The functionality of Eurasian otters (*Lutra lutra*) as top-down predators in marine ecosystems

Jasmine Knight, Marine Biology BSc

Submitted to Swansea University in fulfilment of the requirements for the Degree of MRes Biosciences.

Swansea University

October 2022

Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed..[redacted]..

Date.......31.10.22..

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed...[redacted]..

Date.......31.10.22..

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed...[redacted]..

Date.......31.10.22..

The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

Signed...[redacted]..

Date.......31.10.22..

STATEMENT OF EXPENDITURE

No costs were incurred during the production of this work.

STATEMENT OF CONTRIBUTION

Dr D. W. Forman – dissertation supervisor, conceived and developed idea

Data extracted from the following studies fully cited in references (section 12):

- Parry *et al*., 2011
- Watt, 1991
- Kingston, O'Connell and Fairley, 1999
- Murphy and Fairley, 1985
- Clavero, Prenda and Delibes, 2004
- Harris, 2005 and Maddocks, 2013
- Forman, Gallardo and Knight, 2022

J. D. Gallardo and J.A. Knight collected and processed.

J.A. Knight analysed data and assembled and wrote manuscript.

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J. D. Gallardo my research partner in data collection and processing and my sounding board for all ideas and concepts no matter the time of day.

Dr D.W. Forman my thesis supervisor and font of all *Lutra lutra* based knowledge.

A. Chand for all the help with surveying as well as emotional support during the deadline stress, both times.

W. James, A. Hollamby and E. Wade for all their statistical assistance and reassurance throughout the process.

ETHICS APPROVAL

[redacted]

RISK ASSESSMENT

Field Risk Assessment			
*Grey boxes must be completed by field leader			
College/ PSU	Science	Assessment date	February 2021
Location	The Gower- all field sites	Assessor	J.A. Knight
Activity	Otter signs surveys- spraint collection	Approved by	Dr. D.W. Forman
		Review date (if applicable)	
Associated documents	• E.g. HS plan, participants list, COSHH form		

Part One: Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	Do you need to do anything else to manage this risk?
Uneven/ unstable surfaces and sheer drops	Student/ Supervisor	Slips, trips and falls, injury, drowning	• Wear appropriate footwear • Watch footing • Stay away from cliff/rock edges where possible • Avoid unstable river banks	• First aid kit on hand along with first aid trained/competent individual (either student or supervisor) • Mobile phone on hand for emergencies
Incoming tide	Student/	Stranding,	• Check tide times and survey accordingly	• Mobile phone on hand for

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	Do you need to do anything else to manage this risk?
	Supervisor	drowning, slips, trips and falls	• Keep surveys to safe height/distance from water level • Wear appropriate footwear for substrate type	emergencies • Take extra care when surveying rocks close to the waters edge on the beach
Sunstroke	Student/ Supervisor	Sunstroke/ Sunburn	• Wear sunscreen • Wear protective clothing e.g. hat • Drink plenty of water whilst out in the field	• Bring additional sunscreen for top up's throughout the course of the survey • Prior to the survey ensure each individual has their own water and enough of it for the duration of the survey
Disease Transmission	Student/ Supervisor	Transmission of disease through faecal sample handling	• Wear gloves when collecting samples • Store in appropriate containers (e.g. Ziplock bags or screw top bottles) • Label accordingly • Hand washing/sanitizing when possible after handling samples and containers	• Sanitise hands after glove removal, clean pair of gloves after each change • Santise hands before eating/drinking in the field • Wash hands thoroughly with warm water and antibacterial soap after surveys prior to eating
Drowning	Student/ Supervisor	Hypothermia, illness from waterbourne pathogens, death	• watch footing • don't enter water deeper than calf depth • use of stick/staff for water depth measurement • be aware of weeds, rocks and fast flowing water	• Take extra care when entering and exiting water systems (e.g, streams/rivers) • Take extra care when surveying rocks close to the waters edge on the beach • Mobile phone on hand for

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	Do you need to do anything else to manage this risk?
				emergencies

Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
Ensure all above actions and procedures are followed			YES
Mobile Phone is carried by at least one member of survey team			YES
First aid kit carried and at least one of the team is competent in first aid			YES
Sunscreen and hand sanitiser are on hand, enough for each member of the survey team for the duration of the survey			YES

Desk based work Risk Assessment			
College/ PSU	College of Science	Assessment Date	June 2021
Location	Working from Home	Assessor	J.A. Knight
Activity	Desk based tasks	Review Date (if applicable)	
Associated documents	•	•	

Part 1: Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Repetitive strain	Student	Repeated typing for prolonged periods of time	• Taking regular breaks	4	1	4	NA				
Eye strain	Student	Staring for prolonged periods of time at computer screens	• Taking regular breaks • Wearing glasses • Working in a well lit room	4	1	4	NA				

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Postural issues	Student	Back/neck problems from sitting for prolonged periods of time	• Taking regular breaks • Suitable back support from chair • Ensure computer screen is at a comfortable height	4	1	4	NA				

Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
NA	NA	NA	NA

Risk Assessment for Teaching, Administration and Research Activities

Swansea University; College of Science

[redacted].. **date:** 01/07/21....

Supervisor*: Dr Daniel Forman ....**Signature:** .... **date:** ....

Activity title: Otter Spraint Analysis..**Base location (room no.):** 038..

(* the supervisor for all HEFCW funded academic and non-academic staff is the HOC)

University Activity Serial # (enter Employee No. or STUREC No. ....
Start date of activity (cannot predate signature dates) ....
End date of activity (or 'on going') ....

Level of worker (delete as applicable) ....

PG

Approval obtained for Gene Manipulation Safety Assessment by SU ? not applicable
Licence(s) obtained under "Animals (Scientific Procedures) Act (1986)" ? not applicable
Approval obtained for use of radioisotopes by COS ? not applicable

Record of specialist training undertaken

Course	date
Spraint preparation	01 July 2021

Summary of protocols used; protocol sheets to be appended plus COSHH details for chemicals of category A or B with high or medium exposure

Protocol Details						Protocol Details					
#	Assessment					#	Assessment				
	1st date	Frequency of re-assessment	Hazard category	Secondary containment level	Exposure potential		1st date	Frequency of re- assessment	Hazard category	Secondary containment level	Exposure potential
1						11					
2						12					
3						13					
4						14					
5						15					
6						16					
7						17					
8						18					
9						19					
10						20					

See notes in handbook for help in filling in form **(Continue on another sheet if necessary)**

Bioscience and Geography Protocol Risk Assessment Form

(Expand or contract fields, or append additional sheets as required; insert NA if not applicable)

Protocol #	**Title:** Spraint preparation
Associated Protocols **#..........................**	**Description:** Cleaning of hard prey remains from Eurasion otter (*Lutra lutra*) spraint for identification

Location:

circle which Bioscience and Geography Local Rules apply –

Boat Field Genetic-Manipulation **Laboratory** Office/Facility Radioisotope

Identify here risks and control measures for work in this environment, additional to Local Rules

Chemicals	Quantity	Hazards	Category (A,B,C,D)*	Exp Scor
Biological washing detergent	500 ml	Mild irritation for and skin and eyes	D	LOV

Hazard Category (known or potential)

A (e.g. carcinogen/teratogen/mutagen)

B (e.g. v.toxic/toxic/explosive/pyrophoric)

C (e.g. harmful/irritant/corrosive/high flammable/oxidising)

D (e.g. non classified)

Exposure Potential Circle the **highest Exposure Score** above. Use this to calculate the exposure potential for the entire protocol (see handbook). Indicate this value below.

Low Medium High

Primary containment (of product) sealed flask/bottle/glass/plastic/other (state) :- Plastic bottle

Storage conditions and maximum duration :- 1 year, lab room 038

Secondary containment (of protocol) open bench/fume hood/special (state) :-NA

Disposal e.g. autoclaving of biohazard, SU chemical disposal:- Commercial refuse, recycling

Identify other control measures (circle or delete) - latex/nitrile/heavy gloves; screens; full face mask; dust mask; protective shoes; spillage tray; ear-defenders; other (state):- NA

Justification and controls for any work outside normal hours:- NA

Emergency procedures (e.g. spillage clearance; communication methods):- NA

Supervision/training for worker (circle)

None required **Already trained** Training required Supervised always

Declaration I declare that I have assessed the hazards and risks associated with my work and will take appropriate measures to decrease these risks, as far as possible eliminating them, and will monitor the effectiveness of these risk control measures.

[redacted]..

Name & counter-signature of supervisor.. *Date*........................

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3 DEFINITIONS OF ABBREVIATIONS

B.F.	Body form
E.T.	Ecosystem type
F.O	Frequency of Occurrence
H.C.	Habitat classification
Study 1-7	Study code (1-7)
M	Metres
P.T.	Prey type
R.F.O	Relative Frequency of Occurrence

4 ABSTRACT

Ecological niche (Elton, 1927) has been adapted over the years to fit the various definitions within the broad spectrum of an ecological niche. The term 'trophic niche' is referred to most commonly now and can be measured by width/ breadth using various diversity indices to determine whether a species is a generalist or a specialist (Hutchinson, 1957). This study explores the methodology utilised by existing literature for *Lutra lutra* spraint analysis and subsequent dietary studies. The data from seven studies in the UK and Europe in the last 40 years has been extracted and processed to create a meta-dataset of the relative frequency of occurrence (R.F.O %) of prey within spraints, and four selected prey characteristics or traits; body form, ecosystem type, habitat classification and prey type. Trophic niche analysis using Shannon- Weiner diversity index and Levins measure of niche breadth index indicates the hypothesis that the diet of *Lutra lutra* is more likely to be generalist than specialist is correct (Mean *J'* = 0.75 (± 0.08), mean Levins = 0.35 (± 0.05)). Prey trait analysis demonstrates that the most prevalent body form is fusiform (39.6%), ecosystem type with prey presence at two interfaces was most frequent, (36.4%) demersal is the most common habitat classification (48.7%) and type of food (prey) consumed by the prey species/group is small invertebrates, small crustaceans, fish fry (type 3, 43.5%). Furthermore, Welch's two sample t-test indicates that there is no significant difference between the mean R.F.O (%) of marine prey and non-marine prey at family level (t= 1.97, p= 0.06). The clear need for the standardisation of current approaches towards spraint analysis to improve our understanding of *Lutra lutra's* diet and by extension ecological niche, to ultimately protect this semi-aquatic mammal from potential threats in rapidly changing dynamic coastal and marine environments (Gutiérrez, *et al*., 2019).

5 LAY SUMMARY

The term 'trophic niche' is essentially the diversity of the diet of an individual in relation to its environment, it is used to determine if a species can be considered a generalist (high diversity of prey in diet) or a specialist (more specific prey). This can be measured using various diversity indices to determine whether a species is a generalist or a specialist (Hutchinson, 1957). This study explores the methodology utilised in existing literature for the Eurasion otter (*Lutra lutra*) in spraint analysis and subsequent dietary studies. A spraint is a faecal deposit left by an otter generally as a positional marker for themselves and other otters, they are primarily composed of undigested prey such as fish bones and other hard prey remains (Carss, 1995). These are collected and processed to enable the vertebrae and other hard parts to be identified according to what prey species they have come from. The data from seven coastal otter dietary studies in the UK and Europe in the last 40 years have been extracted and processed to create a meta-dataset of the relative frequency of occurrence (R.F.O %) of prey in spraints as well as four selected prey characteristics or traits of interest; body form, ecosystem type, habitat classification and prey type. Trophic niche analysis using Shannon- Weiner diversity index and Levins measure of niche breadth index indicates the hypothesis that the diet of *Lutra lutra* is more likely to be generalist than specialist is correct (Mean J' = 0.75 (± 0.08), mean Levins = 0.35 (± 0.05). Prey trait analysis demonstrates that the most prevalent body form is fusiform (39.6%), ecosystem type with prey presence at two interfaces was most frequent, (36.4%) demersal is the most common habitat classification (48.7%) and type of food (prey) consumed by the prey species/group is small invertebrates, small crustaceans, fish fry (type 3, 43.5%). Furthermore, Welch's two sample t-test indicates that there is no significant difference between the mean R.F.O (%) of marine prey and non-marine prey at family level ($t = 1.97$, $p = 0.06$). The clear need for the standardisation of current approaches towards spraint analysis to improve our understanding of *Lutra lutra's* diet and by extension ecological niche, to ultimately protect this semi-aquatic mammal from potential threats in rapidly changing dynamic coastal and marine environments (Gutiérrez, *et al*., 2019).

Figure 1. Image from USB microscope of European eel *(Anguilla anguilla*) vertebrae from a sample analysed in study 7 (Gower, Wales, UK)

6 INTRODUCTION

6.1 Ecological trends

The term ‘ecological niche’ was developed by Charles Elton (1927) as “the status of an animal in its community” and states that each species has a unique niche encompassing both its habitat and use of resources (Slagsvold and Wiebe, 2007). It is an ecological concept has been summarised and interpreted by many to fit their own ideals of a niche (Pocheville, 2015). This concept has since been renamed as ‘trophic niche’ to avoid confusion with other interpretations of ecological niche (Whittaker *et al*., 1973), the trophic niche concept encapsulates how an organism utilises resources and increases with environment and community (Parry, 2010). All organisms function within a niche which lies along a continuum of variation between specialists and generalists (Hutchinson, 1957; Ferreras *et al*., 2011).

Due to their ability to change food sources when their preferred food sources are unavailable (Moorhouse- Gann *et al*., 2020), ecological generalists are often found in heterogeneous environments (Kassen, 2002) and tend to stabilise populations (Lambin, Petty and Mackinnon, 2000; Krebs *et al*., 2001). Whereas ecological specialists, having a narrower niche breadth than generalists (Bidart-Bouzat and Kliebenstein, 2011), commonly benefit from homogenous environments and are at greater risk from environmental degradation than ecological generalists according to niche evolution theory (Devictor, Julliard and Jiguet, 2008).

Intraspecific and interspecific competition can also impact trophic niche as multiple species competing for the same resource will result in issues such as a decline in the availability of that resource over time, similarly, overcrowding of a population or even multiple populations of the same species in too small an area, or when a resource is limited can reduce biodiversity both pressures can cause a shift in trophic niche. Competitive interactions both between and within species are important contributors to ecological communities within ecosystems and biomes (Prati *et al*., 2021).

