on the Gower Peninsula revealed that unidentified gobiidae were the most prevalent prey type with a mean RFO of 29.61%, followed by *Cottus gobio* (mean RFO 27.38%) and *Anguilla anguilla* (mean RFO 13.69%) (Fig. 3). However, if we consider the presence/absence data (Fig. 4) we see that unidentified crustacea were prevalent in more spraints than any other prey type (28% of samples) and constituted a much greater proportion of the prey biomass (BIO) examined than any other group.

### 3.2 Combined Dietary Data

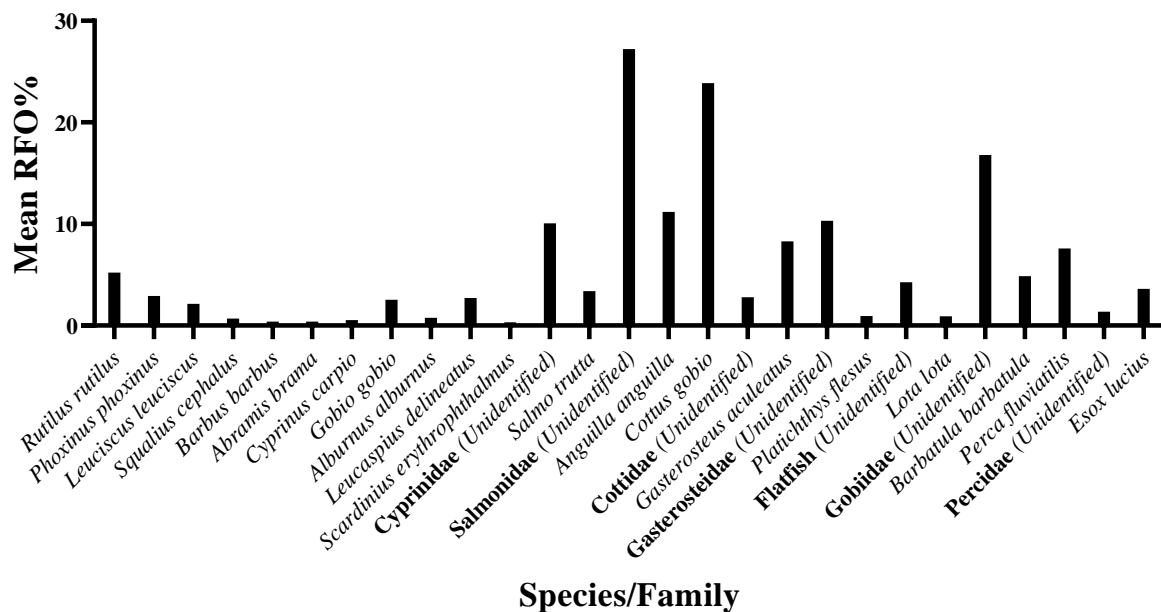


Fig. 6: Mean RFO% of all freshwater species/family freshwater fish prey identified across collected Gower data and collated UK & Ireland otter dietary studies.

Unidentified salmonids were, on average, the highest predated-upon group across sites with a mean RFO of 27.22%. *Cottus gobio* was the second most identified group (mean RFO 23.87%), followed by unidentified gobiidae (mean RFO 16.78%). However, the RFO% of overall unidentified salmonids has been inflated due to high populations reported within the Scottish dietary lists conducted at Burn of Sheeoch and Canny Burn, Aberdeen (RFOs of 89.7% and 90.1%, respectively). If we exclude the two outliers then this group has an RFO% of 11.54%, making it the third most abundant overall.

### 3.3 Statistical Analysis and Combined Effects

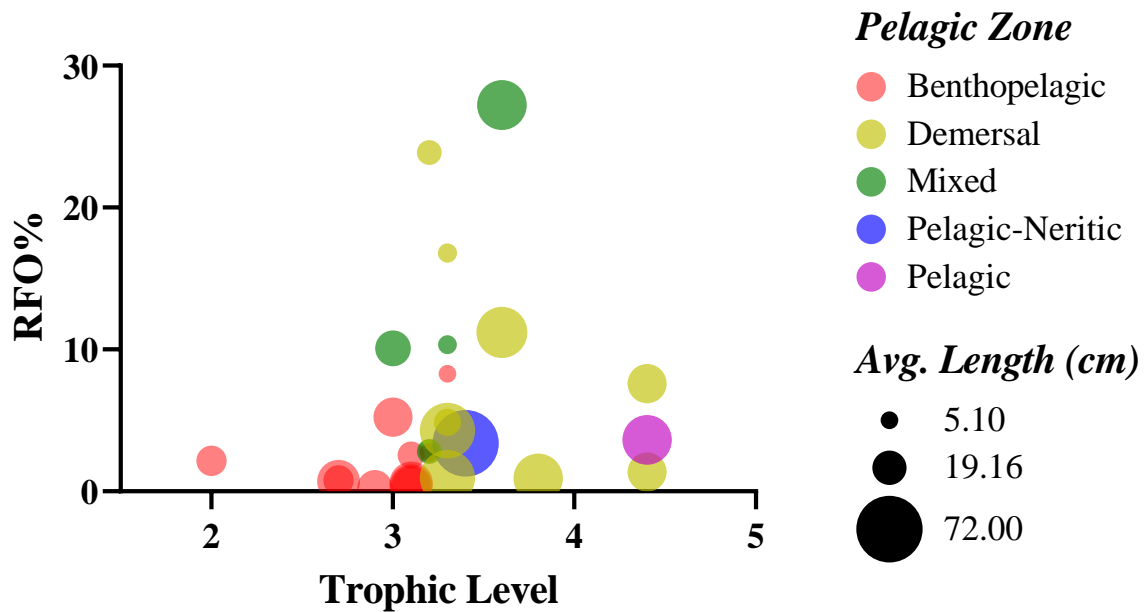


Fig. 7: RFO% of aquatic zone and mean length across trophic levels of freshwater fish occurrences identified from collected data and collated UK & Ireland otter dietary lists.

Our statistical analysis shows that there is not an even distribution among the means of prey within the selected categories, suggesting that there are particular groups within these categories that otters predate upon more greatly than others. This is most prevalent in trophic levels and may be an indication of a selective process, rather than more generalist hunting. When combining our results (Fig. 7) we can see that there may be a range, particularly within TL (3.2-3.6) and prey size (~10-25cm), that otters may prioritise when selecting prey.

Table 3: Results of Kruskal-Wallis tests performed on all five selected categories. All tests performed reported a statistically significant difference between group means across all categories.

