Diet of coastal foraging Eurasian otters (L.) in Pembrokeshire south-west Wales

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Abstract The importance of the marine environment to Eurasian otters is currently poorly understood. Wales is one of the few countries where coastal activity has been recorded and an increase in marine otter sightings could indicate remarkable developments within Welsh populations. The trophic niche of coastal otter populations around Pembrokeshire was investigated over a 12-month period. Marine activity was more widespread than previously thought and marine prey formed the largest component of otter diet, although, otters also consumed freshwater and terrestrial prey throughout the year. Otter diet was very diverse compared to other European coastal populations and a spring contraction in trophic niche width coincided with the estimated timing of breeding activity. Seasonal variation in prey composition was predominantly due to differences in the consumption of alternate prey types. In areas where wetlands are fragmented and populations of freshwater fish are declining, the marine environment may become an increasingly important habitat for otters. It is necessary to define the historical importance of coastal populations to otter conservation. Coastal areas are often subject to pressure from human activities, so the impact of disturbance needs to be assessed. Importantly, there is no verified otter survey method for coastal areas, so the use of marine habitat is likely to be underestimated.

Keywords Eurasian otter · Diet · Coastal · Marine · Foraging · Carnivore

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Introduction

The Eurasian otter *Lutra lutra* (hereafter referred to as the otter) is a semi-aquatic carnivore belonging to the Mustelid family. In many areas of Europe and Asia, otters remain a species of conservation concern following widespread population declines during the 20th century (Ruiz-Olmo et al. 2008). The otter is one of only a few Eurasian carnivores that has evolved the ability to actively forage both in water and on land (Oliveira et al. 2008), and is highly capable of hunting in both freshwater (Carss et al. 1990; Copp and Roche 2003) and marine (Kruuk and Moorhouse 1990; Heggberget 1993) environments. A considerable amount of research has been undertaken on otter diet in freshwater habitats across Europe. In contrast, only a few studies have examined otter diet and behaviour in coastal regions. Research carried out in Scotland since the 1970s elucidated a number of fascinating aspects of the otter's ability to forage in marine waters (e.g. Watson 1978; Kruuk et al. 1987; Kruuk and Moorhouse 1990; Watt 1995), whilst researchers in Norway (Heggberget 1993), Portugal (Beja

1991), Eire (Kingston et al. 1999) and Spain (Clavero et al. 2004) have described various aspects of otter trophic ecology in coastal areas. Very little information is available from coastal otter populations in other areas (Britton et al. 2006; Liles 2003a); consequently, the prevalence of marine activity within this species' European range is currently poorly defined.

Further investigation is required to determine the significance of coastal habitats to the ecology and conservation of otter populations. Moreover, there is little published information on UK otter populations outside of Scotland, despite declines being more severe in Wales (Jones and Jones 2004) and England (Crawford 2003). The coastline of South Wales provides a wealth of opportunities for otters, with large sections of remote or inaccessible coastline that provide potential foraging, resting and breeding sites (Liles 2003a). It is known that otters are widely distributed in Pembrokeshire (Jones and Jones 2004) and preliminary surveys have indicated that otters are utilising coastal areas for foraging and breeding at some locations (Liles 2003a). Accordingly, Pembrokeshire may represent one of the most important areas for otters in Wales, but very little is known about the ecology of the otter population in this region. The Pembrokeshire coast is subject to concurrent conservation and human economic interest. The presence of oil refineries in Milford Haven means that there is also a risk of crude oil spillage, whilst the Pembrokeshire coast has also been identified as a potential site for renewable energy development (Project Management Support Services 2006). Thus, the extent to which otters use marine habitats in Pembrokeshire needs to be determined, so that potential conflict with human industrial and recreational activities can be assessed and incorporated into conservation management plans.

Trophic niche describes the way an organism utilises food resources within its environment (Begon et al. 1996). It is important to study carnivore trophic niches as this determines the fitness of populations and their role in the trophic interactions of food webs (Miller et al. 2001). Dietary data is typically reported using parameters such as niche width, which describes the diversity of prey taken (Sargeant 2007). This study describes the trophic niche of otters inhabiting coastal areas of Pembrokeshire over a 12-month period, addressing three specific aims (a) to determine the extent to which otter populations in Pembrokeshire are using the marine environment and (b) to record the temporal variation in the dietary composition and population total trophic niche width (TNW) of costal otters in Pembrokeshire. (c) Calculate the TNW using data from previous studies conducted in coastal areas of Europe (see Appendix A for a full list of sources included) to provide an overview of the degree of dietary generalisation or specialisation in coastal foraging otter populations.