Factors affecting trophic niche can be both intrinsic and extrinsic, intrinsic influences such as morphological variations among populations (Evangelista, Boiche, Lecerf, and Cucherousset, 2014), how this may be specifically affecting otters is discussed in section 9.3. Extrinsic factors such as, environmental variability, for example polar bears (Ursus maritimus) actively seeking human settlements in search of food due to the drastic changes within their normal territories with ice caps melting at an alarming rate and water temperatures and levels rising affecting both the polar bears ability to hunt their prey, the prey itself and their prey too (Stirling and Parkinson, 2006).

6.2 Carnivore ecology

Carnivores are predators, with small populations as well as low density and reproduction rate (Gittleman *et al*., 2001; Ruiz-Olmo and Jimenez, 2009). Predators, especially keystone predators promote diversity within communities (Leibold, 1996), maintaining the fitness of prey species (Kruuk and Turner, 1967; Brodie and Brodie, 1999). There has traditionally been considerable persecution of top predators by humans through, for example, conflict over livestock (Wolf and Ripple, 2016). There is also the constant threat of habitat loss due to human development expansion across ecosystems causing biodiversity loss on a global scale (Hong and Joo, 2021). The study of carnivore diet advances our understanding of ecological theories such as community regulation through top- down ecology (del Rio *et al*., 2001) and predator prey interactions (Wegge *et al*., 2009). Carnivore diet can also reflect variation, both temporal and spatial, in prey availability (Moorhouse-Gann *et al*., 2020).

6.3 Existing research and wider implications

Many of the studies exploring species richness and distribution patterns consider the relative influence of anthropogenic factors such as disturbance (Barbosa *et al*., 2001). Where it has the effect of human disturbance has been limited to single species or local species largely neglecting trophic niche dynamics across communities (Manlick and Pauli, 2020). There are also fewer studies on marine and coastal otters, with the majority focusing on freshwater habitats (Murphy and Fairley, 1985; Kingston, O'Connell and Fairley, 1999; Martinez-Abrain *et* al., 2020; Otto, 2020).

Improving our understanding of carnivore diet composition is one of the first steps towards developing effective conservation strategies for that species (Otto, 2020). For example, niche overlap can cause interspecific competition between carnivores, especially when human-carnivore conflict is factored in (Manlick and Pauli, 2020). Some of the behavioural mechanisms employed by carnivores to achieve coexistence with humans include avoidance both spatial and temporal as well as high reproduction rate, and if all else fails migration (Lamb *et al*., 2020). Long term conservation of keystone species including carnivorous predators, can lead to umbrella-like protection for other species within the ecosystem (Sergio *et al*., 2008; Wegge *et al*., 2009). Similarly, restoration of trophic complexity involves the restoration of carnivores to modified landscapes is advocated to ensure top-down control is in place for ecosystem functionality (Manlick and Pauli, 2020). Better understanding of the ecological determinants of land use change is imperative for sustainable conservation objectives and long-term research can aid biodiversity restoration, as well as guiding conservation efforts (Hong and Joo, 2021).

6.4 Eurasian otter ecology

Eurasion otters (*Lutra lutra*) operate within a wide variety of habitats, ranging across terrestrial, freshwater, and marine ecosystems (Carss, 1995; Calvero, Prenda and Delibes, 2004; Otto, 2020). Many studies focusing on the Eurasion otter's foraging and dietary ecology consider the otter to be generalists with opportunistic tendencies (Blanco-Garrido, Prenda and Narvaez, 2008; Martinez-Abrain *et* al., 2020). There is debate as to what extent Eurasian otters are generalists as most studies report a preference towards fish, such as salmonid species and European eels (*Anguilla anguilla*), as the primary component of their diet (Almeida *et al*., 2012).

However, it is uncertain as to whether they have a preferred foraging habitat as this inclination towards fish is represented across freshwater, brackish, and marine ecosystems (Clavero, Prenda and Delibes, 2004; Martinez-Abrain *et* al., 2020). Seasonality within different ecosystems is considered a main driver behind this generalist feeding behaviour (Calvero, Prenda and Delibes, 2006) as the availability of prey, the abundance in the environment and ease of capture can vary with the time of year as well as between species (Moorhouse-Gann *et al*., 2020). In the case of the Eurasion otter, the question of whether there is a preference towards available marine prey and if that differs when freshwater and brackish prey are also available (Beja, 1991) remains uncertain.

The semi-aquatic predator is categorised as a top predator (Almeida *et* al., 2013; Ruiz-Olmo and Jimenez, 2009), however there are costs when it comes to feeding in both freshwater and marine environments due to the high energy demands of swimming, as well as the thermoconductivity of the water (Kruuk and Carss, 1996). Furthermore, semi-aquatic Mustelids have higher metabolic basal rates and higher heat loss rates than expected for terrestrial carnivores (Ruiz-Olmo and Jimenez, 2009).

6.5 Threats and conflicts

The Eurasian otter is currently classified as 'Near Threatened' on the IUCN Red List (Roos *et al*., 2015) due to a combination of human and environmental events leading to population declines in the 20th century (Otto, 2020). This is largely due to water pollution across Europe (Martinez-Abrain *et al*., 2020), especially from organochlorine pesticides (Mason, and Macdonald, 1994) and general degradation of habitats frequented by otters (Miranda *et al*., 2008) as well as rising conflicts between otters and anglers and fish farmers who all benefit from fish such as carp (*Cyprinus carpio*) which has become more popular in recent years (Almeida *et al*., 2012). Conflicts between otters and anglers have been well documented all over the world (Goedeke, 2005; Rauschmayer, Wittmer, and Berghöfer, 2008), however in recent years they have become more pronounced, especially across Europe and Asia and particularly between recreational anglers, commercial fishermen and environmentalists advocating for the Eurasian otter (Václavíková, Václavík, and Kostkan, 2011).

Therefore, it is crucial that we understand the composition of their diet and the reasons for it to ensure bespoke conservation initiatives can be established and instigated where required. To reduce these conflicts, more information about the diet and behaviour of otters needs to be made more readily available not just within the scientific and conservation community, but more widespread to ensure that it is reaching the other water users who have been led to believe that the presence of otters is a direct threat to them and are a leading cause of depletion in both farmed and stocked fish (Lyach, and Čech, 2017). Furthermore, depending on which side of the argument is focused on otters are both generalists and specialists, through understanding the trophic niche of otters will allow conservationists to present as evidence to anglers and fishermen that otters are not the enemy they are often perceived to be (Almeida *et al*., 2013) and are in fact a valuable 'signal species' of biodiversity within aquatic ecosystems (Miranda *et al*., 2008).

However, there may be variation between populations throughout the vast area that Eurasian otters inhabit across Europe and Asia, and seasonality (Britton *et al*., 2017) can play a significant part in prey selection largely because of availability of fish, especially within freshwater ecosystems. This research aims to demonstrate that not only are Eurasian otters feeding across a combination of different environments and ecosystems, but also that the prey that they are foraging for is not necessarily the species that is causing anglers and fishermen to both fear and hate otters. If it can be made clear to anglers, fishermen and other water users that the otters are not directly or even indirectly targeting commercially 'valuable' species such as carp and salmonids.

6.6 Aims and objectives

In this study I aim to determine the significance of marine species within the diet of the Eurasian otter, demonstrate the impact of the otter's presence on coastal and marine ecosystems, review the current approaches undertaken in existing research within this area and evaluate a standardised approach to enable comparable and efficient methods for future research.

7 MATERIALS AND METHODS

7.1 Study area

More than 70% of the coastline in Wales is protected to some legislative degree (Phillips *et al*., 2011), including the Gower Peninsular. Situated in south Wales, it was one of the UK's first designated Areas of Outstanding Natural Beauty (AONB) (Bridges, 1997), boasting three National Nature Reserves (NNR's), as well as 25 Sites of Special Scientific Interest (SSSI's). It is also declared as an internationally important RAMSAR site (Phillips *et al*., 2007). The Eurasian otter is considered a top predator of freshwater ecosystems (Taylor *et al*., 2010), and there are many rivers and streams running throughout the Gower Peninsula, many of which are popular among the local Eurasian otter population (Parry *et al*., 2013). The sites we chose to survey vary in habitat type, but all include freshwater and marine interfaces. Survey sites included in this study were chosen based on Dr Forman's personal knowledge and experience, as well as information from Gower, New Naturalist series (Mullard, 2006).

The first survey site as seen in Figure 2, Llangennith, is known as a locally important habitat with rich flora, including rare species such as lesser pondweed (*Potamogeton pusillus*), Himalayan balsam (*Impatiens glandulifera*), and *Odonata spp*. The water filled ditches along the moors act as field boundaries, with the water draining out at Diles Lake on Rhossili beach. Similarly, the combination of open water, reed-swamp, floating fen, damp woodland at Oxwich bay, as well as the adjacent dunes and salt marshes, provides an incredibly biodiverse environment. As a result, the flora and fauna (NNR) including eel (*Anguilla anguilla*), rudd (*Scardinius erythrophthalmus*), roach, brown trout, amphibians, birds, and mammals reflect the variation in habitats. Oxwich bay is also a recognised otter breeding site (national survey monitoring site).

The stream at Penard pill runs underground at Barlands quarry through caves reappearing in lower Bishopston valley where it drains out at Pwll du bay. Species found here include stickleback (*Gasterosteidae*) both three and fifteen-spined, roach (*Rutilus rutilus)*, perch (*Percidae*), brown trout (*Salmo trutta*), thick lipped grey mullet (*Chelon labrusus*), flounder (*Paralichthys dentatus*) and common goby (*Pomatoschistus microps*) (Mullard, 2006). The final survey site included in this study is Clyne valley country park, containing the river Clyne and the remains of copper and arsenic works, which ceased in 1860. The site remains highly contaminated and frequently floods in lower reaches throughout the winter. Species such as brown trout, bullhead (*Cottus gobio*) and stickleback, amongst others, occupy the river. Otter spraints and sightings are frequently recorded by pedestrians and cyclists in this area despite the popularity of the site and proximity to residential areas, cycle paths and busy roads.

Figure 2. Map of survey sites in the Gower peninsula (from left to right) Llangennith, Oxwich bay, Pennard pill and Three cliffs bay, Pwll du bay, Clyne Valley (my maps, Google, 2023).

7.2 Spraint collection and preparation

Initially the plan was to have survey teams of at least three people surveying sites at two-week intervals, to reduce impact of spraint removal on ecosystems. However, due to local lockdowns and covid restrictions the survey team was primarily composed of myself, J. D. Gallardo, and Dr D. W. Forman and/or accompanied by A. Chand on occasion. The surveys were conducted at least two weeks apart when returning to the same survey sites, however most sites were only surveyed once throughout this period, data collection was conducted from March 2021 to January 2022.

The method for collecting spraints from marine ecosystems is generally the same as in most dietary studies involving otter spraint analysis. An area with a length of 100 m was surveyed, upriver from the point of discharge. Each member of the survey team walked along the section, on each side of the river/stream, looking for signs of otter presence, such as otter tracks and flattened vegetation and trampled sections were checked as points of entry. Some were ruled out as many of these sites are popular with dog walkers and could have been created by small dogs entering the water and leaving prints in the soft sediment along the water course and in the riparian strip, the survey team discerned genuine otter prints from dogs where possible and recorded if present. Spraints were most found on small clumps of grass, elevated sections of rock and small ‘walk-ways’ running parallel to the water.

Once located, photos of the spraints as they were found were taken with the GPS function enabled on the Olympus TG4, which gave the eight figure grid reference coordinates of each of the spraint’s locations. Wearing gloves, each individual spraint was carefully collected and stored in an airtight container or Ziplock bag and labelled with the sample number, coordinates, and date. Samples were then stored in a freezer at minus 18° C until further analysis could be performed to prevent further degradation. All spraints were kept separate in individual 300 ml beakers and cleaned by soaking in a solution of 100 ml of warm tap water with 5 ml of a mild biological detergent for 24 hours at room temperature, a glass rod was used to stir the contents and rinsed in between. The samples were then gently rinsed with a slow flow of tap water through a 1 mm sieve over the sink- to remove any remaining "soft" matter and binding agents, leaving the hard prey remains to be air dried and then stored for identification later.

7.3 Identification of prey remains

Identification of hard prey remains consisted primarily of identifying fish vertebrae using a USB microscope attached to a laptop for closer observation of prey remains to improved accuracy of identification. Keys and guides such as 'A guide to the identification of prey remains in Otter spraints' (Webb, Watt and Conroy, 1993) and the 'Archaeological Fish Resource' (Nottingham University, 2021) were also used for identification. Separation of identified vertebrae/other remains was to retain the identified samples for use in future studies and as references throughout the process.

7.4 Meta data collection and processing

For the analysis of data from existing studies, papers were selected based on fitting the criteria necessary for this study i.e., that spraints were from marine ecosystems surveyed in UK and Europe, no earlier than 1980 and the prey list identified to family or species level, with abundance data reported as either total count, frequency of occurrence (F.O %) or relative frequency of occurrence (R.F.O %). Furthermore, the studies needed to include additional information regarding the habitats of the areas surveyed as well as the duration of sample collection and number of samples analysed as well as including a list of prey with corresponding counts or F.O (%) and/or R.F.O (%) as well as totals in order to calculate missing data (F.O % and/or R.F.O %). Additionally, the sampling methodology needed to be relatively standardised and like the methodology used for study 7 (see section 7.2), this was also more difficult than anticipated as many studies used a combination of techniques alongside standard spraint survey and identification, which is very informative however when this data wasn't clearly separated was confusing. As a result, this process was time consuming and made difficult by the inconsistencies in data collection, analysis, and presentation of data within research. While the total number of studies started considerably higher than the final six that were selected and the data from those was collated. This data collected and collated from studies 1-6 was considered compatible and therefore analysed as one dataset alongside the primary data collected at the start of this study.

A summary of the relevant information extracted from these studies (thereafter referred to as studies 1-6 as well as by location) includes authors names, date of publication, and number of spraints analysed can be seen in Table 1. The full version is too large be included, so a brief version has been included in the study matrix found in Appendix A.