	<b>Kruskal-Wallis Statistic</b>	<b>p-value</b>
Trophic Level	87.43	<0.0001
Resilience	10.06	0.0181
Body form	35.47	<0.0001
Mean Adult Length	58.86	<0.0001
Aquatic Zone	37.98	<0.0001

### 3.4 Trophic Level

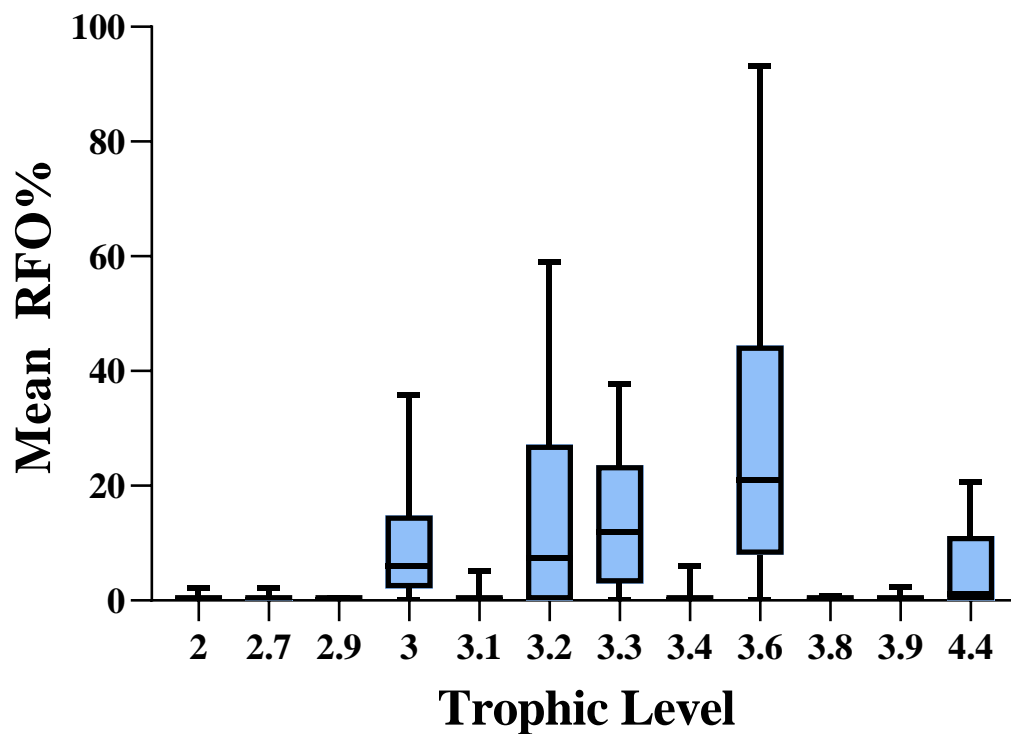


Fig 8: Mean RFO% of trophic levels of all freshwater fish prey identified across collected Gower data and collated UK and Ireland dietary studies.

The results suggest that otters tend to primarily take freshwater fish prey between TL 3.2-3.6. This range represents 13 out of the 27 freshwater species identified across sites, with those at TL 3.6 representing an average of 30.4% of all freshwater fish species predated upon. Results of the Kruskal-Wallis test performed to measure the RFO% of trophic levels between sites reported no statistically significant difference (KW statistic = 12.28,  $p = 0.4231$ ). TL 3 is typically assigned to secondary consumers; opportunistic omnivorous species that consume invertebrates and small fish (Kieckbusch *et al.*, 2004).

Table 4: Primary trophic feeding range and associated species/family groups of prey identified across combined otter dietary data. All information collated using the FishBaseTM online database (Froese & Pauly, 2022).

TL	Noted Species/Groups	General Feeding Notes
3.2	<i>Cottis Gobio</i> , <i>Leucaspius delineates</i> , <i>Phoxinus phoxinus</i> , Unidentified Cottidae	Smaller bottom-dwelling insects, smaller crustaceans. Some examples also feed on plant debris and algae.
3.3	<i>Barbatula barbatula</i> , <i>Gasterosteus aculeatus</i> , <i>Platichthys flesus</i> , Unidentified Gastoridae, Unidentified Gobiidae	Small insects and larvae, amphipods, nematodes, epibenthic meiofauna, crustaceans, mites, and smaller fish.
3.4	<i>Salmo Trutta</i>	Juveniles will primarily feed on small insects and larvae, while adults feed on crustaceans, molluscs, and smaller fish.
3.5	-	-
3.6	<i>Anguilla Anguilla</i> , Unidentified Salmonidae	Similar diet to those observed at TL 3.3, but adults will incorporate slightly larger crustaceans, molluscs, and small fish (including those found at aforementioned trophic levels).

### 3.5 Mean Adult Length

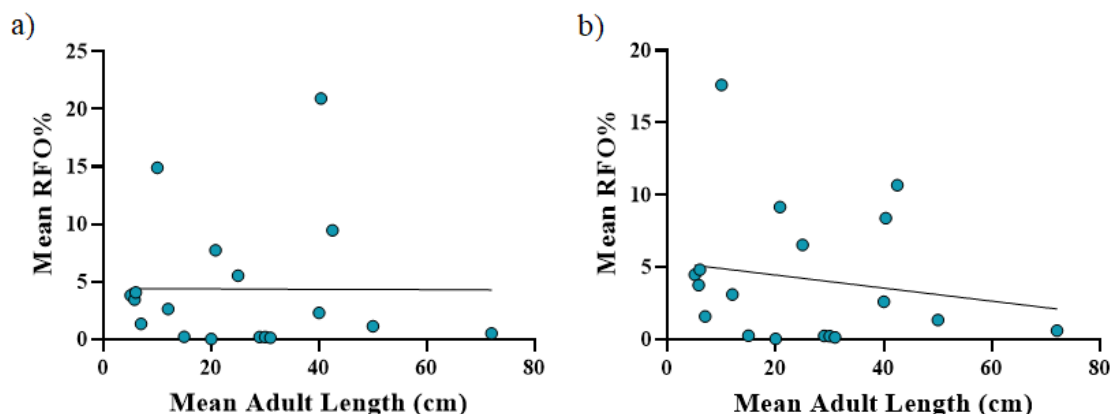


Fig. 9: Comparison of RFO% of freshwater fish species sizes between a) all dietary lists used during analysis (slope = -0.001673) and b) exclusion of study by Carss *et al.* (1990) containing inflated unidentified salmonidae values (slope = -0.04516).

Most freshwater fish predated upon had a mean adult length between 10-25cm. Prey with a mean adult length of 40.4cm were the most prevalent across studies (mean RFO 20.94%). However, this group represents the unidentified salmonidae and, again, has been inflated due to high populations reported in the Burn of Sheeoch and Canny Burn dietary lists used. If we exclude these lists, then prey with a mean length of 10cm were the most prevalent (mean RFO 17.61%) followed by those of 42.5cm (mean RFO 10.68%) and 20.82 (mean RFO% 9.15). The results from our Pearson’s correlation test reported no statistically significant relationship between mean adult length and RFO% ( $r = -0.1189$ ,  $p$  (two-tailed) = 0.5548).

### 3.6 Resilience

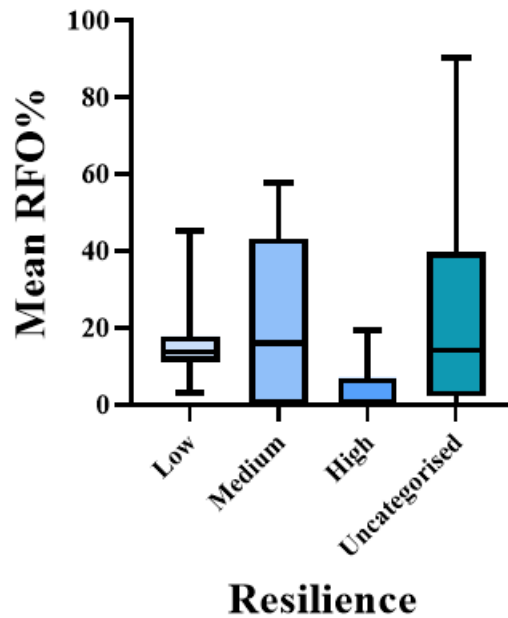


Fig. 10: Mean RFO% of resilience of freshwater fish prey species identified across collected Gower data and collated UK and Ireland dietary studies.