Materials and methods

Study area

The Pembrokeshire Coast National Park covers 416 km of coastline and contains the Pembrokeshire Marine Special Area of Conservation (SAC), one of the largest European Marine Sites in the UK. This encompasses several Special Protection Areas (SPA), Wales' only Marine Nature Reserve and many Sites of Special Scientific Interest. Two of the sampling sites fell within the St David's Peninsula Coast SPA. The Pembrokeshire coastline is heterogeneous including rocky shores, sandy shores, sub-tidal reefs, mudflats, estuaries, lagoons and salt marsh. In places, there are steep cliffs and coastal caves. Many rivers and small streams discharge into the sea along the width of the Pembrokeshire coast, most of which are less than 2 km long (Liles 2003a). The Pembrokeshire coast also contains number of large shallow inlets and bays which slope out gradually from the coast providing a shallow foraging habitat for otters. A number of sampling sites were located within the Milford Haven waterway (Fig. 1), which is also a part of the Pembrokeshire Marine SAC. Pembrokeshire is picturesque and a popular tourist destination, whilst Milford Haven is a busy port used for both industry and leisure purposes.

Sprint collection and dietary analysis

Sprint collections were undertaken by a team of volunteers co-ordinated by the Pembrokeshire Marine SAC officer and Pembrokeshire Biodiversity Partnership Implementation Officer. The aim was to visit a total of 21 confirmed spranting sites (Fig. 1) every month between July 2007 and June 2008. Volunteers were trained by the Pembrokeshire Marine SAC Relevant Authorities Group and Pembrokeshire Biodiversity Partnership to help them identify and collect sprints. During each monthly visit, the volunteers were instructed to search the immediate vicinity of the site and collect up to three sprints for analysis. A three-sprint limit was set as this enabled a year-long study to be undertaken with the logistical and financial resources available. In some cases, this meant that only a sub-set of the available sprints were analysed; however, in many cases, less than three sprints were present. Sprints were placed into individual, sealed and labelled bags and sent to Swansea University where they were stored at −17°C until dietary analysis was undertaken. The criteria for samples to be included in the dietary analysis were that each bag must contain a single sprint. All sprint bags returned were checked to confirm that they contained a single otter sprint. In the event of rejected samples, the reason was recorded. Red fox *Vulpes vulpes*, American mink *Mustela vison* and European polecat

Fig. 1 The Pembrokeshire coast with *stars* indicating sampling sites and *circles* indicating towns (produced using MapInfo Professional© Pitney Bowes Software Inc New York USA) using an OS-base map obtained from EDINA©
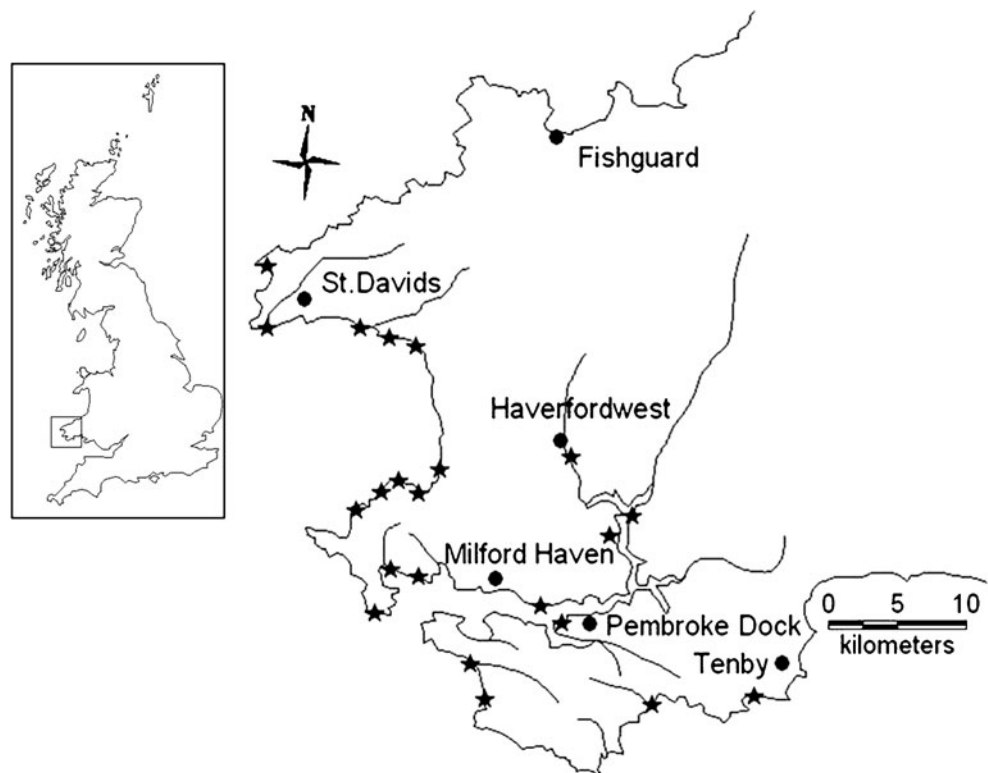
Mustela putorius are present in Pembrokeshire (NBN 2010) and may use coastal areas. Scats from these species are relatively easy to distinguish from otter spraints and a recent molecular study verified the primary author's ability to accurately identify otter spraints (Forman et al., unpublished data).