Table 1. Summary of key information extracted from studies used in collated analysis in this study including author, year, location, duration, and sample size.

Study code	**Author**	**Year**	**Location**	**Duration (months)**	**Sample size**
1	Parry *et al*	2011	Pembrokeshire, Wales, UK	12	180
2	Watt., J	1991	Isle of Mull, Scotland, UK	24	958
3	Kingston *et al*	1999	Arran islands, Ireland	11	1510
4	Murphy. K. P. and Fairley. J.S.	1985	Galway, Ireland	13	1026
5	Clavero *et al*	2004	Tarifa, Spain	36	1882
6	Harris. E. and Maddocks. K	2005/2013	Newport Gwent Levels, Wales, UK	2002-2010	168
7	Forman. D.W, Gallardo. J.D and Knight. J. A	2022	Gower peninsula, Wales, UK	11	44

Figure 3. This map shows the different locations that data was collected for all seven studies analysed, the majority of which were collected in the United Kingdom the studies in Pembrokeshire, Newport Gwent Levels, Gower all being in South and West Wales and the Isle of Mull in Scotland) except for The Arran Islands and Galway, Ireland and Tarifa, Spain. Many of the other European location-based studies were excluded from this study due to inconsistencies in data collection, analysis, and presentation. (my maps, Google, 2023).

This data was then standardised so for each prey entry an R.F.O (%) value was associated and tabulated into the study- prey matrix (Appendix II) the spraint sample numbers for each study and the total number of spraints analysed are recorded in Table 2. The study-prey matrix describes the complete prey list of all seven studies, with the mean R.F.O (%) and prey traits relating to each species' life history were allocated into the four categories of interest: body form, ecosystem type, habitat classification and prey type. This categorical data was collated from online databases such as Fishbase (Froese and Pauly, 2000) and data provided by the MarLIN programme (Marine Biological Association, 2020) for prey that were fish, for the non-fish prey (such as amphibians, crustaceans, insects etc) either phylum or class taxonomic terminology was used.

Frequency of occurrence: F.O. (%) = (number of spraints containing prey type/ total number of spraints) x 100

Relative frequency of occurrence: R.F.O (%) = (number of occurrences by prey type/ sum of all occurrences of all prey types) x 100

Table 2. The number of spraints analysed in each study. This number varies significantly between each study; it is generally considered that the larger the sample size the more representative results. These differences in sample size between studies is just one of the potential issues and complications that arise with collating and comparing data regarding Eurasian otter diet.

Study	Number of spraints (analysed)
1	232
2	958
3	1510
4	1026
5	1882
6	168
7	44
TOTAL	**5820**

The prey matrix (Appendix IV) shows the complete prey list with the mean R.F.O (%) for each prey, as well as body form, ecosystem type, habitat classification and prey type for each species. To create the figures in section 8.4 each prey trait required a numerical value for each subcategory ready for analysis in Microsoft Excel (Version 2203). Tables 3, 4 and 5 are the corresponding classification keys for body form, habitat classification and prey type. The values for ecosystem type were created by counting the number of interfaces the prey is found in (1-4).

Table 3. Body form classification key, this was used to quantify these categories for analysis and to produce figures (see section 8.4).

Classification	Body form
1	Anguilliform
2	Elongated
3	Fusiform
4	Short and/or deep
5	Amphibian
6	Crustacean
7	Insect
8	Mammal
9	Mollusc
10	Reptile
11	Avian

Table 4. Habitat classification key

Classification	Habitat Classification
1	Benthic
2	Benthopelagic
3	Demersal
4	Reef associated
5	Pelagic
6	Pelagic- neritic
7	Other

Table 5. Prey type classification key

Classification	Prey type
1	Herbivourous only
2	Detritis only
3	Small invertebrates, small crustaceans, fish fry
4	Small fish and as well as invertebrates and crustaceans
5	Majority of diet is fish and/or cephalopods
6	Other

These classification keys were used to create the second study prey matrix with numerical values rather than categorical labels (Appendix C). The prey matrix was further separated into two tables with one dedicated to named species e.g., *Anguilla anguilla, Spinnachia spinnachia* etc. (Table 9), and one with all prey categorised to family taxonomic level (Table 10). This was necessary to analyse the significance of marine species in the diet across all the studies as not all the studies identified prey to species level.

7.5 Analysis

For each study Shannon- Weiner diversity Index and Levins standardised Indices were performed, the *H'* and *J'* values for diversity and evenness are reported alongside the Levins value for niche breadth in Table 8 (Bibi and Ali, 2013). While Levins indicates how species utilise habitats in accordance with the availability of resources (Feinsinger, Spears and Poole, 1981) whereas the Shannon- Weiner diversity index is measuring both the richness of a population as well as the evenness of the selection, in this study prey richness and evenness.

Shannon- Weiner Diversity Index formula: $H' = -\sum Pi \ln Pi$, $J' = H'/\text{Log}N$

Where H' is the Shannon-Weiner measure of diversity (niche breadth), Pi is the proportion of species in the sample, and lnPi is the natural logarithm of Pi, and where J' is the evenness measure of Shannon-Weiner function and N is the total number of possible resource states.

Levins niche breadth index formula: $B' = Y^2/\sum Nj^2$

Where, B' is Levins measure of niche breadth, Nj is the number of individuals found in or using the resource and Y is the total number of individuals sampled (Krebs, 1998).

The proportion of categorical variables (prey traits) in relation to R.F.O (%) to describe the potential relationship between each prey trait and R.F.O (%) overall is explored in section 8.4. In terms of inferential statistics, non-parametric testing e.g., chi squared test for analysis of statistical significance between observed and expected values, have been used by other otter dietary studies such as Murphy and Fairley, (1985) and Lanszki and Lanszkiné Széles (2006). However, these tests are not applicable in this study due to sample size limitations and the exploratory nature of the study calling for predominantly descriptive analysis rather than inferential statistics. Welch's two sample t-test assuming unequal variance can be used for two samples of differing length and variance, which is why it was used to compare the statistical significance of marine and non-marine prey (section 8.5).

8 RESULTS

8.1 Prey list

The final prey list seen in Table 5 is presented with the total number of studies (one to seven) each prey species/group is recorded as being present in, they are ordered from highest to lowest.

Table 6. Comprehensive prey list with total number of studies they are listed in (*Bufo bufo* included in species list of one study as an example of anuran, but not directly recorded in any study, included for posterity)

Prey list	**Total number of studies (1-7) prey recorded**
Anguilla anguilla (European eel)	7
Unidentified *Labridae* (wrasse)	6
Unidentified *Gobiidae* (gobies)	6
Gasterosteus aculeatus (three-spined stickleback)	5
Unidentified C*rustacea* (crustacean)	5
Unidentified *Blenniidae* (blennies)	5
Unidentified *Pleuronectidae* (flatfish)	5
Salmo trutta (sea trout)	4
Solea solea (sole)	4
Spinachia spinachia (fifteen-spined stickleback)	4
Unidentified *Avian* (bird)	4
Unidentified *Amphibia* (amphibian)	4
Ciliata mustela (five-bearded rockling)	3
Conger conger (conga eel)	3
Unidentified *Cottidae* (sea scorpion)	3
Cottus gobio (bullhead)	3
Pholis gunnellus (butterfish)	3
Scophthalamus rhombus (brill)	3
Unidentified *Mammalian* (mammal)	3
Unidentified *Cyprinid* (carp/minnow)	3
Unidentified *mollusca* (mollusc)	3
Unidentified *Gadidae* (cod)	3
Callionymus lyra (dragonet)	2
Carcinus maenas (common shore crab)	2
Cobitis paludica (loach)	2
Crenilabrus melops (corkwing wrasse)	2
Esox lucius (pike)	2
Gaidropsarus mediterraneus (shore rockling)	2
Limanda limanda (dab)	2
Perca fluviatilis (European perch)	2
Phoxinus phoxinus (minnow)	2
Platichthys flesus (flounder)	2

Pleuronectes platessa (plaice)	2
Squalius pyrenaicus (chub)	2
Syngnathus acus (greater pipefish)	2
Unidentified *Insecta* (insect)	2
Abramis brama (common bream)	1
Atherina spp (sand smelt)	1
Barbatula barbatula (stone loach)	1
Cancer pagurus (edible crab)	1
Chirolophis ascanii (Yarrell's blenny)	1
Ciliata septentrionalis (northern rockling)	1
Ctenolabrus rupestris (goldsinny wrasse)	1
Leuciscus leuciscus (dace)	1
Enchelyopus cimbrius (four-bearded rockling)	1
Gadus morhua (cod)	1
Gobius pagenellus (rock goby)	1
Lepadogaster lepadogaster (shore's clingfish)	1
Liparis montagui (Montagu's sea snail)	1
Lipophrys pholis (shanny)	1
Muglidae (grey mullet)	1
Myoxocephalus scorpius (bullhead)	1
Nerophis lumbriciformis (worm pipefish)	1
Paracentrotus lividus (sea urchin)	1
Pollachius pollachius (pollack)	1
Pollachius virens (saithe)	1
Procambrus clarkii (red swamp crayfish)	1
Rana temporaria (common frog)	1
Rutilus rutilus (roach)	1
Salmo salar (Atlantic salmon)	1
Scardinius erythropthalmus (rudd)	1
Sorex Araneus (common shrew)	1
Sprattus sprattus (sprat)	1
Squalius cephalus (chub)	1
Taurulus bubalis (sea scorpion)	1
Tinca tinca (tench)	1
Trisopterus minutus (poor cod)	1
Tritus spp (newts)	1
Zeugopterus punctatus (topknot)	1
Zoarces viviparpus (eelpout)	1
Bufo bufo (common toad)	0

The most commonly occurring species across all seven studies is *Anguilla anguilla*, followed by *Labridae* and *Gobiidae,* all three of which are primarily marine and brackish species. Most of the prey identified to species level are only recorded to have been present in one or two studies such as *Abramis brama* (common bream) and *Gaidropsarus mediterraneus* (shore rockling). Interestingly, both the fresh water dwelling three-spined stickleback (*Gasterosteus aculeatus*) and strictly marine fifteen-spined stickleback (*Spinachia spinachia*) were present in more than three studies (five and four respectively). Crustaceans were also recorded as present in five studies, but only one species of decapod, *Carcinus maenas* (common shore crab) was identified to species level in more than one study. Similarly, *Rana temporaria* (common frog) the only amphibian identified to species level, *Tritus spp* (newts) were recorded as present in one study and *Bufo bufo* (common toad) were included in a description of possible *Anuran* spp but not directly identified.

8.2 Prey matrix

The prey matrix (Appendix II) shows the complete prey list broken down by study with the mean R.F.O (%) for each example of prey as well as body form, ecosystem type, habitat classification and prey type for each species. The prey matrix was further separated into two tables with one dedicated to named species (e.g., *Anguilla Anguilla*, *Spinnachia spinnachia* etc) (Table 9) and one with all prey categorised at family level (Table 10). This was necessary to analyse the significance of marine species in the diet across all the studies as not all the studies identified prey to species level (see section 9.3).

Table 7. Modal analysis of prey traits for each study with the most common prey traits for body form, ecosystem type, habitat classification and prey type as well as the average for each.

Study	Body form	Ecosystem type	Habitat classification	Prey type
1	3	2	3	3
2	3	1	3	3
3	3	3	3	3
4	3	2	3	3
5	3	3	7	3
6	3	2	3	3
7	3	2	3	3
AVERAGE	**3.00**	**2.14**	**3.57**	**3.00**

Table 7 shows the modal value of each categorical variable for each study and each prey trait as well as the average for all studies on the bottom row. The only outliers in this dataset appear to be the body form for study 5 (Tarifa, Spain), 3.5, and the ecosystem type for study 2 (Isle of Mull, Scotland), 1.

8.3 Trophic niche analysis

Shannon -Weiner diversity Index was calculated for the R.F.O (%) values for each prey entry for all seven studies, both the H value for diversity and J value for evenness are included in Table 7 along with Levins niche breadth calculation, for equations see section 7.4.

Table 8. Trophic statistics from Shannon- Weiner diversity index (*H* and *J* values) and Levins niche breadth analysis for each study

Study code	*H'*	*J'*	Levins
1	2.86	0.97	0.53
2	2.51	0.85	0.32
3	2.04	0.69	0.36
4	2.38	0.81	0.54
5	2.69	0.91	0.24
6	2.14	0.73	0.25
7	1.82	0.27	0.21
AVERAGE	2.35 (± 0.14)	0.75 (± 0.08)	0.35 (± 0.05)

The Shannon- Weiner *H* values for diversity) for studies 1-6 are similar (2.04- 2.86), *J* values for evenness) for studies 1-6 are all similar (0.69-0.97) however study 7 (Gower, Wales) is an outlier (*H'*= 1.82 and *J'* = 0.27). These results indicate that there is a higher level of diversity in studies 1-6. Levins is more evenly distributed with all studies (0.21-0.54) indicating from the samples in studies 1-7 *Lutra lutra* is leaning towards the specialist end of the spectrum of specialist- generalist, and that they may be favouring specific environments, potentially marine associated environments.

8.4 Prey trait analysis

A count of each prey trait category was conducted for each summary with totals overall proportions were calculated these are found in Appendices E and F.

For each prey trait this data is presented as both a bar chart of total number of occurrences overall (Figure 3) and a 100% stacked bar chart of the proportion of each trait category for each study (Figure 4). See section 7.4 (Tables 3-5) for prey trait classification keys, ecosystem type is classified in this study by how many interfaces prey species/group are found in (1-4) see section 2.4.

The most common prey body form was fusiform (39.6%), followed by elongated (14.9%) and anguilliform (11%), reptile was the least common (0.6%) only occuring once in study 5 (Tarifa, Spain) see Appendix E, Table E1. The most common number of ecosystem interfaces the prey occupy is two (36.4%), followed by one (33.1%), with the least common being four (5.2%), most species occur across multiple interfaces. Demersal is the most common habitat classification (48.7%) with other being the next highest number (20.8%) and pelagic-neritic being the least common (1.3%). The prey type category most common was Type 3 (43.5%) with Type 1 being the least common (1.95%).