If we exclude occurrences classed as “uncategorised”, most prey items fall into the “medium” resilience category (mean RFO 19.88%), followed by “low” (mean RFO 15.36%) and then “high” (mean RFO 3.82%). Most occurrences, however, were labelled as “uncategorised” and account for an average of 25.52% of prey taken. There are currently 90 known freshwater species found across the UK and Ireland that could potentially be present within the uncategorised group (Froese & Pauly, 2022), of which 5 are categorised as “high” (5.5%), 66 as “medium” (73.3%), 18 as “low” (20%) and 1 as “very low” (1.1%). Considering this ratio

within the uncategorised group, we may potentially assume that most freshwater fish prey taken have a species doubling time of 1.4 - 4.4 years.

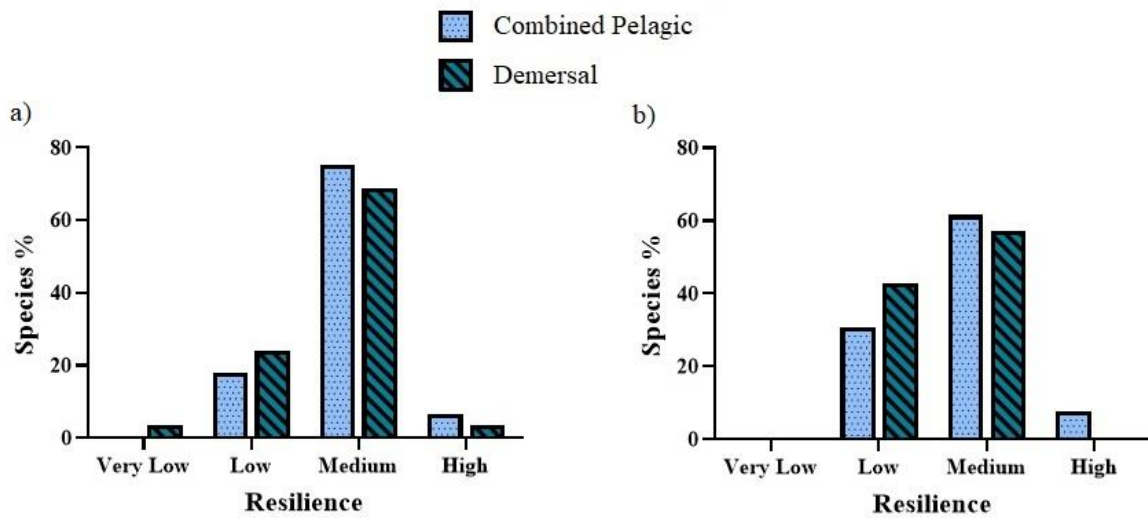


Fig. 11: Comparison of resilience categories between pelagic and demersal fish species a) present across the UK and Ireland and b) identified across collected and collated otter dietary lists used during study. “Combined Pelagic” group consists of all pelagic, pelagic-neritic and benthopelagic species.

### 3.7 Body Form

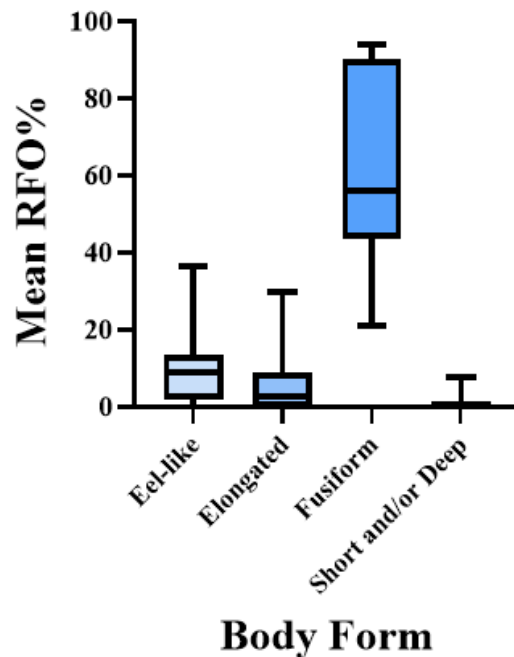


Fig 12: Mean RFO% of body form of freshwater fish prey species identified across collected Gower data and collated UK and Ireland dietary studies.

Results show strong selection toward fusiformes (mean RFO 61.61%). Eel-like (mean RFO 9.47%) and elongated (mean RFO 6.17%) made up much less of the total prey catchment, while short and/or deep occurrences were minimal (mean RFO 1.13%). No occurrences of flat or compressiform were recorded.

### 3.8 Aquatic Zone

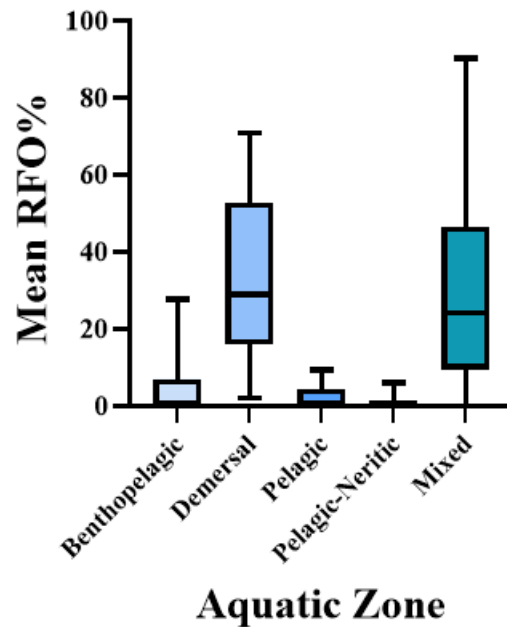


Fig 13: Mean RFO% of aquatic zone of freshwater fish prey species identified across collected Gower data and collated UK and Ireland dietary studies.

Most prey species/groups fall into the “demersal” and “uncategorised” categories, with mean RFOs of 33.98% and 33.22% respectively. Species in the “benthopelagic” (mean RFO 4.67%), “pelagic” (mean RFO 2.23%) and “pelagic-neritic” (mean RFO 0.52%) categories were much less present across dietary lists. However, of the 90 potential species that could occur within the “uncategorised” category; 50 are benthopelagic, 29 are demersal, 3 are pelagic and 8 are pelagic-neritic. This means that the potential for a much higher true percentage of benthopelagic prey species must be taken into consideration when reviewing these results.

## 4.0 Discussion

While the results show a wide range of prey species that otters are predating upon, and variation of species taken between different sites, they also suggest narrow ranges within the chosen categories that are being selected for. This is particularly prevalent within the TL and size categories and alludes that otters within the UK and Ireland lean more towards selective/specialist hunting strategies than more generalist feeding. At the very least, we may consider that while they might still be considered generalist in terms of prey species, they are more specialist in prey functionality. This might allow us to predict more accurately how a population of otters might affect a freshwater system and the populations of prey species present within. To understand how these patterns may affect ecosystem functionality, we need to understand the functions that prey within these ranges typically provide to the system around them and interpret how disruption to their populations may affect their ecosystem.