Otter diet was determined through the identification of hard prey remains in spraints. Prior to analysis, spraints were soaked individually in 250-ml beakers containing a saturated solution of biological detergent for a period of at least 24 h. The spraints were then rinsed through a 420-μm sieve and turned out onto a sheet of paper roll, with care taken to ensure that all remains were removed from the sieve. The spraint remains were left to dry for a period of at least 24 h. All spraints were analysed using an Olympus SZ40© dissection microscope (Olympus UK Ltd, Watford). Prey remains were indentified using published keys (Day 1966; Watson 1978; Miranda and Escala 2002; Conroy et al. 2005) and a reference collection containing vertebrae and mouth parts of 39 fish species, three amphibian species and two reptile species. Where possible, remains were identified to family or species level.

The results of the dietary analysis were expressed using the Relative Frequency of Occurrence (RFO%) method described by Watson (1978) as

$$\text{RFO\%} = \frac{Number\ of\ occurrences\ of\ a\ prey\ category}{Sum\ of\ occurrences\ of\ all\ prey\ categories} \times 100$$

The limitations of using spraint analysis to study diet are well documented (Carss and Elston 1996; Carss and Parkinson 1996). The relative frequency of occurrence method has been shown to produce a relatively accurate interpretation of diet by feeding trials on captive otters (Erlinge 1968; Carss and Parkinson 1996; Jacobsen and Hansen 1996). In order to determine the extent of marine foraging the proportions of marine fish, freshwater fish and non-fish prey in otter diet were assessed. Fish prey was classified as marine or freshwater using the classifications of Wheeler (1969). A full year of spraints was only available from one site, severely reducing the power of statistical analysis of spatial trends in diet. Consequently, a spatial analysis was not undertaken.

Data analysis

All analyses were conducted using SPSS 13.0 (SPSS Inc, Chicago, USA). Prior to analysis, the distribution of all data were assessed using a Kolmogorov–Smirnov test and the equality of variance tested using a Levene's test. Significance (p) was set at 0.05. Population TNW was calculated using the Shannon–Wiener standardised measure (H'), described by Krebs (1989) as

$$H' = \Sigma Pj \log ePj$$

Pj=Proportion of individuals found in or using a resource states

Variation in proportion of marine and freshwater prey and seasonal variation in TNW was investigated using one-way analysis of variance (ANOVA). Seasonal variation in dietary composition was investigated using Renkonen's index of percentage similarity, described by Krebs (1989) as

$$P = \%\Sigma minimum(P_{1i}P_{2i})$$

P=Percentage of similarity between sample 1 and 2
P_{1i}=Percentage of species in community 1 sample
P_{2i}=Percentage of species in community 2 sample

The top ten prey types were determined using the overall RFO% values. To reduce discrepancies caused by using many different levels of taxonomic classification fish were grouped to family level, with the exception of flatfish which is routinely grouped as an order in otter dietary studies (Watson 1978; Kruuk and Moorhouse 1990; Watt 1995; Kingston et al. 1999). Non-fish prey were organised to class level, as is normal practice in otter dietary studies. The top ten prey types were then used to investigate seasonal variation in diet composition through one-way ANOVA. Where significant results were detected, a least significant difference post hoc test was applied to investigate which pairings differed significantly.