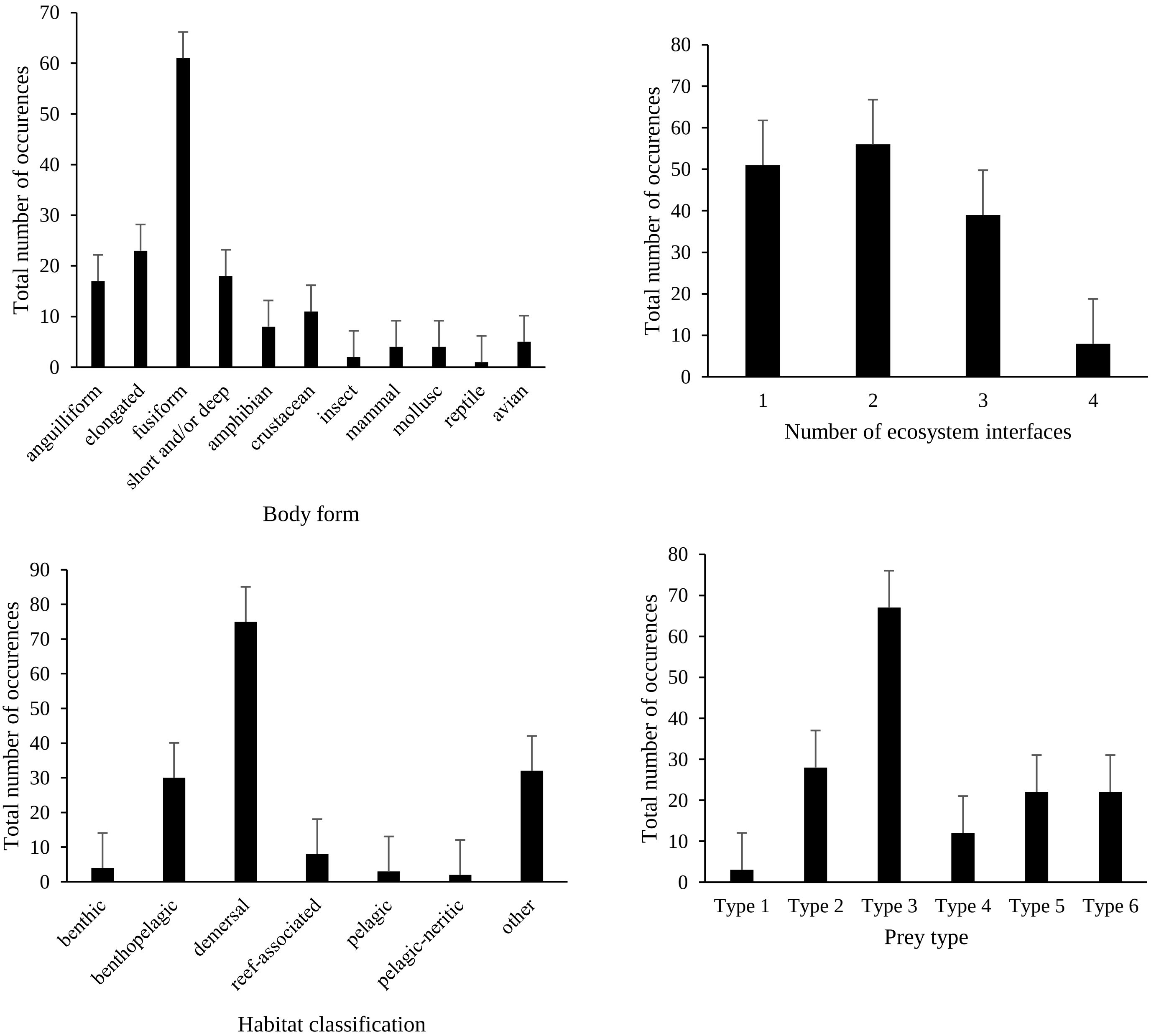

Figure 4. Total number of occurrences of each prey trait across all seven studies (+SE). The total number of occurrences of each prey trait (bodyform, ecosystem type, habitat classification and prey type) is more varied than initially expected, however the most and least common in each category is not surprising. As this study is exploratory as opposed to defining it would be difficult to quantify which of these characteristics is the most important in this study as each offers different insights into the otter's diet and feeding habits, especially within marine ecosystems.

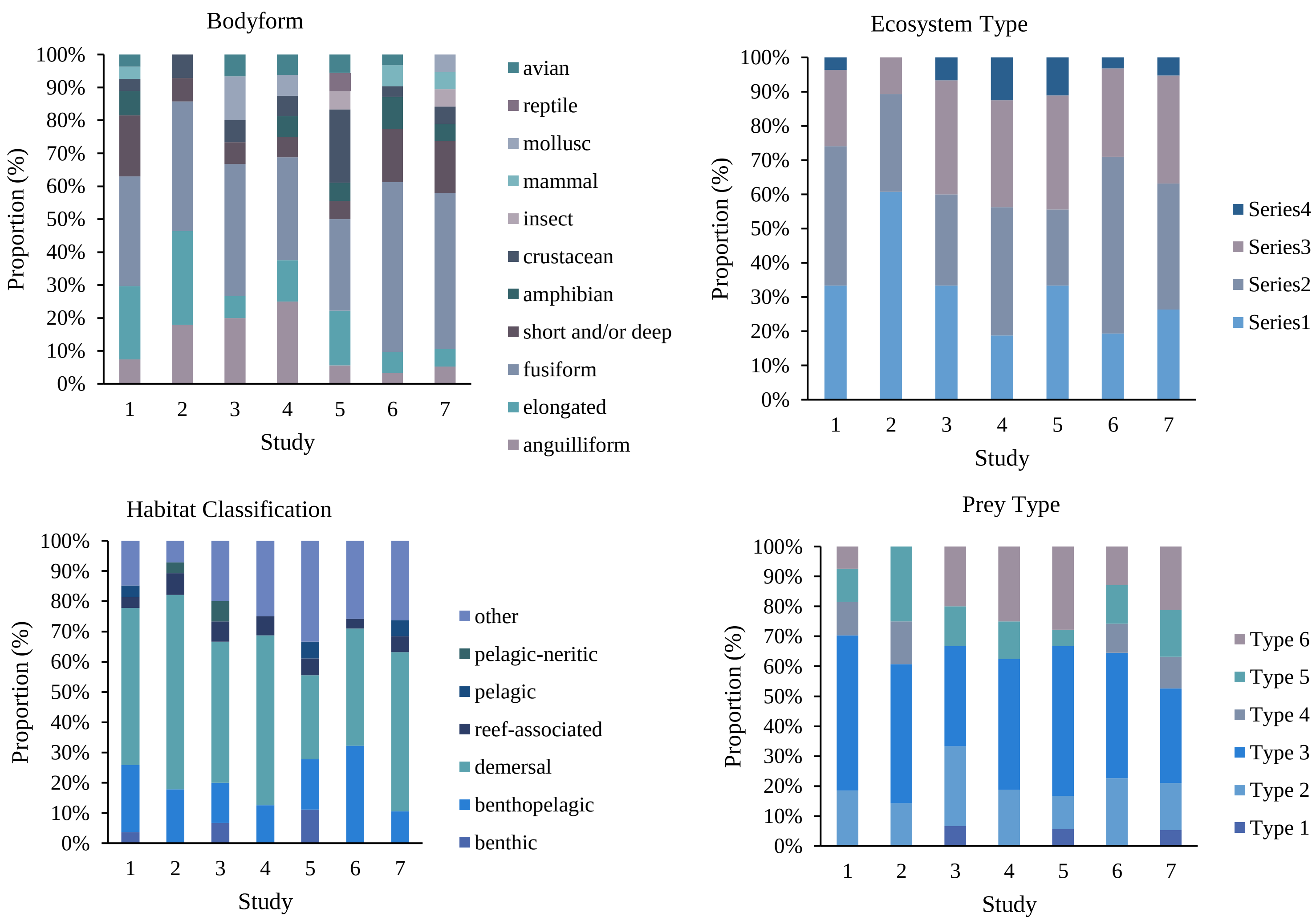

Figure 5. Proportion (%) of each prey trait in each of the seven studies. The proportion of each prey trait (bodyform, ecosystem type, habitat classification and prey type) varies between each study and therefore each location. Despite many of the studies being in relatively close proximity and/ or similar habitats e.g., study 1 (Pembrokeshire) and 7 (Gower) are the closest (geographically and in habitat type) and yet they still differ greatly. It is also important to recognise the nature of this study in its raw comparative form is still only comparing data from seven studies in a small section of the otters known potential environment (i.e., Europe and Asia).

8.5 Significance of marine species

To investigate the significance of marine species the prey matrix (Table 9) is split into species level identification and a second prey matrix with family level identification (all prey within each family aggregated into one entry for marine and one for non-marine if necessary (Table 10).

Table 9. Prey matrix (identified to species level only) with the mean R.F.O (%) for all occurrences across studies (1-7), chosen prey traits; body form, ecosystem type, habitat classification and prey type.

Prey species	Mean R.F.O (%) (± 2.03)	Body form	Ecosystem type	Habitat classification	Prey type
Abramis brama (common bream)	0.03	fusiform	FW/B	benthopelagic	5
Anguilla anguilla (eel)	12.98	anguilliform	M/B/FW	demersal	5
Atherina spp (sand smelt)	0.07	elongated	M/B	pelagic	3
Barbatula barbatula (stone loach)	0.14	fusiform	FW	demersal	3
Bufo bufo (common toad)	0.00	amphibian	FW/T	other	3
Callionymus lyra (dragonet)	0.07	elongated	M	demersal	3
Cancer pagurus (edible crab)	0.25	crustacean	M	other	3
Carcinus maenas (common shore crab)	2.15	crustacean	M/B	other	2
Chirolophis ascanii (Yarrell's blenny)	0.05	elongated	M	benthopelagic	3
Ciliata mustela (five-bearded rockling)	5.59	elongated	M	demersal	2
Ciliata septentrionalis (northern rockling)	0.02	elongated	M/B	demersal	3
Cobitis paludica (loach)	0.16	elongated	FW	benthopelagic	1
Conger conger (conga eel)	0.80	anguilliform	M	demersal	5
Cottidae (sea scorpion)	4.55	fusiform	M/B	demersal	2
Cottus gobio (bullhead)	0.68	fusiform	FW/B	demersal	2
Crenilabrus melops (corkwing wrasse)	0.14	fusiform	M	reef-associated	3
Ctenolabrus rupestris (goldsinny wrasse)	0.06	fusiform	M	reef-associated	3
Leuciscus leuciscus (dace)	0.94	fusiform	FW/B	benthopelagic	2
Enchelyopus cimbrius (four-bearded rockling)	0.04	elongated	M	demersal	3
Esox lucius (pike)	1.40	elongated	FW/B	pelagic	5
Gadus morhua (cod)	0.43	fusiform	M/B	benthopelagic	5
Gaidropsarus mediterraneus (shore rockling)	5.18	elongated	M/B	demersal	4
Gasterosteus aculeatus (three-spined stickleback)	0.34	fusiform	M/FW/B	benthopelagic	3

Gobius paganellus (rock goby)	0.02	fusiform	M/FW/B	demersal	3
Lepadogaster lepadogaster (shore's clingfish)	0.17	elongated	M	demersal	3
Limanda limanda (dab)	0.16	short and/ or deep	M	demersal	4
Liparis montagui (Montagu's sea snail)	0.03	elongated	M	demersal	3
Lipophrys pholis (shanny)	0.86	fusiform	M	demersal	2
Myoxocephalus scorpius (bullhead)	0.02	fusiform	M/B	demersal	4
Nerophis lumbriciformis (worm pipefish)	0.51	anguilliform	M	demersal	3
Paracentrotus lividus (sea urchin)	0.37	echinoderm	M	benthic	1
Perca fluviatilis (european perch)	3.24	fusiform	FW/B	demersal	4
Pholis gunnellus (butterfish)	0.17	anguilliform	M/B	demersal	2
Phoxinus phoxinus (minnow)	0.53	fusiform	FW/B	demersal	3
Platichthys flesus (flounder)	0.70	short and/ or deep	M/FW/B	benthopelagic	2
Pleuronectes platessa (plaice)	1.00	short and/ or deep	M/B	demersal	2
Pollachius pollachius (pollack)	0.51	fusiform	M	benthopelagic	5
Pollachius virens (saithe)	3.26	fusiform	M	demersal	5
Procambrus clarkii (red swamp crayfish)	0.05	crustacean	FW	benthic	3
Rana temporaria (common frog)	0.06	amphibian	FW/T	other	3
Rutilus rutilus (roach)	0.61	fusiform	FW/B	benthopelagic	2
Salmo trutta (sea trout)	0.06	fusiform	M/FW/B	pelagic-neritic	5
Salmo salar (Atlantic salmon)	0.06	fusiform	M/FW/B	benthopelagic	5
Scardinius erythropthalmus (rudd)	0.18	fusiform	FW/B	benthopelagic	2
Scophthalamus rhombus (brill)	3.74	short and/or deep	M	demersal	4
Solea solea (sole)	0.03	short and/ or deep	M/B	demersal	3
Sorex Araneus (common shrew)	3.89	mammal	T	other	3
Spinachia spinachia (fifteen-spined stickleback)	0.06	elongated	M/B	benthopelagic	3
Sprattus sprattus (sprat)	0.34	fusiform	M/B	pelagic-neritic	2
Squalius cephalus (chub)	0.21	fusiform	FW/B	benthopelagic	4
Squalius pyrenaicus (chub)	0.29	fusiform	FW	benthopelagic	3
Syngnathus acus (great pipefish)	0.67	anguilliform	M	demersal	3
Taurulus bubalis (sea scorpion)	0.03	fusiform	M/B	demersal	3
Tinca tinca (tench)	0.03	fusiform	FW/B	demersal	2

Trisopterus minutus (poor cod)	0.02	fusiform	M	benthopelagic	5
Zeugopterus punctatus (topknot)	0.13	short and/or deep	M	demersal	4
Zoarces viviparpus (eelpout)	0.13	elongated	M/B	demersal	3

Table 10. Prey matrix identified to family (or higher) taxonomic classification, for all family entries mean R.F.O (%) for each entry combined aggregated into one for marine ecosystems and one for non-marine.