### 4.1 Trophic Level

Most of the freshwater fish species recorded in the dietary lists are between trophic levels 3.2-3.6. The primary food source of fish identified within this range are small, predominantly benthic invertebrates and, as such, the presence of a top predator in the environment acting as a control agent for these fish may correlate with population increases of small invertebrates within the system. Small, benthic invertebrates play crucial roles within their ecosystem by helping release bound nutrients into the system through feeding, excretion, and burrowing activities (Covich *et al.*, 1999) in addition to accelerating nutrient transfer processes to other systems (Clarke *et al.*, 1997; Wallace *et al.*, 1997). They are also a staple food-source for many terrestrial and aquatic vertebrates (Malmqvist, 2002) and an increase in their populations can offer greater food availability for other species, potentially increasing overall biodiversity. Many of these invertebrates are also predatory themselves and can help control populations of other invertebrates within the system (Wellborn *et al.*, 1996), demonstrating the positive top-down cascading effects that a top-predator can impart throughout the lower trophic levels.

These top-down control effects have been previously recorded to promote ecosystem growth, increase biodiversity, and positively affect ecosystem functionality with other carnivore species such as wolves (*Canis lupus*) (Dobson, 2014), pine-martens (*Martes martes*) (Sheehy *et al.*, 2018), lynx (*Lynx lynx*) (Elmhagen *et al.*, 2010) and other freshwater predators such as largemouth bass (*Micropterus salmoides*) (Mittelbach *et al.*, 1995). Understanding the function



of prey species that are likely to be predominantly predated upon, and the cascading effects fluctuations in their population may have on other species, can help us determine the how to better predict the implications of otter re-introduction and management.

#### *4.2 Mean Adult Length*

While our results demonstrated that there was no statistically significant relationship between RFO% and the mean adult length of prey, our data does not consider the actual size of fish being predated upon and could lead to misinterpretations regarding potential prey size selection. Intra-species size fluctuations of prey are important to note as an individual's characteristics, behaviour, energetic value, and trophic function can change with life-stage (Thorstad *et al.*, 2012). Actual size is less important when we consider some of the smaller prey species recorded, such as *Cottus gobio*, but becomes more important with larger species, such as the salmonids.

In a study by Sittenhaler *et al.* (2019), three size categories of salmonids were established to measure size selection of prey taken by otters (small = <12cm, medium = 12-25cm, large = >25cm). They reported that otters primarily predated on salmonids of medium size (RFO 47-68%) while generally avoiding smaller individuals (RFO 13-38%) and only taking larger individuals when energetically efficient (RFO 10-19%). These results were not proportionate with the availability of each size class present and gives us an indication of selection in otter foraging. Medium-sized salmonids, on average, tend to inhabit shallower waters than those of other size classes (Armstrong *et al.*, 2003), which plays better to the otter's hunting strengths and makes them more energetically efficient prey. Most salmonid species also do not reach sexual maturity until reaching sizes well into the "large" category (Froese & Pauly, 2022), meaning that predation on a salmonid population should affect breeding fishes much less so than non-breeding fishes. The study also showed that otters supplemented their diet with smaller, less energetically beneficial prey types to maximise foraging efficiency according to the optimal foraging theory (MacArthur & Pianka, 1966). This gives us a perfect example of both opportunistic/generalist and selective/specialist hunting behaviours by otters, further strengthening the argument that we must consider both strategies simultaneously.

While size and trophic level are usually strongly correlated with each other among fish species (Dantas *et al.*, 2019), the nature of whether this relationship is either positive or negative is

dependent on fish functional/morphological traits such as body depth, mouth width and tooth shape. (Keppler *et al.*, 2020). This means that while we might link size to prey selection, size alone cannot be used as a predictor for the trophic functionality of a fish species. However, we might use size to infer other cascading effects on trophic structure, such as the abundance of parasites within a system. For example, helminths are macroparasitic worms that often reside within the intestinal tracts, body cavity, muscle tissue, or organs of their hosts (Bell & Burt, 1991; Castro, 2011). They usually travel up trophic levels in larval or juvenile forms via predator-prey interactions and typically choose predatory species as their definitive hosts, where they reach their adult stages (Parker *et al.*, 2015). Studies show that, on average, fish <20cm in length have twice the proportion of larval helminth taxa than those >100cm, meaning that smaller fish generally make better hosts for larval parasites (Poulin & Leung, 2011). These parasites usually require three hosts to complete their life cycles: an invertebrate first intermediate host, a fish second intermediate host, and a definitive host (Chub 1980). While there are several helminth taxa that specialise on inhabiting mammals such as otters as their definitive hosts (Torres *et al.*, 2004; Mulville, 2016), there are also many examples that culminate their life histories in fish, amphibian, and bird hosts (Holland & Kennedy, 1997). By prioritising smaller fish, otters may be able to reduce the amount of ideal secondary host bodies present for the latter mentioned groups of parasites and lower overall helminth abundance within a system. The detrimental effects helminths can have on both the individual host and overall ecosystem health are well documented (Shah *et al.*, 2013; Akinya *et al.*, 2019; Desai *et al.*, 2021), and so reductions in their population should correlate with an increase in system-wide health.

### 4.3 Resilience

There are two terms used when describing a species ability to react to disturbances within a system. “Resistance” is the ability of a species to withstand a disturbance and “resilience” refers to the fecundity, or doubling time, of a species (Mahardja *et al.*, 2021). Thus, we can use resilience to infer an assemblages’ ability to return to its previous structure following a disturbance event (Connel & Sousa, 1983). There are two ways we can approach this statement. First, we can predict how environmental disturbances might affect fish assemblages, potentially affecting otter’s foraging/feeding patterns by switching to more prominent prey types and altering the effect their diet has on ecosystem functionality. Secondly, we can also consider the

otter itself as a disturbance factor in a system where the predator is absent and estimate how its (re)introduction might affect fish assemblages.

In a study by Rose (2005) it was reported that pelagic fish are both more likely to respond to changes in their environment than demersal fish species and are also likely to do so more quickly due to having typically higher resistance and resilience levels. This difference in resilience levels between groups was also observed in our data, both across the dietary lists selected for our analysis and across all present freshwater fish species found within the UK and Ireland (Fig. 11). Demersal fish species with, on average, lower resilience levels are more susceptible to environmental disturbance factors such as flooding (Pearsons *et al.*, 1992), pollutants (Ibrahim *et al.*, 2014), and human disturbance (Vasconcelos *et al.*, 2017) than pelagic species with higher resistance and resilience levels. This highlights a potential area for disturbance in otter foraging, as our data shows that otters predate upon demersal freshwater fish more so than pelagic species within the UK and Ireland.