Results

Distribution and habitat use of coastal otters in Pembrokeshire

Otter spraints were successfully collected at all study sites and there was evidence that use of marine, freshwater and terrestrial habitats was widespread. Non-fish prey was recorded at 66.7% (14/21) of sites, whilst both marine and freshwater prey was recorded in spraints at 76.2% (16/21) of sites, including sites situated well within the estuary. Interestingly, spraints containing only prey originating from marine habitats were recorded at just 14.3% (3/21) of sites. Two sites returned no samples that passed the inclusion criteria.

Trophic niche and temporal variation in diet

In total, 232 spraints were collected of which 180 passed the criteria to be included in the dietary analysis. The most frequent reason for rejection was the presence of multiple spraints in one bag. There were 578 prey occurrences and 30 different prey types were identified. Fish constituted 85.3% of the overall RFO% (Table 1). Sticklebacks (12.8%), gobies (12.5%), eels (10.9%) and blennies (10.4%) were the most frequent prey items overall. Crustaceans (6.6%),

Table 1 Otter diet on the Pembrokeshire coast July 2007–June 2008 expressed as relative frequency of occurrence (RFO%)

Prey type	Taxonomic name	RFO%
Fish		85.3
Freshwater fish		29.3
Bullhead	*Cottis gobio*	2.4
Chub	*Leuciscus cephalus*	0.5
European eel	*Anguilla anguilla*	10.9
Minnow	*Phoxinus phoxinus*	0.2
Pike	*Esox lucius*	0.2
Salmonidae	Salmonidae sp	2.8
Three-spined stickleback	*Gasterosteus aculeatus*	6.6
Unidentified Cyprinidae	Cyprinidae sp	5.7
Marine fish		55.7
Blennies	*Blennidae sp*	10.4
Brill	*Scophthalmus rhombus*	0.3
Dab	*Limanda limanda*	1
Eelpout	*Zoarcidae*	0.9
Fifteen spined stickleback	*Spinachia spinachia*	6.2
Five-bearded rockling	*Gaidropsarus vulgaris*	1.9
Flounder	*Platichthys flesus*	1.4
Four-bearded rockling	*Enchelyopus cimbrius*	6.6
Gobies	*Gobiidae sp*	12.5
Pipefish	*Sygnathidae*	1.9
Plaice	*Pleuronectes platessa*	0.5
Wrasse	*Labridae sp*	4.3
Unidentified Cottidae	Cottidae sp	2.8
Unidentified flatfish	Hetrosomata sp	5
Unidentified fish		0.3
Insects		0.9
Coleoptera	*Dysticus sp*	0.7
Odonata	*Ashena sp*	0.2
Crustacean	*Crustacean*	6.3
Amphibian		3.5
Anuran sp	*Rana temporaria, Bufo bufo*	1.9
Newts	*Triturus sp*	1.6
Mammalian		0.7
Avian		3.3
Total		100

Number of spraints=180

amphibians (3.5%) and birds (3.3%) were the most frequent non-fish prey items with insects and mammals occurring at relatively low frequencies. Crustacean remains were mostly *Carcinus sp*, the majority of bird remains were from the Rallidae family and the mammalian remains were predominantly rabbit. A very small number of fish remains were not identifiable through either the reference collection or the published keys, which suggests they are potentially previously unrecorded otter prey items.

Marine fish constituted the largest component of otter diet throughout the year (Fig. 2). There was no significant seasonal variation in the proportion of marine ($F_{3, 10}=0.3$, $p=0.8$) or freshwater fish ($F_{3, 10}=0.4$, $p=0.3$) in otter diet.