Family (or higher)	**Mean R.F.O (%) (±0.50)**	**Ecosystem type**
Amphibia	1.54	FW/T
Anguillidae	12.98	M/B/FW
Atherinidae	0.07	M/B
Avian	0.72	M/B/FW
Blenniidae	3.18	M
Callionymidae	0.07	M
Clupeidae	0.06	M/B
Cobitidae	0.16	FW
Congridae	0.80	M
Cottidae	3.87	M/B
Cottidae	4.55	FW/B
Crustacea	3.26	FW
Crustacea	5.05	M/B
Cyprinidae	0.03	M
Cyprinidae	3.27	FW/B
Esocidae	0.04	FW/B
Gadidae	9.52	M/B
Gasterosteidae	5.18	FW/B
Gasterosteidae	3.89	M/B
Gobiesocidae	0.02	M
Gobiidae	10.04	M/FW/B
Insecta	0.42	NA
Labridae	7.41	M
Liparidae	0.16	M
Lotidae	6.98	M
Mammalia	0.16	T
Mollusca	2.05	NA
Muglidae	1.64	M/FW/B
Nemacheilidae	0.14	FW
Parechinidae	0.51	M
Percidae	0.37	FW/B
Pholidae	3.24	M/B
Pleuronectidae	3.50	M
Salamandridae	0.23	FW/T
Salmonidae	0.67	M/FW/B

Scophthalmidae	0.19	M
Soleidae	3.74	M/B
Stichaeidae	0.05	M
Syngnathidae	0.30	M
Zoarcidae	0.13	M/B

Welch's two sample t test assuming unequal variances conducted on marine and non-marine prey to family level and produced a t-statistic of 1.97 (p-value of 0.06) for two tailed analyses. Therefore, we cannot reject the null hypothesis that there is no significant difference between the mean R.F.O (%) of marine and non-marine prey consumed by *Lutra lutra* across the seven studies explored in this study.

9 DISCUSSION

The underlying theme of most carnivore research is to not only extend understanding but to ultimately utilise that understanding to protect and conserve that species. The aims of this study focused on the significance of marine prey within the diet of the Eurasian otter, *Lutra lutra*, the impact this has on the marine and coastal ecosystems as well as reviewing the current approaches to this research. The results of this study rely predominantly on measures of central tendency such as the mode, median and mean are used to demonstrate the distribution of the data, all means are presented with ± standard error. The limitations of statistical analysis in this study pertain primarily to the descriptive rather than inferential nature of this study. However, the results from both the Shannon- Weiner diversity index and Levins niche breadth index are indicative of the Eurasian otter being a generalist- specialist. This is not surprising as other otter species have been described in a similar way such as sea otters, *Ehydra lutris* spp, (David and Bodkin, 2021). The results of this study have also been positive in that there is clear evidence that the otter is feeding in marine and coastal habitats, on marine and brackish prey as well as in freshwater and terrestrial. It can be interpreted from the results that while we cannot reject the null hypothesis that there is no significant difference between the mean R.F.O (%) of marine and non-marine prey consumed by *Lutra lutra*, there is clearly more than an inconsequential amount of marine prey within the diet of the otter. This suggests that otters are feeding in marine and coastal ecosystems at least as often as in freshwater ecosystems, because of this it is important to understand the significance of the otter feeding in these ecosystems for not only the otter, but also the species eaten and on a wider scale the other species within these ecosystems including to an extent humans.

9.1 Trophic niche width/breadth analysis

While only a minority of terrestrial carnivores are thought to be obligate specialists, otters have the most restricted trophic niche of all mustelids (Je drzejewska *et al*., 2001). Shannon- Weiner analysis and Levins niche breadth index are both used as an illustration of the breadth of species diversity (different values from different parts of analysis) in this study both Shannon-Weiner *H'* value for diversity and *J'* value for evenness amongst prey have been used to analyse the trophic niche. Levins index is also a measure of niche breadth, with the species weighted by the number of different environments utilised, however it is biased towards rarity.

Both the Shannon-Weiner and Levins indices for the combined data sampled in this study recorded in Table 7, provide the average statistics for all seven studies (*H'* = 2.35 (± 0.14), *J'*= 0.75 (± 0.08), and Levins = 0.35 (± 0.05)) which indicate that *Lutra lutra* is a generalist forager, with the average values for *J'* and Levins both being close to 0. While the measurements of niche width/breadth can be indicative of an individual's ecological specialisation (Olalla-Tárraga *et al.,* 2017), whether it is a generalist or specialist (or somewhere in between) its only investigating one aspect (in this instance prey species diversity) but it does not provide the whole picture (Sargeant, 2007). The bulk of otters' diet is approximately 95% fish (Smiroldo *et al*., 2019), *Lutra lutra* are highly dependent on fish (Krawczyk *et al*., 2016) therefore it is an energy trade off when feeding on other prey as the energetic value is lower (Krawczyk *et al*., 2016), given the metabolically costly lifestyle of the otter (Kruuk, 2006) this is indicative of *Lutra lutra's* opportunistic feeding when fish stocks are low.

9.2 Prey trait analysis

The most interesting prey trait analysed in this study was body form, purely because of the significance of the species that fit within each body form category and the implications that this may have relating to how the otters are foraging. The most prevalent body form in this dataset is fusiform (39.6%), elongated and anguilliform were also present in high proportions (14.9% and 11% respectively). Fusiform is one of the most common body form types in fish species inhabiting shallow coastal and marine waters (Martinez, *et al*., 2021), therefore, it is not surprising that it is highly common in studies surveying marine and coastal ecosystems. There could also be a potential connection between body form and swim type as they are linked (Blake, 2004) and whether this may affect which prey otters choose as they use both sight and touch to forage for prey (Taylor *et al*., 2010). This also links back to habitat classification as the position of prey in the water column can be indicative of swim type and by extension body form. It is also interesting that while *Anguilla anguilla* was the most common prey species (evidence of it found in all seven studies), anguilliform was not the most common body form category. This may suggest that perhaps stocks of eels are dropping or that they are just more difficult to catch, due to the opportunistic nature of otters and/or the metabolic cost of diving to forage, it could also relate back to the catadromous nature of eels that they may only be being caught by otters at certain times, perhaps when they are more vulnerable.

9.3 Significance of marine prey

The comparison of marine and non- marine prey does not have a statistically significant difference according to Welch's two sample t- test ($t = 1.97$, $p = 0.06$). However, there is clearly a high proportion of marine prey found in the diet of *Lutra lutra* from studies across the UK and Europe (Table 10). Interestingly there is a strong presence of strictly marine species, such as *Gobiidae* and *Labridae* as well as the more transient prey such as *Anguilla Anguilla* and *Salmonidae,* which frequent multiple ecosystems at different life stages (Moriarty and Dekker, 1997; Ludwig *et al*., 2002). The occurrence of prey species at multiple interactions of marine, brackish, and freshwater ecosystems (most common number of interface interactions across the studies was two (see Figure 4). The need for comprehension of the significance of ecosystem interfaces (Copp, Daverat and Bašić, 2021) to *Lutra lutra* especially marine/brackish ecosystems as optimal foraging sites due to the availability of a wider selection of prey (both fish and non-fish) than either marine or freshwater alone. The increasing anecdotal evidence of *Lutra lutra* predating on octopus more and more around the coasts of the UK and Europe (predominantly on social media groups), raises concerns regarding potentially another consequence of rising sea temperatures, increasing numbers of octopus in popular otter foraging areas, or due to an increase in otters foraging in different coastal areas (Parry *et al*., 2011) and the implications on the ecosystem because of this.

It is thought that otters predominantly forage for demersal prey (Watt, 1991; Watt, 1995; McMahon and McCafferty, 2006), the results of this study to demonstrate that demersal was the most common category within habitat classification (48.7%). This could reflect the opportunistic generalist tendencies of the otter as they catch whatever is swimming in proximity while on a dive for prey (Kruuk and Carss, 1996). To conserve energy and avoid the expenditure incurring from chasing pelagic prey (Reid *et al.*, 2013) or from diving deeper to predate upon the slower moving but deeper dwelling benthic and benthopelagic species, they hunt what is readily available at the most cost-effective depth (Figures 3 and 4). There is still a considerable proportion of flatfish species, which are mostly benthopelagic and demersal, present in the spraints, the majority of these are primarily marine and brackish species such as *Limanda limanda* (dab), *Scophthalamus rhombus* (brill), *Pleuronectes platessa* (plaice) and *Platichthys flesus* (flounder). This could suggest that the presence of benthopelagic flatfish species in marine and brackish ecosystems are nutritionally beneficial to warrant the additional depth of a dive. It would be interesting moving forward with this research to compare the most prevalent habitat classification between marine and non-marine prey as there may be a difference between foraging in the tidal controlled open water of marine and brackish ecosystems (McCluskie, 1998) and the more enclosed ecosystems of rivers, ponds, and lakes further away from the point of discharge (Beja, P.R., 1991). There has also recently been research conducted into the potential physical evolutionary traits of *Lutra lutra* feeding more and more in marine environments, including skull shape (Russo *et al*., 2022). Not only is this considered to be diet based but also potentially influenced by the habitat they primarily forage in with differences between freshwater lakes and rivers, coastal/ estuarine and marine/ island. When considering the varied geographical locations and habitats samples were collected in from the seven studies included in this study this would be an interesting factor to investigate in the future.

9.3.1 Impact of marine prey in otter diet

The most common prey type of the prey species remains found in *Lutra lutra* spraints in studies from the UK and Europe was Type 3, 43.5%, and the least common was Type 1, 1.95% (see Table 5). Figures 3 and 4 demonstrate the overall prevalence of prey type within prey species as well as the proportion of each prey type for each study. This identification of the most common prey type of prey species may be indicative of the greater impacts of the presence of *Lutra lutra* foraging within an ecosystem, further analysis is needed to determine what exactly the trickle-down effects of the otter feeding on this prey will have on these prey types in both the short and long term. In addition, extraneous factors such as prey availability, seasonality and threats to ecosystem dynamics will need to be considered. The bulk of otters' diet is approximately 95% fish (Smiroldo *et al*., 2019), *Lutra lutra* are highly dependent on fish (Krawczyk *et al*., 2016) therefore it is an energy trade off when feeding on other prey as the energetic value is lower (Krawczyk *et al*., 2016), given the metabolically costly lifestyle of the otter (Kruuk, 2006) this is indicative of *Lutra lutra's* opportunistic feeding when fish stocks are low. However, all otter species rely heavily on crustacean and decapods in their diet (Watt, 1991) due to the nature of most dietary analysis (e.g., spraint analysis), there could be an underestimation of the significance of crustaceans in the diet of *Lutra lutra*, a transitional interface species operating across marine, freshwater, and terrestrial ecosystems (Parry *et al.*, 2011).

9.4 Existing literature and limitations

One of the fundamental aims of this study was to review the current approaches to this research and evaluate a standardised approach. Collating the data from existing studies for comparison was made difficult by the lack of consistency throughout the studies in methodology and analysis. This has previously been referred to in research by Krawczyk *et al*. (2016). Some of the inconsistencies include discrepancies in collection frequency and volume of samples as well as sampling areas themselves, which are mostly designated from local knowledge. There is also variation within the statistical analysis of samples, the range of variables from frequency of occurrence, relative frequency of occurrence etc made it difficult to compare the studies. For example, R.F.O was used as one of the primary units of measurement rather than F.O in this study as this was the most used measure of prey frequency. Furthermore, not all the studies included in this analysis, reported the necessary information to utilise F.O. However, one of the issues of only using R.F.O is that it does not account for biomass of prey (Krawczyk *et al*., 2016). Furthermore, some of the formulas for various units of measurement are referred to as different things in each study, there are inconsistencies across the existing literature. There is also dispute over the trophic niche classification of *Lutra lutra* with some studies referring to the otter species as generalist (Moorhouse-Gann *et al*., 2020), others as opportunistic (Almeida *et al*., 2012) and some as specialist (Je drzejewska *et al*., 2001; Bonesi and Macdonald, 2004), should the term be specialist-generalists. Similarly, a lot of research refers to *Lutra lutra* as nocturnal, however like most carnivores, crepuscular may be more accurate (Ruiz-Olmo, Saavedra, and Jiménez, 2001).

There are also limitations within the fundamental methodology of spraint collection and analysis for dietary studies such as inconsistencies in collection frequency and number between studies. It is also difficult to quantify certain data from spraint analysis (Bearhop *et al*., 2004; Syväranta *et al*., 2013). Likewise there are the limitations of the spraints themselves as only hard remains are analysed, there is bias towards species with a greater number of vertebrae such as *Anguilla anguilla* (Heggberget and Moseid, 1994; Moriarty and Dekker, 1997) also bias towards smaller sized prey, as larger prey such as *Salmonidae* spp when caught only the most nutritionally valuable parts may be consumed by the otter, meaning there may be less vertebrae and other hard parts ingested and therefore less to identify (Heggberget and Moseid, 1994)). Furthermore, not all prey species will leave hard remains e.g., cephalopods (Beja, 1997), it is also more difficult to identify remains of amphibians to species level than fish (Smiroldo *et al*., 2019). Given these biases it is therefore not surprising that most studies examining otter diet focus on assessing influence of fish availability (Remonti *et al*., 2008), there is also significantly more focus on freshwater habitats and less on marine or on the freshwater and marine interfaces including brackish and estuarine ecosystems. Taking all these factors and biases into consideration, are other methods of dietary analysis such as stable isotope analysis the way forward, however, there are still limitations with this method as only a subset of ecological niche is explored (Swanson *et al*., 2015).

9.5 Future proofing, conservation, and management

As more coastal areas are urbanised (Bulleri and Chapman, 2010), wetland areas are fragmented (Amezaga and Santamaría, 2000; Das, Shit and Bera, 2021), river systems become less habitable (Birk and Willby, 2010), fish stocks continue to decrease (Parry *et al*., 2011) and amphibian populations decline (Krawczyk *et al*., 2016), the Eurasian otter will search for higher energetic value prey (Krawczyk *et al.*, 2016) likely in coastal areas. This could present problems as the value of the marine environment changes (Barbier, 2020; McLeod and Leslie, 2009; Worm *et al*., 2009) however with no established coastal otter surveying method, the significance of the marine environment has most likely been underestimated previously (Parry *et al*., 2011).