If we consider the otter itself as the disturbance factor, then our data shows that they primarily affect freshwater fish species with medium resilience levels, followed by low resilience. While we reported a mean RFO% of 19.88% and 15.36% for these groups respectively, we assume that the true figures are higher while still maintaining this pattern. Given that otters are generally solitary and have relatively large home ranges (McCarthy & Hassett, 1993; Kruuk, 2006), we would expect to see an overall reduction in the populations of species predated upon but only to a point of equilibrium between predator and prey communities. This is under the assumption that habitat availability is not a limiting factor for otters, which could lead to overcrowding, increased predation pressures on prey species, and potential destabilisation of a system. We could also see the presence of otters affecting the resilience levels of species through disturbance pressures. For example, some bivalve species have been shown to increase resilience levels when faced with increased predation risks (Belgrad *et al.*, 2021). With otters potentially removing some of their predators through top-down control, we might expect an overall reduction in the resilience levels of bivalve assemblages due to reduced predation pressures. However, as we have previously mentioned how top-down control of one species can afford more resources to competing species (see 4.1 Trophic Level), this newly available resource should be exploited by other predators. As bivalves have also been recorded in otter diet, we might then expect to see an overall increase in the resilience levels of bivalves in the presence of otters, further protecting them against disturbance factors and strengthening the system at the primary level. This is a good example of the complexities behind trophic food

webs and ecological function and highlights the need for further research into this field to fully understand and predict the implications of predator reintroduction on species resilience.

#### 4.4 Body form

The majority of freshwater fish recorded were fusiforms (mean RFO 61.61%), but it is unclear as to whether this is an indication of preferential selection by otters or if fusiform prey is simply far more abundant than those of other body types within these systems. A review of freshwater fish species present within the UK & Ireland shows that 77.77% are classed as fusiforms, which would account for the high percentage recorded in this study but does not tell us much in terms of function or selection. A more correct approach to analysing body form in relation to ecological function may be to inspect the individual factors it is associated with, rather than using such a broad categorisation. These are habitat use, locomotion, and swim type (Villéger *et al.*, 2017; Wiedmann *et al.*, 2014). As we will discuss habit usage further on (see 4.5 Aquatic Zone), here we shall discuss how locomotion and swim type might be associated with the trophic system. Swim type refers to the physio-mechanical adaptations of a fish in relation to propulsion and movement (Sfakiotakis *et al.*, 1999) and is intrinsically linked with locomotion. Therefore, for the purpose of this discussion we will assume that any potential trophic effects or selection relating to swim type will be covered by locomotion speciality. Previous studies have characterised fish locomotion adaptations into three broad specialisation categories: acceleration specialists, cruising specialists, and manoeuvrability specialists (Webb 1984<sub>b</sub>). Webb (1984<sub>a</sub>) reported that locomotor specialists underutilise small food items, such as benthic invertebrates, and that this niche is then exploited by typically smaller, locomotor generalists. The latter group represents most recorded freshwater fishes predated upon by otters and may give an indication as to potential selection of prey.

If we review Fig. 3, we can see that pike (*Esox lucius*) is reported as a peak acceleration specialist. While it only represented a small proportion of overall prey (mean RFO 3.62%), it was recorded as a food source of otters in the collated data and so we can use this peak as a point of reference when trying to determine a theorised range of otter prey. We can also see salmon located closer to the generalist region of the graph, but more specialised towards cruising. While our own values for salmonids are inflated, they still represent a substantial prey type for otters. These can also be used as another reference point as no freshwater prey species recorded in our data is more adapted than the salmonids towards cruising speciality. If we

consider the morphological adaptations, size and prey of the other fish groups identified in our dietary analysis, we might assume them to primarily be locomotion generalists and to be attributed to the central region of the graph. This presents us with a potential selection range of otter prey based on locomotive function. It suggests that otters prioritise locomotive generalists, and occasionally can take prey more specialised in acceleration or cruising. However, none of the evidence suggests predation of fish more specialised in manoeuvrability. Whether this is due to a lack of manoeuvrability specialists within the otter's hunting range or if high manoeuvrability is a limiting factor in successful prey catchment remains unclear. Kruuk *et al.* (1990) reported that otters do not often chase their prey in open water, but instead rely heavily on touch to identify prey when foraging. This means that highly manoeuvrable prey might prove too energetically expensive to pursue and thus result in the selection of easier targets, although further research is needed to corroborate this statement. These locomotion types can also predict prey catchment success rates of fish (Table 2), which may give some indication of the effects disruptions to their populations have on trophic function. If we consider that most of the otter's freshwater fish prey comprises of locomotion generalists, who themselves have a prey catchment success rate of around 40-50%, then a reduction in their populations should positively correlate with an increase of species at lower trophic levels.

#### 4.5 Aquatic Zone

The "aquatic zone" (or habitat use) is intrinsically linked with many of the other categories used, and many of the trophic effects previously listed due to otter diet overlap with this category. The majority of freshwater fish prey recorded were found to occupy the demersal zone (mean RFO 33.98%), with benthopelagic species assumed to be the second-most prevalent (mean RFO 4.67%). As with our analysis of trophic level, this further strengthens the argument that the presence of otters may have a positive effect on benthic macro-/meiofauna and small invertebrate populations/diversity through top-down control of their predators. As such, we might expect to see an increase in primary production at the demersal level which can have cascading effects throughout the water column and higher trophic levels.

These results are also in line with the most common observed foraging techniques used by otters. Kruuk *et al.* (1990) describe the most observed strategy used by otters in open water, both marine and freshwater, as "patch fishing". This technique involves the otter diving straight down towards the benthic zone and resurfacing in the same spot after a short time to consume

its prey at the surface. This is then repeated across a relatively small patch of water, which is often revisited. It is important to note that otters are not usually observed submerging their heads before initiating these dives, and so it is thought that these are recognised sites of easier access and higher catchment success. This strategy demonstrates a high degree of specialisation and forward thinking. While otter's foraging plasticity and ability to switch strategies/prey types in response to fluctuating prey availability suggests a more generalist approach, we argue that the repeated recorded usage of these foraging techniques and high levels of demersal/benthic prey items found in spraints across the UK and Ireland suggest that otters will primarily revert to these strategies and zones if prey is available in sufficient quantities.

This high usage of benthic foraging grounds by otters also presents a potential area for disruption which should be considered. Today, the UK faces major water quality issues (Cruddas & Roberts, 2021), and the Environment Agency and Natural England (2021) have recently deemed only 14% of river systems in England and Wales to be of "good" ecological quality. Dumping of pollutants, particularly nitrogen and phosphorous (Bunting *et al.*, 2007; Rothwell *et al.*, 2022), can cause eutrophication of water systems: the over-enrichment of a waterbody with nutrients and minerals, associated with oxygen depression and toxicity (Whelan *et al.*, 2022). This increase in nutrients may produce additional production in pelagic fish (Breitburg, 2002), but this is not the case for demersal species (Eby & Crowder, 2002). Eutrophication can especially cause oxygen depletion near the sediment-water interface, with resulting hypoxia and/or anoxia proving fatal to benthic invertebrate populations (Powers *et al.*, 2005). This has already been demonstrated to be of great disturbance to demersal fish and crab assemblages (Peterson *et al.*, 2000), which in turn may change the foraging habits of otters through reduced availability of these prey types. Prey-switching has been commonly reported in otters when their primary food sources become scarce due to factors such as seasonality and prey species decline (Pagacz & Witzuk, 2010; Moorhouse-Gann *et al.*, 2020), so it is unlikely that otters won't simply change their foraging patterns to accommodate the absence of their primary prey types. However, these changes could alter the effects that otter diet has on its environment, and the energy costs and benefits of foraging itself. The nature of the long-term effects of both factors are unknown but deemed potentially impactful enough on both trophic health/function and otter wellbeing that they merit further investigation.