There was variation in the composition of otter diet over the study period (Table 2). However, dietary composition in spring was relatively similar to all other seasons, with a mean similarity of 88% (±6 SE). The mean level of similarity between all seasons was 72% (±5 SE). Dietary composition in summer 2008 had a lower similarity with all other seasons. There was also a low level of similarity in the composition of diet between winter and summer. The highest similarity in diet was between winter 2007–2008 and spring 2008, when diet was dominated by gobies (winter RFO=13.1%, spring RFO=18.9%) and amphibians (winter RFO=6.93%, spring RFO=9.43%). There was also a high degree of similarity between autumn 2007 and spring 2008. The 10 most important prey types were determined using the overall RFO% values (Table 3). This excluded 20 prey types, with overall RFO values <3%. One-way ANOVA showed that the occurrence of eels varied significantly between seasons ($F_{3, 10}=9.08$, $p=0.006$) and post hoc tests indicated that eel RFO% was significantly lower in winter and spring than in summer ($p<0.05$). No other major prey type displayed significant seasonal variation in occurrence.

Population total niche width

The mean population TNW calculated for otter diet at Pembrokeshire coastal sites was 0.88 (±0.2 SE) and trophic niche richness was 20.2 (±2.3 SE; Table 4). One-way

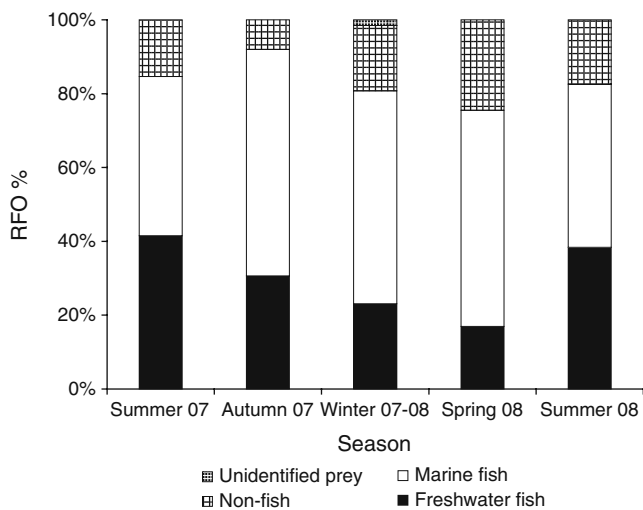
Fig. 2 Seasonal variation in the relative frequency of occurrence (RFO%) of freshwater fish marine fish non-fish and unidentified prey in otter sprints analysed from Pembrokeshire between July 2007– June 2008 (summer 2007 $n=23$, autumn 2007 $n=35$, winter 2007– 2008 $n=53$, spring 2008 $n=40$, summer 2008 $n=7$)

ANOVA demonstrated significant seasonal variation in trophic niche width ($F_{3, 10}=7.1$, $p=0.01$) and post hoc tests indicated that niche width was narrower in spring than in all other seasons ($p<0.05$). Comparing the TNW value obtained by this study to those from other locations across the otter's range it can be seen that diet on the Pembrokeshire coast is particularly diverse (Table 5).

Discussion

Use of the coastal habitats by otter populations

This study confirms that use of the marine environment is widespread in coastal otter populations across Pembrokeshire, with a diet that contains a larger proportion of marine prey than recorded during a preliminary study (Liles 2003a). Marine activity has recently been recorded in otters inhabiting other coastal areas of Wales (Parry and Forman, unpublished data) and England (Jaggs 2009). Whether this represents a current trend for increased use of the marine environment by otters inhabiting coastal areas of the UK is unclear. We propose two possible explanations for the widespread marine activity of otters in Pembrokeshire, and the increasing number of records of marine activity in Wales. Firstly, there is historical evidence that prior to the declines of the twentieth century otters were regularly foraging in the sea off the coastline of Wales (Dillwyn 1848). However, a survey of the Welsh coastal sites undertaken in the 1980s found no evidence of coastal otter activity (Andrew Crawford personal communication). Therefore, as otter populations in Wales recover (Jones and Jones 2004) use of the marine environment may be increasing due to density-dependent effects. Otters are territorial (Kruuk and Moorhouse 1991) and individuals may be displaced into coastal areas when there are high population densities in inland freshwater systems. The last National Otter Survey of Wales returned 97% (64/66) of sites in Pembrokeshire as positive (Jones and Jones 2004), which suggests that there is potential for intraspecific competition for inland territories. However, this study demonstrates that otters in Pembrokeshire are using marine, freshwater and terrestrial habitats, indicating that otters at coastal sites do not appear to be restricted from accessing inland habitats.