A lot of the current approaches to otter diet analysis dietary studies solely exploring trophic niche could potentially be missing information (Pineda-Munoz and Alroy, 2014). The F.O (%) and R.F.O (%) from abundance data provide us with a snapshot-insight into the range of different prey species consumed by the otter (Beja, 1997). However, additional analysis on size of hard remains can only extend that picture especially in terms of understanding potential implications of predation in relation to prey species life history traits not explored in this study such as fecundity, longevity, maturation age, maximum total length, parental care, and spawning season duration (Bertram and Leggett, 1994). The relevance of horizon scanning (Sutherland and Woodruff, 2009; Herbert-Read *et al*., 2022) is becoming increasingly important when considering conservation in the face of global warming (Duarte *et al*., 2020), rising sea levels (Learmonth *et al*., 2006), rain distribution (Poloczanska *et al*., 2007). The impact that these threats pose to both the physical ecosystems as well as the ecosystem and community dynamics and the repercussions of these on predators such as *Lutra lutra*.

In this study one of the most chosen prey is *Anguilla anguilla* which is a species that frequents all three (freshwater, brackish and marine) ecosystems, in terms of impacts on these ecosystems now there is no definitive answer as to whether coastal foraging has either a positive or negative impact. However, it could be inferred by the presence of marine prey in the otter's diet that the strain on freshwater stocks may be lessened when under pressure from extraneous pressures (Aprahamian and Walker, 2008; Johnson *et al*., 2009). Furthermore, it could be argued that the evidence of otters feeding in coastal and marine ecosystems should reduce tensions between anglers, and those working within freshwater aquaculture who believe the otters are in direct competition with them (Almeida *et al*., 2012; Lyach, and Čech, 2017). This is clearly not the whole picture and hopefully this research and future studies investigating the significance of marine prey will help to diffuse these tensions as our understanding of otters foraging and feeding patterns continues to develop.

Equally, as the potential for human and otter conflicts to increase (Duarte *et* al., 2020; Mirzajani *et al.*, 2021) over the marine ecosystem as a resource due to human activities in coastal areas increases exponentially (Parry *et al*., 2011; Paudyal *et al*., 2019). We could examine examples of biologically similar species (e.g., *Lontra felina*) for warnings regarding human- otter conflict in rapidly changing marine and coastal ecosystems (Yom-Tov *et al*., 2006; Gutiérrez, *et al*., 2019). We could also look to *Lontra felina* or (sea cats) as other carnivores constrained to marine and coastal environments, as well as sea otters (*Enhydra lutris* spp), grey seals (*Halichoerus grypus*) and the common seal (*Phoca vitulina*). While there are differences biologically (Kuhn *et al*., 2010, Tinker *et al.*, 2018), there are strong similarities between the ecosystems foraging is undertaken in and pressures experienced from human interactions (Bosetti and Pearce, 2003; Valqui, 2012), as well as other potential external factors such as the implications of climate change (Loy, and Duplaix, 2020; Santillán, Saldaña-Serrano, and De-La-Torre, 2020). Similarly, there is a gap in research concerning interactions between *Lutra lutra* and both the grey and common seal (Boyi *et al*., 2022) and the implications of niche overlap potentially causing competition between these predatory semi-aquatic mammals (Brooks *et al*., 2010; Hadi *et al*., 2012).

These multi species interactions, alongside further research into the wider implications of the role of the Eurasian otter in coastal and marine ecosystems could help us to find better ways to protect both the ecosystems themselves as well as these specialist- generalist carnivores who are finding ways to survive in the face of adversity from all angles.

10 CONCLUSIONS

While only a minority of terrestrial carnivores are thought to be obligate specialists, otters have the most restricted trophic niche of all mustelids (Je drzejewska *et al*., 2001). The impact of changing environments due to urbanisation, socio-economic growth/decline, and global warming need to be considered and evaluated for conservation and management of both *Lutra lutra* and its prey species as well as the habitats they are found in. The next steps for this research going forward are to develop a consistent and standardised protocol for the methodology of collection, analysis, and reporting of otter spraints in dietary studies. Furthermore, the combination of other dietary analysis techniques alongside traditional spraint analysis could be beneficial in improving our understanding of the role of *Lutra lutra* within the marine and coastal ecosystems they are utilising more frequently and ultimately improving our conservation and management of both.

11 APPENDIX

11.1 Appendix A

Table A1. Brief summary of key information extracted from studies used in collated analysis in this study (study matrix) including author, year, location, duration (months), brief habitat description, sample size, seasonality, quantitative vs qualitative. The brief habit description is summarised from papers and categorised on the predominant habitat.

Study code	Author	Year	Location	Duration (months)	Habitat description	Sample size	Seasonality	Quantitative (Y/N)
1	Parry *et al*	2011	Pembrokeshire, Wales, UK	12	Mixed-rocky shore, lowland, sandy beach and estuary	180	Y	Y
2	Watt., J	1991	Isle of Mull, Scotland, UK	24	Rocky shore	958	Y	Y
3	Kingston *et al*	1999	Arran islands, Ireland	11	Mixed-rocky shore and lowland	1510	Y	Y
4	Murphy. K. P. and Fairley. J.S.	1985	Galway, Ireland	13	Rocky shore	1026	Y	Y
5	Clavero *et al*	2004	Tarifa, Spain	36	Sandy beaches and estuaries	1882	NA	Y
6	Harris. E. and Maddocks. K	2005/2013	Newport Gwent Levels, Wales, UK	2002-2010	Lowlands	168	NA	Y
7	Forman. D.W, Gallardo. J.D and Knight. J. A	2022	Gower peninsula, Wales, UK	11	Mixed-rocky shore, lowland, sandy beach and estuary	44	NA	N

11.2 Appendix B

Table B1. Complete study-prey matrix with individual R.F.O (%) for each prey from each study and chosen prey trait categories; body form, ecosystem type, habitat classification and prey type.

Study code	Prey species/group	R.F.O (%)	Body form	Ecosystem type	Habitat classification	Prey type
1	*Cottis gobio* (bullhead)	2.4	fusiform	FW/B	demersal	2
1	*Leuciscus cephalus* (chub)	0.5	fusiform	FW/B	benthopelagic	4
1	*Anguilla anguilla* (eel)	10.9	anguilliform	M/B/FW	demersal	5
1	*Phoxinus phoxinus* (minnow)	0.2	fusiform	FW/B	demersal	3
1	*Esox lucius* (pike)	0.2	elongated	FW/B	pelagic	5
1	*Salmonidae spp*. (salmonidae spp)	2.8	fusiform	M/FW/B	benthopelagic	5
1	*Gasterosteus aculeatus* (3 spined stickleback)	6.6	fusiform	M/FW/B	benthopelagic	3
1	*Cyprinidae spp* (not ID ciprinid spp)	5.7	fusiform	FW/B	demersal	3
1	*Blennidae spp* (blennies)	10.4	elongated	M	demersal	2
1	*Scophthalamus rhombus* (brill)	0.3	short and/or deep	M	demersal	4
1	*Limanda limanda* (dab)	1	short and/ or deep	M	demersal	4
1	*Zoarces viviparpus* (eelpout)	0.9	elongated	M/B	demersal	3
1	*Spinachia spinachia* (15 spined stickleback)	6.2	elongated	M/B	benthopelagic	3
1	*Gaidropsarus vulgaris* (5 bearded rockling)	1.9	elongated	M	demersal	3
1	*Plaitichthys flesus* (flounder)	1.4	short and/ or deep	M/FW/B	benthopelagic	2
1	*Enchelyopus cimbrius* (4 bearded rockling)	6.6	elongated	M	demersal	3
1	*Gobbidae* spp (gobies)	12.5	fusiform	M/B/FW	demersal	3
1	*Synathidae* (pipefish)	1.9	eel - like	M	demersal	3
1	*Pleuronectes platessa* (plaice)	0.5	short and/ or deep	M/B	demersal	2
1	*Labridae* (wrasse)	4.3	fusiform	M	reef- associated	3
1	*Cottidae* spp (no ID Cottidae)	2.8	fusiform	M/FW/B	demersal	3
1	*Heterosomata* spp (no ID flatfish)	5	short and/ or deep	M	benthopelagic	2
1	Marine crab	6.3	crustacean	M/B	benthic	3
1	*Rana temporaria, Bufo bufo* (Anuran spp)	1.9	amphibian	FW/T	other	3
1	*Tritus spp* (Newts)	1.6	amphibian	FW/T	other	3
1	Mammal remains (not ID)	0.7	mammal	T	other	6
1	Avian remains (not ID)	3.3	avian	M/B/FW/T	other	6
2	Salmo trutta (sea trout)	0.11	fusiform	M/FW/B	pelagic-neritic	5
2	Anguilla anguilla (eel)	7.41	anguilliform	M/B/FW	demersal	5
2	Conger conger (conga eel)	0.11	anguilliform	M	demersal	5
2	Gadus morhua (cod)	9.80	fusiform	M/B	benthopelagic	5
2	Pollachius virens (saithe)	3.59	fusiform	M	demersal	5
2	Pollachius pollachius (pollack)	6.97	fusiform	M	benthopelagic	5
2	Trisopterus minutus (poor cod)	0.22	fusiform	M	benthopelagic	5
2	Ciliata mustela (5 bearded rockling)	10.24	elongated	M	demersal	2
2	Ciliata septentrionalis (northern rockling)	0.11	elongated	M/B	demersal	3

2	Gaidropsarus mediterraneus (shore rockling)	0.11	elongated	M/B	demersal	4
2	Gobius pagenellus (rock goby)	2.40	fusiform	M/FW/B	demersal	3
2	Ctenolabrus rupestris (goldsinny wrasse)	0.98	fusiform	M	reef-associated	3
2	Crenilabrus melops (corkwing wrasse)	0.44	fusiform	M	reef-associated	3
2	Pholis gunnellus (butterfish)	13.40	eel- like	M/B	demersal	2
2	Chirolophis ascanii (Yarrell's blenny)	0.33	elongated	M	benthopelagic	3
2	Lipophrys pholis (shanny)	0.22	fusiform	M	demersal	2
2	Myoxocephalus scorpius (bullhead)	5.99	fusiform	M/B	demersal	4
2	Taurulus bubalis (sea scorpion)	4.68	fusiform	M/B	demersal	3
2	Callionymus lyra (dragonet)	0.11	elongated	M	demersal	3
2	Lepadogaster lepadogaster (shore's clingfish)	0.11	elongated	M	demersal	3
2	Liparis montagui (Montagu's sea snail)	1.09	elongated	M	demersal	3
2	Spinachia spinachia (15 spined stickleback)	16.34	elongated	M/B	benthopelagic	3
2	Synathus acus (great pipefish)	0.11	anguilliform	M	demersal	3
2	Nerophis lumbriciformes (worm pipefish)	0.11	anguilliform	M	demersal	3
2	Zeugopterus punctatus (topknot)	0.11	short and/or deep	M	demersal	4
2	Limanda limanda (dab)	0.22	short and/ or deep	M	demersal	4
2	Carcinus maenas (shore crab)	12.96	crustacean	M/B	other	2
2	Cancer pagurus (edible crab)	1.74	crustacean	M	other	3
3	*Sprattus sprattus* (sprat)	0.4	fusiform	M/B	pelagic-neritic	2
3	*Anguilla anguilla* (eel)	7.2	anguilliform	M/B/FW	demersal	5
3	*Conger conger* (conga eel)	0.7	anguilliform	M	demersal	5
3	*Gasterosteus aculeatus* (3 spined stickleback)	1.5	fusiform	M/FW/B	benthopelagic	3
3	*Gadidae* (rockling)	27	elongated	M/B	demersal	3
3	*Labridae* (wrasse)	25.4	fusiform	M	reef-assiciated	3
3	*Gobiidae* (gobies)	1.7	fusiform	M/FW/B	demersal	3
3	*Blennidae spp* (blennies)	4.2	fusiform	M	demersal	2
3	*Pholis gunnellus* (butterfish)	1	anguilliform	M/B	demersal	2
3	*Cottidae* (sea scorpion)	6.6	fusiform	M/B	demersal	3
3	*Heterosomata spp* (no ID flatfish)	1.9	short and/ or deep	M	benthopelagic	2
3	*Crustacea* (crustacean spp)	6.4	crustacean	M/FW/B	other	6
3	*Mollusca* (mollusc spp)	9.7	mollusc	M/FW/B	other	6
3	*Avian remains* (not ID)	0.1	avian	M/B/FW/T	other	6
3	*Paracentrotus lividus* (sea urchin)	3.6	mollusc	M	benthic	1
4	*Anguilla anguilla* (eel)	14.38	anguilliform	M/B/FW	demersal	5
4	*Conger conger* (conga eel)	4.79	anguilliform	M/B/FW	demersal	5
4	*Sygnathidae* (pipefish)	0.96	anguilliform	M	demersal	3
4	*Gadidae* (rocklings)	17.89	elongated	M/B	demersal	3
4	*Labridae* (wrasse)	9.90	fusiform	M	reef-associated	3
4	*Gobiidae* (gobies)	9.90	fusiform	M/FW/B	demersal	3
4	*Blennidae spp* (blennies)	2.24	fusiform	M	demersal	2
4	*Pholis gunnellus* (butterfish)	8.31	anguilliform	M/B	demersal	2