#### 4.6 Inferred Trophic Effects and Issues with Classification

While otters' generalist qualities and hunting plasticity are irrefutable, to say that otter diet is reflective of the prey species assemblage present within a system is simply incorrect. We found sufficient evidence of inter- and intra-species prey selection, both in our results and the reviewed literature, and consistent use of benthic/demersal foraging grounds to suggest specialist hunting behaviours. Most importantly, while prey assemblages varied across dietary lists, we found no statistically significant difference in the mean RFO% of trophic levels of prey between them. This suggests a consistent, narrow trophic range (3.2-3.6) across freshwater fish assemblages that otters will primarily predate upon.

Most prey items taken are small-medium (~10-25cm) demersal fish which provide less energy but are also less energetically expensive to predate (Moorhouse-Gann *et al.*, 2020). These fish generally appear in higher numbers across dietary lists, particularly *Cottus gobio*, and their high volume is thought to compensate for the lower biomass of individual fishes. The other are slightly larger, more free-swimming fish such as the salmonids. These provide more energy but are also more energetically expensive to predate upon. They are generally seen in lower numbers except in areas where their populations are inflated, such as in parts of Scotland and Northern Ireland. However, within the salmonids we see a selective preference towards mid-sized fishes (~12-25cm) which, on average, frequent shallower waters. This provides some overlap between both groups in habitat space use and size, which plays to the otter's primary hunting methods and strengths).

The data suggests demersal/benthic zones as the otter's optimal/primary foraging grounds. However, it is unclear if this is due to preference or if this could be a result of the reduction of salmonid populations in more southern regions of the UK and Ireland (Fausch, 2007). While species such as *Cottus gobio* and *Anguilla anguilla* were prominent prey types across most of the selected dietary studies, their RFO% dramatically dropped, or were not recorded at all, at Scottish and Irish sites where salmonid RFO% increased. This alludes to potential selective decisions between energy cost/gain and BIO previously discussed, where greater concentration of salmonid allows for easier capture than in southern regions. It also suggests that increasing salmonid populations may reduce predation pressures on demersal species considerably.

While there have been many case studies on otter reintroduction across Europe (Sjöåsen, 1997; Saavedra & Sargatal, 1998; Hobbs *et al.*, 2006; Koelewijn *et al.*, 2010; Romanowski *et al.*,

2013), it is surprising that there is so little data on the trophic/cascading effects otter reintroduction and diet has on an ecosystem. We may, however, infer some of these effects by comparing our results with similar studies on other carnivore species. Studies have demonstrated the important role that predators have in contributing to a stable and diverse ecosystem, and that their presence causes both behavioural changes and/or decreased population density in prey species (Winnie Jr. & Creel, 2017). When reviewing the trophic effects predators can impart on an ecosystem through top-down control of herbivorous species, we first typically see a reduction in prey populations and an increase in predator-avoidance behaviours (Hoeks *et al.*, 2020). These behaviours mean that prey species reduce their overall foraging times and often avoid more optimal feeding grounds where they may be more vulnerable to predation. This reduces inter-species competition for resources and has a positive cascading effect on vegetation density and diversity (Calcagno *et al.*, 2011), which usually leads to an increase in species biodiversity at lower trophic levels. If we consider that most freshwater fish predated upon by otters are classed as secondary consumers, then we should expect to see population increases in smaller herbivorous fish and invertebrates, which could lead to a reduction of algae and further protect the demersal zone against potential algal blooms, eutrophication, and disruption of otter's primary foraging methods and prey types.

We might also see otters act as a potential control agent for some invasive species, provided they occupy similar trophic niches and functional/morphological categories as recorded native prey. This has already been observed with some invasive prey types (Britton *et al.*, 2017; Dettori *et al.*, 2021; Pezy *et al.*, 2022), although some studies have suggested a lag phase between invasive species introduction and predation by otters (Prigioni *et al.*, 2006). The effectiveness of such control measures, however, needs to be considered on a species-to-species level. Blanco-Garrido & Prenda (2007) reported that otters actively avoided invasive pumpkinseed (*Lepomis gibbosus*) in Italy due to their apparent dislike of handling spiny prey, another example of selection. Upon review of the locomotion and morphological qualities of *L.gibbosus* (Muhawenimana *et al.*, 2021), we could go a step further and say that the morphology of these fish suggest a speciality towards acceleration and perhaps they also lie outside of the theorised range of fish species predated upon by otters due to the energetic cost of catchment success.

It has been previously reported that predator hunting speciality tends to increase with latitudinal gradient, while generalism typically decreases (Andersson & Erlinge, 1977; Hanski *et al.*,



1991). For some predators this is due a reduction in prey diversity as we go from southern to northern regions, and similar patterns have been suggested for otters within Europe. Clavero *et al.* (2003) reported that otters tended to act more as highly specialised piscivores in more northern, temperate regions of Europe that do not suffer dry seasons, whereas greater environmental fluctuations in Mediterranean areas reflected more generalist feeding ecology. Considering this, it may be more correct to assume otters in the UK and Ireland primarily as piscivorous specialists when planning reintroduction and management strategies, with the assumption that their high adaptability may change their trophic impacts when faced with disturbances to their primary prey types and/or habitats.

While the results and opinions derived from this study should be corroborated with more raw data and extended analysis, at the very least this should encourage dialogue on how we classify the feeding ecology of these animals to aid us in making more accurate predictions on the potential cascading trophic effects otter diet might have on an ecosystem.

#### *4.7 Limitations & The Need for Standardisation*

As previously mentioned, there were many limitations presented within this study. While it is the opinion of the author that this paper still presents valid arguments and results, they should only be considered as indications towards potential patterns and only with more robust analysis and methods can we gather more precise results. To that end, we have identified limitations in three areas: study limitations, data limitations, and standardisation limitations.

Firstly, the COVID-19 pandemic forced limitations on the study parameters due to restrictions of movement imposed during data collection periods. This meant that we could not reliably schedule collection dates and measure potential differences in diet across seasons, which we propose as an important factor to this type of study.

While reviewing otter dietary lists for use in this study, molecular analysis appeared a more robust method of spraint analysis than traditional bone ID methods. While it was originally considered for this study, time and cost prevented us from using this method. However, we propose molecular analysis to be a superior ID method for this type of study as it provides complete species-level analysis, whereas many of the lists reviewed that used traditional ID methods often contained unidentified family-level groups. We found this to be particularly

prevalent across studies with unidentified cyprinidae/leuciscidae and salmonidae family groups. A complete species-level analysis allows us to assign values more accurately to prey within functional and morphological categories, rather than using mean/combined family-level values, thus providing us with much more accurate results.

Prey functional and morphological category selection was also limited by the availability of online data. There were many more categories considered, but the selected five were some of the few where data was readily available for all species. Generation time, sexual maturity, fishing vulnerability, and climate vulnerability are some examples of categories we originally considered, but the data were simply not available for all species. As our understanding of prey species increases, so too will our ability to accurately predict the effects of their predators on a system.