An alternative explanation is that the marine environment has always been a component of the habitat niche of coastal otter populations in the UK, but marine activity has been under-recorded in the past due to difficulties in surveying such terrain. The standardised UK otter survey technique is more appropriately designed for linear riparian systems (Mason and MacDonald 1986), and unfortunately no validated method for monitoring otters in coastal areas exists. Detection probabilities are likely to be lower in

Table 2 Renkonen's Percentage similarity index values, between seasons, in otter diet on Pembrokeshire 2007–2008

Renkonen's Similarity%	Summer 2007	Autumn 2007	Winter 2007–2008	Spring 2008
Summer 2007	–	–	–	–
Autumn 2007	72.0	–	–	–
Winter 2007–2008	54.6	73.0	–	–
Spring 2008	81.8	82.4	100	–
Summer 2008	50.9	64.7	62.3	80.3

coastal areas than in riparian systems, due to the influence of tides that frequently wash away otter signs (Kruuk 1992). Given the increased awareness of otter activity in many coastal areas in Europe (Beja 1991; Heggberget 1993; Kingston et al. 1999; Clavero et al. 2004), the development of a robust otter coastal survey monitoring tool would be timely and of significant utility.

The diet and trophic niche of otters inhabiting coastal areas

Marine fish formed the largest proportion of otter diet throughout the year, clearly indicating that marine prey are an important resource for otters inhabiting coastal areas of Pembrokeshire. In contrast to the study of Clavero et al. (2006), freshwater and terrestrial prey was frequently recorded in spraints collected throughout the year on both rocky and sandy shores. Slow swimming, demersal fish were the most frequent marine and freshwater prey items, indicating that otters foraging on the Pembrokeshire coast caught prey with similar life histories in different habitats. Otters may frequently forage at the demersal zone as it represents an edge, a habitat feature commonly used by foraging carnivores (Andren and Angelstam 1988).

The data indicates that some marine prey items occurred more frequently in otter diet during spring, which could reflect increased use of marine habitats. Gobies, flatfish, blennies, crabs and amphibians, were all frequent prey taken during this most trophically challenging period (Kruuk 2006). Amphibians are relatively plentiful during winter and spring due to this group's tendency to aggregate in large numbers to spawn (Duellman and Trueb 1986); consequently, they often form an important component of otter diet during this period (Weber 1990). It is worthy of note that coastal foraging otters follow this widespread trend in otter ecology. It is now common knowledge that there are significant pressures affecting amphibian populations throughout the world (IUCN 2008). This prey group clearly forms an important component of otter diet at a critical time of year in many areas (the commencement of breeding; Kruuk et al. 1987). The impact of possible widespread amphibian declines on otter reproductive success, and wider trophic cascade effects (Dunne et al. 2002) clearly warrants further urgent investigation.

Otters are believed to be vulnerable during winter, largely due to decreased prey availability and the increased metabolic cost of foraging at lower ambient temperatures (Kruuk et al. 1987; Kruuk and Balharry 1990). This could lead to otters increasing their range, foraging in different habitats or taking alternative prey (Beja 1997; Roche 2001). It is possible that otters switched prey in freshwater areas during winter, in response to the reduced availability of eels. The Renkonen's index values indicated considerable

Table 3 Rank importance and seasonal variation in the relative frequency of occurrence (RFO%) of the top ten prey types in otter spraints analysed from Pembrokeshire between July 2007–June 2008

Prey Category	Summer 2007	Autumn 2007	Winter 2007–2008	Spring 2008	Summer 2008	Overall rank
Angullidae	22.8	11.7	3.1	5.7	14.3	3
Blennidae	14.0	9.5	7.7	13.2	4.8	4
Crustacean	8.8	2.9	6.2	11.3	14.3	= 7
Cottidae	5.3	6.6	5.4	3.8	0	9
Cyprinidae	7.1	7.3	8.5	5.7	0	= 7
Gadidae	5.3	13.1	6.9	7.6	9.5	5
Gasterosteidae	7.0	12.4	14.6	5.7	14.3	1
Gobiidae	14.0	12.4	13.1	18.9	9.5	2
Labridae	3.5	1.5	4.6	5.7	4.8	10
Pleuronectiformes	5.3	11.00	9.2	15.7	9.5	6

Summer 2007 $n=23$, autumn 2007 $n=35$, winter 2007–2008 $n=53$, spring 2008 $n=40$, summer 2008 $n=7$

Table 4 Seasonal variation in trophic niche richness and total niche width values of the coastal otter population in Pembrokeshire 2007–2008