4	*Cottidae* (sea scorpion)	7.03	fusiform	M/B	demersal	3
4	*Spinachia spinachia* (15 spined stickleback)	2.56	elongated	M/B	benthopelagic	3
4	*Gasterosteus aculeatus* (3 spined stickleback)	0.96	fusiform	M/FW/B	benthopelagic	3
4	*Pleuronectidae* (flatfish)	1.92	short and/ or deep	M/B	demersal	2
4	*Rana temporaria* (Anuran spp)	0.32	amphibian	FW/T	other	6
4	Avian remains (not ID)	0.32	avian	M/B/FW/T	other	6
4	*Crustacea* (crustacean spp)	14.06	crustacean	M/FW/B	other	6
4	*Mollusca* (mollusc spp)	4.47	mollusc	M/FW/B/T	other	6
5	*Anguilla anguilla* (eel)	12.8	anguilliform	M/B/FW	demersal	5
5	*Muglidae* (Grey mullet)	11.5	fusiform	M/FW/B	benthopelagic	2
5	*Soleidae* (flatfish)	7.7	short and/ or deep	M/B	demersal	3
5	*Gobiidae* (gobies)	6.2	fusiform	M/FW/B	demersal	3
5	*Labridae* (wrasse)	7.6	fusiform	M	reef-associated	3
5	*Blennidae spp* (blennies)	5.2	fusiform	M/FW/B	demersal	2
5	*Gadidae* (rocklings)	1.4	elongated	M/B	demersal	3
5	*Atherina spp* (sand smelt)	0.5	elongated	M/B	pelagic	3
5	*Squalius pyrenaicus* (chub)	1.1	fusiform	FW	benthopelagic	3
5	*Cobitis paludica* (loach)	0.9	elongated	FW	benthopelagic	1
5	Crustaceans	30	crustacean	M/FW/B	other	6
5	*Procambrus clarkii* (red swamp crayfish)	22.8	crustacean	FW	benthic	3
5	marine crab	2.1	crustacean	M/B	benthic	3
5	small crustaceans	5.1	crustacean	M/FW/B	other	6
5	Amphibian	6.5	amphibian	FW/T	other	3
5	Reptiles	1.8	reptilian	T	other	6
5	Insects	2.8	insect	M/FW/B/T	other	6
5	Bird remains (not ID)	0	avian	M/B/FW/T	other	6
6	*Scophthalamus rhombus* (brill)	0.84	short and/or deep	M	demersal	4
6	*Cottus gobio* (bullhead)	2.10	fusiform	FW/B	demersal	2
6	*Squalius* spp (chub)	0.42	fusiform	FW/B	benthopelagic	4
6	*Abramis brama* (common bream)	0.21	fusiform	FW/B	benthopelagic	5
6	Leuciscus leuciscus (dace)	0.42	fusiform	FW/B	benthopelagic	2
6	*Callionymus lyra* (dragonet)	0.42	elongated	M	demersal	3
6	*Anguilla anguilla* (eel)	24.53	anguilliform	M/B/FW	demersal	5
6	*Spinachia spinachia* (15 spined stickleback)	2.10	elongated	M/B	benthopelagic	3
6	*Plaitichthys flesus* (flounder)	2.31	short and/ or deep	M/FW/B	benthopelagic	2
6	*Gobbidae* spp	7.97	fusiform	M/FW/B	demersal	3
6	*Labridae* spp	0.21	fusiform	M	reef-associated	3
6	*Phoxinus phoxinus* (Minnow)	1.05	fusiform	FW/B	demersal	3
6	*Perca fluviatilis* (european perch)	0.21	fusiform	FW/B	demersal	4
6	*Pleuronectes platessa* (plaice)	4.40	short and/ or deep	M/B	demersal	2
6	*Rutilus rutilus* (roach)	0.42	fusiform	FW/B	benthopelagic	2
6	*Scardinius erythropthalmus* (rudd)	0.42	fusiform	FW/B	benthopelagic	2
6	*Salmo salar* (Atlantic salmon)	0.42	fusiform	M/FW/B	benthopelagic	5
6	*Salmonidae*	0.63	fusiform	M/FW/B	benthopelagic	5

6	*Solea solea* (sole)	0.21	short and/ or deep	M/B	demersal	3
6	*Barbatula barbatula* (stone loach)	1.05	fusiform	FW	demersal	3
6	*Tinca tinca* (Tench)	0.21	fusiform	FW/B	demersal	2
6	*Gasterosteus aculeatus* (3 spined stickleback)	19.71	fusiform	M/FW/B	benthopelagic	3
6	*Cyprinidae*	7.55	fusiform	FW/B	demersal	3
6	Unidentified Flatfish	5.24	short and/ or deep	M/FW/B	demersal	6
6	Crustacean	0.21	crustacean	M/FW/B	other	6
6	*Rana temporaria* (common frog)	0.00	amphibian	FW/T	other	3
6	*Tritus spp* (Newts)	0.00	amphibian	FW/T	other	3
6	Unidentifed *Anuran*	1.89	amphibian	FW/T	other	3
6	*Sorex Araneus* (common shrew)	0.21	mammal	T	other	3
6	Unidentified mammalian	0.21	mammal	T	other	6
6	Unidentified Avian	1.26	avian	M/B/FW/T	other	6
7	Cyprinidae	2.96	fusiform	FW/B	demersal	3
7	Gasterosteidae	7.51	fusiform	M/B/FW	benthopelagic	3
7	Percidae	2.40	fusiform	FW/B	demersal	4
7	Anguillidae	13.69	anguilliform	M/B/FW	demersal	5
7	Cobitidae	0.19	fusiform	FW	demersal	1
7	Cottidae	27.38	fusiform	FW/B	demersal	2
7	Salmonidae	0.75	fusiform	M/B/FW	benthopelagic	5
7	Gobiidae	29.61	fusiform	M/FW/B	demersal	3
7	Soleidae	13.29	short and/or deep	M/B	demersal	3
7	Scophthalmidae	0.13	short and/or deep	M	demersal	4
7	Pleuronectidae	0.65	short and/or deep	M/B	demersal	2
7	Blenniidae	0.02	fusiform	M	demersal	2
7	Esocidae	0.06	elongated	FW/B	pelagic	5
7	Labridae	0.25	fusiform	M	reef-associated	3
7	Crustacea	0.56	crustacean	M/B/FW	other	6
7	Insecta	0.15	insect	M/B/FW/T	other	6
7	Amphibia	0.19	amphibian	FW/T	other	3
7	Mammalia	0.04	mammal	T	other	6
7	Mollusca	0.17	mollusc	M/B/FW/T	other	6

11.3 Appendix C

Table C1. Complete study-prey matrix with individual R.F.O (%) for each prey from each study and chosen prey trait categories; body form, ecosystem type, habitat classification and prey type in numerical format (classification keys in section 7.3).

Study code	Prey species/group	R.F.O (%)	Body form	Ecosystem type	Habitat classification	Prey type
1	*Cottis gobio* (bullhead)	2.4	3	2	3	2
1	*Leuciscus cephalus* (chub)	0.5	3	2	2	4
1	*Anguilla anguilla* (eel)	10.9	1	3	3	5
1	*Phoxinus phoxinus* (minnow)	0.2	3	2	3	3
1	*Esox lucius* (pike)	0.2	2	2	5	5
1	*Salmonidae spp*. (salmonidae spp)	2.8	3	3	2	5
1	*Gasterosteus aculeatus* (three-spined stickleback)	6.6	3	3	2	3
1	*Cyprinidae spp* (not ID ciprinid spp)	5.7	3	2	3	3
1	*Blennidae spp* (blennies)	10.4	2	1	3	2
1	*Scophthalamus rhombus* (brill)	0.3	4	1	3	4
1	*Limanda limanda* (dab)	1	4	1	3	4
1	*Zoarces viviparpus* (eelpout)	0.9	2	2	3	3
1	*Spinachia spinachia* (fifteen-spined stickleback)	6.2	2	2	2	3
1	*Gaidropsarus vulgaris* (five-bearded rockling)	1.9	2	1	3	3
1	*Platichthys flesus* (flounder)	1.4	4	3	2	2
1	*Enchelyopus cimbrius* (four-bearded rockling)	6.6	2	1	3	3
1	*Gobiidae* (gobies)	12.5	3	3	3	3
1	*Syngnathidae* (pipefish)	1.9	1	1	3	3
1	*Pleuronectes platessa* (plaice)	0.5	4	2	3	2
1	*Labridae* (wrasse)	4.3	3	1	4	3
1	Unidentified *Cottidae* (sea scorpion)	2.8	3	3	3	3
1	*Heterosomata* spp (no ID flatfish)	5	4	1	2	2
1	Marine crab	6.3	6	2	1	3
1	*Rana temporaria, Bufo bufo* (Anuran spp)	1.9	5	2	7	3
1	*Tritus spp* (newts)	1.6	5	2	7	3
1	Unidentified *Mammalian* (mammal)	0.7	8	1	7	6
1	Unidentified *Avian* (bird)	3.3	11	4	7	6
2	*Salmo trutta* (sea trout)	0.11	3	3	6	5

2	*Anguilla anguilla* (European eel)	7.41	1	3	3	5
2	*Conger conger* (conga eel)	0.11	1	1	3	5
2	*Gadus morhua* (cod)	9.80	3	2	2	5
2	*Pollachius virens* (saithe)	3.59	3	1	3	5
2	*Pollachius pollachius* (pollack)	6.97	3	1	2	5
2	*Trisopterus minutus* (poor cod)	0.22	3	1	2	5
2	*Ciliata mustela* (five-bearded rockling)	10.24	2	1	3	2
2	*Ciliata septentrionalis* (northern rockling)	0.11	2	2	3	3
2	*Gaidropsarus mediterraneus* (shore rockling)	0.11	2	2	3	4
2	*Gobius paganellus* (rock goby)	2.40	3	3	3	3
2	*Ctenolabrus rupestris* (goldsinny wrasse)	0.98	3	1	4	3
2	*Crenilabrus melops* (corkwing wrasse)	0.44	3	1	4	3
2	*Pholis gunnellus* (butterfish)	13.40	1	2	3	2
2	*Chirolophis ascanii* (Yarrell's blenny)	0.33	2	1	2	3
2	*Lipophrys pholis* (shanny)	0.22	3	1	3	2
2	*Myoxocephalus scorpius* (bullhead)	5.99	3	2	3	4
2	*Taurulus bubalis* (sea scorpion)	4.68	3	2	3	3
2	*Callionymus lyra* (dragonet)	0.11	2	1	3	3
2	*Lepadogaster lepadogaster* (shore's clingfish)	0.11	2	1	3	3
2	*Liparis montagui* (Montagu's sea snail)	1.09	2	1	3	3
2	*Spinachia spinachia* (fifteen-spined stickleback)	16.34	2	2	2	3
2	*Synathus acus* (great pipefish)	0.11	1	1	3	3
2	*Nerophis lumbriciformis* (worm pipefish)	0.11	1	1	3	3
2	*Zeugopterus punctatus* (topknot)	0.11	4	1	3	4
2	*Limanda limanda* (dab)	0.22	4	1	3	4
2	*Carcinus maenas* (shore crab)	12.96	6	2	7	2
2	*Cancer pagurus* (edible crab)	1.74	6	1	7	3
3	*Sprattus sprattus* (sprat)	0.4	3	2	6	2
3	*Anguilla anguilla* (European eel)	7.2	1	3	3	5
3	*Conger conger* (conga eel)	0.7	1	1	3	5

3	*Gasterosteus aculeatus* (three-spined stickleback)	1.5	3	3	2	3
3	*Gadidae* (rockling)	27	2	2	3	3
3	*Labridae* (wrasse)	25.4	3	1	4	3
3	*Gobiidae* (gobies)	1.7	3	3	3	3
3	*Blennidae spp* (blennies)	4.2	3	1	3	2
3	*Pholis gunnellus* (butterfish)	1	1	2	3	2
3	*Cottidae* (sea scorpion)	6.6	3	2	3	3
3	*Heterosomata spp* (unidentified flatfish)	1.9	4	1	2	2
3	*Crustacea* (crustacean)	6.4	6	3	7	6
3	*Mollusca* (mollusc)	9.7	9	3	7	6
3	Unidentified *Avian* (bird)	0.1	11	4	7	6
3	*Paracentrotus lividus* (sea urchin)	3.6	9	1	1	1
4	*Anguilla anguilla* (European eel)	14.38	1	3	3	5
4	*Conger conger* (conga eel)	4.79	1	3	3	5
4	*Sygnathidae* (pipefish)	0.96	1	1	3	3
4	*Gadidae* (rocklings)	17.89	2	2	3	3
4	*Labridae* (wrasse)	9.90	3	1	4	3
4	*Gobiidae* (gobies)	9.90	3	3	3	3
4	*Blennidae* (blennies)	2.24	3	1	3	2
4	*Pholis gunnellus* (butterfish)	8.31	1	2	3	2
4	*Cottidae* (sea scorpion)	7.03	3	2	3	3
4	*Spinachia spinachia* (fifteen-spined stickleback)	2.56	2	2	2	3
4	*Gasterosteus aculeatus* (three-spined stickleback)	0.96	3	3	2	3
4	*Pleuronectidae* (flatfish)	1.92	4	2	3	2
4	*Rana temporaria* (common frog)	0.32	5	2	7	6
4	Unidentified *Avian* (bird)	0.32	11	4	7	6
4	*Crustacea* (crustacean)	14.06	6	3	7	6
4	*Mollusca* (mollusc)	4.47	9	4	7	6
5	*Anguilla anguilla* (European eel)	12.8	1	3	3	5
5	*Muglidae* (grey mullet)	11.5	3	3	2	2
5	*Soleidae* (flatfish)	7.7	4	2	3	3
5	*Gobiidae* (gobies)	6.2	3	3	3	3
5	*Labridae* (wrasse)	7.6	3	1	4	3
5	*Blennidae spp* (blennies)	5.2	3	3	3	2