Lastly, while gathering online otter dietary list data, we noticed a pervasive lack of standardisation of methods and data presentation across papers. Many of the papers reviewed presented their findings using one of, or a combination of, three main units/formulas: relative frequency of occurrence (RFO%), frequency of occurrence (FO%), and relative proportion of occurrence (PFO%).

$$RFO\% = \frac{\text{Number of occurrences of a prey type}}{\text{Total number of occurrences for all prey types}} \times 100$$

$$FO\% = \frac{\text{Number of spraints in which prey type occurs}}{\text{Total number of spraints}} \times 100$$

$$PFO\% = \frac{\text{Number of spraints in which prey type occurs}}{\text{Total number of occurrences for all prey types}} \times 100$$

It is not the reporting of different metrics that causes issue, as they can be used to describe different things or correspond to different data types. However, many papers failed to report data which would naturally be recorded by the study and would allow for easy conversion of results into another metric by outside studies (i.e. number of spraints collected). There were also multiple accounts found where metrics and formulas were simply interchanged, thus nullifying results altogether. During our original analysis, it became apparent that there were inconsistencies in the overall data. We reverse-engineered the results of previously selected

papers reporting their results as RFO%, but that had failed to report which formula they had used in their analysis, and found that the wrong formula had been used in many cases. This forced us to reject many of the dietary lists that had reported their results as RFO% from our original list of studies, which consisted of more than 30 papers. It is the opinion of the author that these are self-imposed and avoidable limitations on a branch of study where there is still so much ground-level work to be done. By limiting the collective data pool available to researchers, we impose serious limitations on the speed in which we advance our understanding in this field.

## 5.0 Conclusion

The results of this study should encourage discussion on how we classify predator feeding ecology in general. In the reviewed literature otters were widely described as generalist predators, with fewer describing them as specialists and less so as both. While we highlighted key factors that suggest otters as both specialists and generalists, there were also elements of otter feeding ecology that are not in line with these classifications. Classifying these animals as one or the other invites preconceived notions on how otters might affect a system that may not reflect reality. Classing them as both does not allow us to clearly predict effects and defeats the purpose of classifications altogether. While we could, and sometimes do, consider these classifications as a spectrum, it is the opinion of the author that perhaps otters should not be classed outright as either and that this highlights a potential gap in our terminology. However, this in itself requires much more debate and research so for the purpose of this study we use the existent terminology.

Although there is a lack of data available for many of the prey species discussed, we conclude that there is still sufficient evidence presented in these findings to consider otter freshwater feeding ecology in the UK and Ireland to be more specialist than generalist. The findings of this study suggest a narrow trophic range of freshwater fish that otters primarily exploit. There is sufficient overlap between size, space usage, and trophic levels of prey that suggest specialised selection. On top of this, freshwater fish prey trophic levels remained consistent across reviewed dietary lists, further demonstrating this selective pattern in otter diet. As previous studies on otter feeding ecology report a shift to more specialist behaviours in northern temperate regions than in Mediterranean habitats, we suggest that the otters should be considered more as a piscivorous specialists than generalists when formulating re-introduction and management strategies targeted at the UK and Ireland.

While our predicted trophic effects are speculative, we believe that otters may provide beneficial effects to freshwater systems in line with top-down cascading effects reported with more researched carnivore species. We believe there is potential for otters to increase a system's resistance to environmental pressures through top-down control of secondary consumers, increasing primary production at the demersal zone. An increase in predator avoidance behaviours and reductions in prey populations should also increase available resources to competing species and allow for an increase in overall biodiversity. Top-down

control of smaller fish species may also indirectly reduce the number of ideal secondary hosts bodies available for helminth parasites, which could potentially positively correlate with an increase to system-wide health. We may also see otters beneficially contributing to a systems' health through the control of invasive species, if said species occupy similar trophic and morphological categories as recorded native prey. Given the potential ecological benefits that otters could provide to our poor-quality freshwater systems, we strongly encourage more research into understanding the mechanisms behind otter feeding ecology and the potential cascading effects their diet may impart on a system.

We also propose a review of the methodologies used and presentation of data within this field of study. While we do not suggest that different methods are not useful to individual studies, nor that the methodologies presented here are necessarily the most accurate, the lack of standardisation and omittance of key points of data across multiple studies reviewed hinders the collaborative efforts of researchers. There is still an enormous amount of work to undertake before we can fully understand the intricacies and trophic effects of otter feeding ecology. By not working collaboratively we risk imposing limitations on the speed at which we advance our knowledge within this field.

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## Appendix 1

Table 5: Dietary list of all prey types identified within spraint samples collected on the Gower Peninsula, Wales, between 31/05/2021 - 14/01/2022. Results expressed as percentage frequency of occurrence (FO% = number of spraints in which prey type occurs / total number of spraints) and percentage frequency of occurrence (RFO% = number of occurrences of a prey type / total number of occurrences for all prey types). Values in bold are considered incorrect as individual occurrences could not readily be identified.

Species	FO%	RFO%
Cyprinidae (Unidentified)	20	2.96
<i>Gasterosteus aculeatus</i>	48.89	7.51
Percidae (Unidentified)	22.22	2.4
<i>Anguilla anguilla</i>	40	13.69
Cobitidae (Unidentified)	6.67	0.19
<i>Cottus gobio</i>	55.56	27.38
<i>Salmo trutta</i>	17.78	0.75
Gobiidae (Unidentified)	48.89	29.61
<i>Solea solea</i>	37.78	13.29
Scophthalmidae (Unidentified)	4.44	0.13
<i>Pleuronectes platessa</i>	11.11	0.65
Blenniidae (Unidentified)	2.22	0.02
<i>Esox lucius</i>	4.44	0.06
Labridae (Unidentified)	8.89	0.25
Crustacea (Unidentified)	62.22	<b>0.58</b>
Insecta (Unidentified)	13.33	<b>0.15</b>
Anura (Unidentified)	11.11	0.19
<i>Rattus rattus</i>	2.22	0.04
Mollusca (Unidentified)	15.56	0.17

## Appendix 2

Table 6: Collated UK and Ireland otter dietary lists selected for analysis. Study by Carrs *et al.* (1990) provided two dietary lists (Burn of Sheeoch and Canny Burn).

No.	Study	Author(s)	Collection Year	Sprints
1	Seasonal analysis of total Gower diet and niche breadth (Unpublished)	D. Forman	2005-2007	Not Reported
2	Importance of small fishes and invasive crayfish in otter <i>Lutra lutra</i> diet in an English chalk stream	J.R. Britton, M. Berry, S. Sewell, C. Lees & P. Reading	2014-2015	140
3	Dietary complexity and hidden costs of prey switching in a generalist top predator	R.J. Moorhouse-Gann, E.F. Kean, G. Parry, S. Valladares & E.A. Chadwick	1995-2010	610
4	Diet of coastal foraging Eurasian otters ( <i>Lutra lutra</i> L.) in Pembrokeshire south-west Wales	G.S. Parry, S. Burton, B. Cox & D.W. Forman	2007-2008	180
5	Do Eurasian otters <i>Lutra lutra</i> (L.) in the Somerset Levels prey preferentially on non-native fish species?	R. Miranda, G.H. Copp, J. Williams, K. Beyer & R.E. Gozlan	2004-2005	358
6	The diet of otters <i>Lutra lutra</i> (L.) in the Clare river system	S. Breeathnach & J.S. Fairly	1991-1992	1709
7	Distribution, density, diet, and habitat of the otter in relation to land use in the araglin valley, Southern Ireland	P. Ottino & P. Giller	1995-1996	287
8	Fish selection by riverine Eurasian otters in lowland England	K.R. Grant & L.A. Harrington	2003-2006	108
9	Status and diet of the otter <i>Lutra lutra</i> in Northern Ireland	S.J. Preston, A.A. Portig, W.I. Montgomery, R.A. McDonald & J.S. Fairley	2002	210
10	A study of the diet and distribution of the Eurasian otter ( <i>Lutra lutra</i> ) on the water of Leith, Edinburgh	B.A. MacFarlane	2019-2020	102
11	Predation on adult Atlantic Salmon, <i>Salmo salar</i> L., by otters, <i>Lutra lutra</i> L., within the River Dee system, Aberdeenshire, Scotland	D.N. Carss, H. Kruuk & J.W.H. Conroy	1989-1990, 1989-1991	220, 39

## Appendix 3

Table 7: Spraint samples collected on the Gower Peninsula used in supplementary Gower dietary list.

Sample No.	Site	Collection Date	Coordinates
1	Pwlldu Bay	31/05/2021	N 51° 33' 55", W 4° 3' 24"
2	Pwlldu Bay	31/05/2021	N 51° 33' 55", W 4° 3' 24"
3	Pwlldu Bay	31/05/2021	N 51° 33' 55", W 4° 3' 24"
4	Pwlldu Bay	31/05/2021	N 51° 33' 55", W 4° 3' 24"
5	Pwlldu Bay	31/05/2021	N 51° 33' 55", W 4° 3' 24"
6	Pwlldu Bay	31/05/2021	N 51° 33' 55", W 4° 3' 24"
7	Pwlldu Bay	31/05/2021	N 51° 34' 6", W 4° 3' 39"
8	Pwlldu Bay	11/06/2021	N 51° 33' 55", W 4° 3' 24"
9	Pwlldu Bay	11/06/2021	N 51° 33' 55", W 4° 3' 23"
10	Hillend	14/06/2021	N 50° 35' 50", W 4° 17' 41"
11	Hillend	14/06/2021	N 50° 35' 50", W 4° 17' 41"
12	Hillend	14/06/2021	N 50° 35' 50", W 4° 17' 41"
13	Hillend	14/06/2021	N 50° 35' 50", W 4° 17' 39"
14	Hillend	14/06/2021	N 50° 35' 50", W 4° 17' 39"
15	Clyne Valley	29/06/2021	N 51° 35' 56", W 3° 59' 58"
16	Three Cliffs	31/07/2021	N 51° 34' 57", W 4° 6' 9"
17	Three Cliffs	31/07/2021	N 51° 34' 57", W 4° 6' 9"
18	Three Cliffs	31/07/2021	N 51° 34' 56", W 4° 6' 6"
19	Three Cliffs	31/07/2021	N 51° 34' 56", W 4° 6' 6"
20	Three Cliffs	31/07/2021	N 51° 34' 56", W 4° 6' 6"
21	Three Cliffs	31/07/2021	N 51° 34' 56", W 4° 6' 6"
22	Three Cliffs	31/07/2021	N 51° 34' 56", W 4° 6' 6"
23	Three Cliffs	29/08/2021	N 51° 34' 57", W 4° 6' 9"
24	Three Cliffs	29/08/2021	N 51° 34' 56", W 4° 6' 6"
25	Three Cliffs	29/08/2021	N 51° 34' 56", W 4° 6' 6"
26	Three Cliffs	29/08/2021	N 51° 34' 56", W 4° 6' 6"
27	Three Cliffs	14/01/2022	N 51° 34' 56", W 4° 6' 6"
28	Three Cliffs	14/01/2022	N 51° 34' 47", W 4° 6' 13"
29	Three Cliffs	14/01/2022	N 51° 34' 47", W 4° 6' 13"
30	Three Cliffs	14/01/2022	N 51° 34' 47", W 4° 6' 13"
31	Three Cliffs	14/01/2022	N 51° 34' 47", W 4° 6' 13"
32	Three Cliffs	14/01/2022	N 51° 34' 47", W 4° 6' 13"
33	Three Cliffs	14/01/2022	N 51° 34' 47", W 4° 6' 13"
34	Three Cliffs	14/01/2022	N 51° 34' 47", W 4° 6' 13"
35	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
36	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"

<b>37</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
<b>38</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
<b>39</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
<b>40</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
<b>41</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
<b>42</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
<b>43</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"
<b>44</b>	Three Cliffs	14/01/2022	N 51° 34' 53", W 4° 6' 19"

## Appendix 4

Table 8: Mean RFO% and category classification for each freshwater fish prey type identified in collected data and collated UK and Ireland dietary studies.

Species	Mean RFO%	TL	Body Form	Mean Adult Length (cm)	Resilience	Aquatic Zone
<i>Rutilus rutilus</i>	5.218	3	Fusiform	25	Medium	Benthopelagic
<i>Phoxinus phoxinus</i>	2.917	3.2	Fusiform	7	Medium	Demersal
<i>Leuciscus leuciscus</i>	2.14	2	Fusiform	15	Medium	Benthopelagic
<i>Squalius cephalus</i>	0.693	2.7	Fusiform	30	Medium	Benthopelagic
<i>Barbus barbus</i>	0.38	3.1	Fusiform	30	Low	Benthopelagic
<i>Abramis brama</i>	0.38	3.1	Fusiform	25	Low	Benthopelagic
<i>Cyprinus carpio</i>	0.547	3.1	Fusiform	31	Medium	Benthopelagic
<i>Gobio gobio</i>	2.545	3.1	Fusiform	12	Medium	Benthopelagic
<i>Alburnus alburnus</i>	0.76	2.7	Fusiform	15	Medium	Benthopelagic
<i>Leucaspius delineatus</i>	2.7	3.2	Fusiform	6	Medium	Benthopelagic
<i>Scardinius erythrophthalmus</i>	0.255	2.9	Fusiform	20	Low	Benthopelagic
Unidentified Cyprinidae	10.068	3	Fusiform	20.82	Uncategorised	Uncategorised
<i>Salmo trutta</i>	3.375	3.4	Fusiform	72	Medium	Pelagic-Neritic
Unidentified Salmonidae	27.215	3.6	Fusiform	40.4	Uncategorised	Uncategorised
<i>Anguilla anguilla</i>	11.191	3.6	Eel-like	42.5	Low	Demersal
<i>Cottus gobio</i>	23.868	3.2	Fusiform	10	Medium	Demersal
Unidentified Cottidae	2.8	3.2	Fusiform	10	Uncategorised	Uncategorised
<i>Gasterosteus aculeatus</i>	8.275	3.3	Fusiform	5.1	High	Benthopelagic
Unidentified Gasterosteidae	10.325	3.3	Fusiform	5.8	Uncategorised	Benthopelagic
<i>Platichthys flesus</i>	0.945	3.3	Short and/or Deep	50	Medium	Demersal
Unidentified flatfish	4.27	3.3	Short and/or Deep	50	Uncategorised	Demersal
<i>Lota lota</i>	0.9	3.8	Elongated	40	Low	Demersal
Unidentified Gobiidae	16.783	3.3	Elongated	6	Medium	Demersal
<i>Barbatula barbatula</i>	4.858	3.3	Fusiform	12	Medium	Demersal
<i>Perca fluviatilis</i>	7.58	4.4	Fusiform	25	Low	Demersal
Unidentified Percidae	1.35	3.9	Fusiform	29	Uncategorised	Uncategorised
<i>Esox lucius</i>	3.616	4.4	Elongated	40	Low	Pelagic