5	*Gadidae* (rocklings)	1.4	2	2	3	3
5	*Atherina* spp (sand smelt)	0.5	2	2	5	3
5	*Squalius pyrenaicus* (chub)	1.1	3	1	2	3
5	*Cobitis paludica* (loach)	0.9	2	1	2	1
5	*Crustacea* (crustacean)	30	6	3	7	6
5	*Procambrus clarkii* (red swamp crayfish)	22.8	6	1	1	3
5	Marine crab	2.1	6	1	1	3
5	Small crustaceans	5.1	6	3	7	6
5	Unidentified *Amphibia* (amphibian)	6.5	5	2	7	3
5	Unidentified *Reptilia* (reptile)	1.8	10	1	7	6
5	Unidentified *Insecta* (insect)	2.8	7	4	7	6
5	Unidentified *Avian* (bird)	0	11	4	7	6
6	*Scophthalamus rhombus* (brill)	0.84	4	1	3	4
6	*Cottus gobio* (bullhead)	2.10	3	2	3	2
6	*Squalius* spp (chub)	0.42	3	2	2	4
6	*Abramis brama* (common bream)	0.21	3	2	2	5
6	*Leuciscus leuciscus* (dace)	0.42	3	2	2	2
6	*Callionymus lyra* (dragonet)	0.42	2	1	3	3
6	*Anguilla anguilla* (European eel)	24.53	1	3	3	5
6	*Spinachia spinachia* (fifteen-spined stickleback)	2.10	2	2	2	3
6	*Platichthys flesus* (flounder)	2.31	4	3	2	2
6	*Gobbidae* (gobies)	7.97	3	3	3	3
6	*Labridae* (wrasse)	0.21	3	1	4	3
6	*Phoxinus phoxinus* (minnow)	1.05	3	2	3	3
6	*Perca fluviatilis* (European perch)	0.21	3	2	3	4
6	*Pleuronectes platessa* (plaice)	4.40	4	2	3	2
6	*Rutilus rutilus* (roach)	0.42	3	2	2	2
6	*Scardinius erythropthalmus* (rudd)	0.42	3	2	2	2
6	*Salmo salar* (Atlantic salmon)	0.42	3	3	2	5
6	*Salmonidae* (salmonids)	0.63	3	3	2	5
6	*Solea solea* (sole)	0.21	4	2	3	3
6	*Barbatula barbatula* (stone loach)	1.05	3	1	3	3
6	*Tinca tinca* (tench)	0.21	3	2	3	2
6	*Gasterosteus aculeatus* (three-spined stickleback)	19.71	3	3	2	3
6	*Cyprinidae* (carp/minnow)	7.55	3	2	3	3

6	Unidentified flatfish	5.24	4	3	7	6
6	*Crustacea* (crustacean spp)	0.21	6	3	7	6
6	*Rana temporaria* (common frog)	0.00	5	2	7	3
6	*Tritus spp* (newts)	0.00	5	2	7	3
6	Unidentifed *Anuran* (amphibian spp)	1.89	5	2	7	3
6	*Sorex Araneus* (common shrew)	0.21	8	1	7	3
6	Unidentified *Mammalian* (mammal)	0.21	8	1	7	6
6	Unidentified *Avian* (bird)	1.26	11	4	7	6
7	*Cyprinidae* (carp/minnow)	2.96	3	2	3	3
7	*Gasterosteidae* (sticklebacks)	7.51	3	3	2	3
7	*Percidae* (perch)	2.40	3	2	3	4
7	*Anguillidae* (European eel)	13.69	1	3	3	5
7	*Cobitidae* (loaches)	0.19	3	1	3	1
7	*Cottidae* (bullhead)	27.38	3	2	3	2
7	*Salmonidae* (salmonids)	0.75	3	3	2	5
7	*Gobiidae* (gobies)	29.61	3	3	3	3
7	*Soleidae* (flatfish)	13.29	4	2	3	3
7	*Scophthalmidae* (flatfish)	0.13	4	1	3	4
7	*Pleuronectidae* (flatfish)	0.65	4	2	3	2
7	*Blenniidae* (blennies)	0.02	3	1	3	2
7	*Esocidae* (pike)	0.06	2	2	5	5
7	*Labridae* (wrasse)	0.25	3	1	4	3
7	*Crustacea* (crustacean)	0.56	6	3	7	6
7	*Insecta* (insect)	0.15	7	4	7	6
7	*Amphibia* (amphibian)	0.19	5	2	7	3
7	*Mammalia* (mammal)	0.04	8	1	7	6
7	*Mollusca* (mollusc)	0.17	9	3	7	6

11.4 Appendix D

Table D1. Prey matrix with mean R.F.O (%) and ± standard error for each prey species/group for all studies combined and the chosen prey traits for each prey species/group; body form, ecosystem type, habitat classification and prey type.

Prey species/group	Mean R.F.O (%) (± 0.28)	Body form	Ecosystem type	Habitat classification	Prey type
Abramis brama (common bream)	0.029	fusiform	FW/B	benthopelagic	5
Anguilla anguilla (eel)	12.983	anguilliform	M/B/FW	demersal	5
Atherina spp (sand smelt)	0.071	elongated	M/B	pelagic	3
Barbatula barbatula (stone loach)	0.143	fusiform	FW	demersal	3
Bufo bufo (common toad)	0.000	amphibian	FW/T	other	3
Callionymus lyra (dragonet)	0.073	elongated	M	demersal	3
Cancer pagurus (edible crab)	0.249	crustacean	M	other	3
Carcinus maenas (common shore crab)	2.151	crustacean	M/B	other	2
Chirolophis ascanii (Yarrell's blenny)	0.047	elongated	M	benthopelagic	3
Ciliata mustela (five-bearded rockling)	5.591	elongated	M	demersal	2
Ciliata septentrionalis (northern rockling)	0.016	elongated	M/B	demersal	3
Cobitis paludica (loach)	0.156	elongated	FW	benthopelagic	1
Conger conger (conga eel)	0.800	anguilliform	M	demersal	5
Cottidae (sea scorpion)	2.347	fusiform	M/B	demersal	2
Cottus gobio (bullhead)	4.554	fusiform	FW/B	demersal	2
Crenilabrus melops (corkwing wrasse)	0.677	fusiform	M	reef-associated	3
Ctenolabrus rupestris (goldsinny wrasse)	0.140	fusiform	M	reef-associated	3
Leuciscus leuciscus (dace)	0.057	fusiform	FW/B	benthopelagic	2
Enchelyopus cimbrius (four-bearded rockling)	0.943	elongated	M	demersal	3
Esox lucius (pike)	0.037	elongated	FW/B	pelagic	5

Gadus morhua (cod)	1.400	fusiform	M/B	benthopelagic	5
Gaidropsarus mediterraneus (shore rockling)	0.430	elongated	M/B	demersal	4
Gasterosteus aculeatus (three-spined stickleback)	5.181	fusiform	M/FW/B	benthopelagic	3
Gobius paganellus (rock goby)	0.343	fusiform	M/FW/B	demersal	3
Lepadogaster lepadogaster (shore's clingfish)	0.016	elongated	M	demersal	3
Limanda limanda (dab)	0.174	short and/ or deep	M	demersal	4
Liparis montagui (Montagu's sea snail)	0.156	elongated	M	demersal	3
Lipophrys pholis (shanny)	0.031	fusiform	M	demersal	2
Muglidae (grey mullet)	1.643	fusiform	M/FW/B	benthopelagic	2
Myoxocephalus scorpius (bullhead)	0.856	fusiform	M/B	demersal	4
Nerophis lumbriciformis (worm pipefish)	0.016	anguilliform	M	demersal	3
Paracentrotus lividus (sea urchin)	0.514	echinoderm	M	benthic	1
Perca fluviatilis (european perch)	0.371	fusiform	FW/B	demersal	4
Pholis gunnellus (butterfish)	3.244	anguilliform	M/B	demersal	2
Phoxinus phoxinus (minnow)	0.171	fusiform	FW/B	demersal	3
Platichthys flesus (flounder)	0.529	short and/ or deep	M/FW/B	benthopelagic	2
Pleuronectes platessa (plaice)	0.700	short and/ or deep	M/B	demersal	2
Pollachius pollachius (pollack)	0.996	fusiform	M	benthopelagic	5
Pollachius virens (saithe)	0.513	fusiform	M	demersal	5
Procambrus clarkii (red swamp crayfish)	3.257	crustacean	FW	benthic	3
Rana temporaria (common frog)	0.046	amphibian	FW/T	other	3
Rutilus rutilus (roach)	0.057	fusiform	FW/B	benthopelagic	2
Salmo trutta (sea trout)	0.609	fusiform	M/FW/B	pelagic-neritic	5
Salmo salar (Atlantic salmon)	0.057	fusiform	M/FW/B	benthopelagic	5
Scardinius erythropthalmus (rudd)	0.057	fusiform	FW/B	benthopelagic	2

Scophthalamus rhombus (brill)	0.176	short and/or deep	M	demersal	4
Solea solea (sole)	3.741	short and/ or deep	M/B	demersal	3
Sorex Araneus (common shrew)	0.029	mammal	T	other	3
Spinachia spinachia (fifteen-spined stickleback)	3.886	elongated	M/B	benthopelagic	3
Sprattus sprattus (sprat)	0.057	fusiform	M/B	pelagic-neritic	2
Squalius cephalus (chub)	0.343	fusiform	FW/B	benthopelagic	4
Squalius pyrenaicus (chub)	0.214	fusiform	FW	benthopelagic	3
Syngnathus acus (great pipefish)	0.287	anguilliform	M	demersal	3
Taurulus bubalis (sea scorpion)	0.669	fusiform	M/B	demersal	3
Tinca tinca (tench)	0.029	fusiform	FW/B	demersal	2
Trisopterus minutus (poor cod)	0.031	fusiform	M	benthopelagic	5
Tritus spp (newts)	0.229	amphibian	FW/T	other	3
Zeugopterus punctatus (topknot)	0.016	short and/or deep	M	demersal	4
Zoarces viviparpus (eelpout)	0.129	elongated	M/B	demersal	3
Unidentified *Avian* (bird)	0.717	avian	M/B/FW	other	6
Unidentified *Mammalian* (mammal)	0.134	mammalian	T	other	6
Unidentified *Cyprinid* (carp/minnow)	2.309	fusiform	FW/B	demersal	3
Unidentified *Amphibia* (amphibian)	1.499	amphibian	FW/T	other	3
Unidentified *Crustacea* (crustacean)	2.651	crustacean	M/B/FW	other	6
Unidentified M*ollusca* (mollusc)	2.049	mollusc	NA	other	6
Unidentified *Insecta* (insect)	0.421	insect	NA	other	6
Unidentified *Labridae* (wrasse)	6.593	fusiform	M	reef-associated	3
Unidentified *Gobiidae* (gobies)	9.701	fusiform	M/FW/B	demersal	3
Unidentified *Blennidae* (blennies)	3.151	fusiform	M	demersal	2
Unidentified *Gadidae* (cod)	6.613	elongated	M/B	demersal	3

Unidentified *Heterostomata* (flatfish)	1.729	short and/ or deep	M	demersal	2
Unidentified *Pleuronectidae* (flatfish)	0.367	short and/or deep	M/B	demersal	2

11.5 Appendix E

Count of each prey trait and total number of prey species/groups within each study (1-7)

Table E1. Count of each body form type and total number of prey species/groups within each study (1-7)

Study	anguilliform	elongated	fusiform	short and/or deep	amphibian	crustacean	insect	mammal	mollusc	reptile	avian	TOTAL
1	2	6	9	5	2	1	0	1	0	0	1	**27**
2	5	8	11	2	0	2	0	0	0	0	0	**28**
3	3	1	6	1	0	1	0	0	2	0	1	**15**
4	4	2	5	1	1	1	0	0	1	0	1	**16**
5	1	3	5	1	1	4	1	0	0	1	1	**18**
6	1	2	16	5	3	1	0	2	0	0	1	**31**
7	1	1	9	3	1	1	1	1	1	0	0	**19**
TOTAL	**17**	**23**	**61**	**18**	**8**	**11**	**2**	**4**	**4**	**1**	**5**	**154**

Table E2. Count of each number of ecosystem interfaces and total number of prey species/groups within each study (1-7)

Study	1	2	3	4	TOTAL
1	9	11	6	1	**27**
2	17	8	3	0	**28**
3	5	4	5	1	**15**
4	3	6	5	2	**16**
5	6	4	6	2	**18**
6	6	16	8	1	**31**
7	5	7	6	1	**19**
TOTAL	**51**	**56**	**39**	**8**	**154**

Table E3. Count of each habitat classification and total number of prey species/groups within each study (1-7)

Study	benthic	benthopelagic	demersal	reef-associated	pelagic	pelagic-neritic	other	TOTAL
1	1	6	14	1	1	0	4	**27**
2	0	5	18	2	0	1	2	**28**
3	1	2	7	1	0	1	3	**15**
4	0	2	9	1	0	0	4	**16**
5	2	3	5	1	1	0	6	**18**
6	0	10	12	1	0	0	8	**31**
7	0	2	10	1	1	0	5	**19**
TOTAL	**4**	**30**	**75**	**8**	**3**	**2**	**32**	**154**

Table E4. Count of each prey type and total number of prey species/groups within each study (JK1-7)

Study	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	TOTAL
1	0	5	14	3	3	2	**27**
2	0	4	13	4	7	0	**28**
3	1	4	5	0	2	3	**15**
4	0	3	7	0	2	4	**16**
5	1	2	9	0	1	5	**18**
6	0	7	13	3	4	4	**31**
7	1	3	6	2	3	4	**19**
TOTAL	**3**	**28**	**67**	**12**	**22**	**22**	**154**

11.5 Appendix F

Overall proportion of each prey trait for the combined seven studies.

Table F1. Overall proportion (%) of each body form from the combined seven studies

Body form	Overall Proportion (%)
Anguilliform	11.0
Elongated	14.9
Fusiform	39.6
Short and/or deep	11.7
Amphibian	5.2
Crustacean	7.1
Insect	1.3
Mammal	2.6
Mollusc	2.6
Reptile	0.6

Table F2. Overall proportion (%) of each ecosystem type across the seven studies

Ecosystem type	Overall Proportion (%)
1	33.1
2	36.4
3	25.3
4	5.2

Table F3. Overall proportion (%) of each habitat classification across the seven studies

Habitat classification	Overall Proportion (%)
Benthic	2.6
Benthopelagic	19.5
Demersal	48.7
Reef-associated	5.2
Pelagic	1.9
Pelagic-neritic	1.3
Other	20.8

Table F4. Overall proportion (%) of each prey type across the seven studies

Prey type	Overall Proportion (%)
Type 1	1.9
Type 2	18.2
Type 3	43.5
Type 4	7.8
Type 5	14.3
Type 6	14.3

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