Season	Number of spraints	Niche richness	Total niche width Shannon–Wiener (H')
Summer 2007	23	22	0.95
Autumn 2007	35	26	0.90
Winter 2007–2008	54	23	0.91
Spring 2008	40	17	0.68
Summer 2008	7	13	0.96
Mean (± SE)	31.8±10.2	20.2±2.3	0.88±0.2

seasonal variation in dietary composition. The low sample size collected in summer 2008 probably contributed to the low level of dietary similarity between this period and other seasons in the study. However, there was a large amount of variation in dietary composition between other seasons as well, notably between summer 2007 and winter 2007–2008. Despites this, only one major prey type showed significant seasonal variation in occurrence in otter diet. Seasonal variations in carnivore diet are likely to reflect seasonal trends in prey availability. A winter decrease in eel predation has been recorded previously and is thought to be due to the over-wintering behaviour of eels reducing their availability to otters (Jenkins et al. 1979). The disparity in dietary composition between winter and summer demonstrates that the composition of otter diet on the Pembrokeshire coast varies seasonally, but the lack of variation in the most frequent prey types indicates that it is the composition of alternative prey that is subject to the most variation, which is a common feature of populations composed of individual specialists (Bolnick et al. 2007).

Table 5 Total niche width values for otter diet, calculated using data provided in selected coastal studies across their range

Study Location	Total niche width Shannon–Wiener (H')
Eire Murphy and Fairley 1985	0.84
Eire (Kingston et al. 1999)	0.73
Norway (Heggberget 1993)	0.78
Norway (Heggberget and Moseid 1994)	0.79
Pembrokeshire Wales	0.92
Portugal (Beja 1991)[a]	0.70
Portugal (Beja 1997)	0.69
Scotland (Watson 1978)	0.81
Scotland (Watt 1995)[a]	0.80
Scotland (Yoxon 1999)	0.76
Spain (Clavero et al. 2004)	0.76
Wales (Parry, unpublished)	0.69
Mean (±SE)	0.77±0.2

[a] Mean niche width value across all sites

The otters had a broad TNW (0.92), a feature of all the coastal otter populations included in the analysis (Table 5), indicating a broad trend for high trophic diversity in coastal otter populations (see also Jędrzejewska et al. 2001). It is interesting to note that the TNW of the Pembrokeshire population was the greatest of all the studies sampled. This can be explained by two factors. Firstly, in contrast to many previous studies of coastal otter populations (Watson 1978; Kruuk and Moorhouse 1990; Heggberget and Moseid 1994; Kingston et al. 1999), otters on the Pembrokeshire coast regularly foraged inland. Secondly, otter diet is thought to reflect the complexity of the surrounding environment (Clavero et al. 2004). The Pembrokeshire coastline is a heterogeneous network of habitats bordered by extensive riparian systems, providing a complex and diverse prey base. Trends in otter trophic diversity may differ between coastal and freshwater habitats due to differences in prey assemblages, particularly in the diversity of fish communities. As opportunistic foragers (Kruuk and Moorhouse 1990; Watt 1995), otters would be expected to have a broad trophic niche where there is a diverse prey base. This study demonstrates that otters living in coastal areas can potentially forage in marine, freshwater and terrestrial habitats, and as such have access to a higher diversity of prey than inland populations (Jędrzejewska et al. 2001). Trophic niche width is also very broad in another coastal foraging otter, the Sea Cat *Lutra feline* (Medina-Vogel et al. 2004), and this could be a common feature of semi-aquatic carnivores foraging at the freshwater/marine interface.

The broad overall TNW trophic niche width indicates a generalist foraging strategy on the Pembrokeshire coast. However, there was a significant contraction of niche width in spring, which suggests that otters are highly facultative foragers (Glasser 1984) adapting their strategy according to changes in their environment. The observed seasonal trend in TNW contrasts previous dietary studies of otters (Brzeziński et al. 2006; Prigioni et al. 2006a, b) and other carnivore species (Sinclair and Zeppelin 2002; Zalewski 2004; Rosalino et al. 2005), in which niche width undergoes a significant increase during winter. Trends in niche width are usually attributed to seasonal reductions in the availability of preferred prey, as foraging theory predicts

dietary diversification when preferred prey types are scare (MacArthur and Pianka 1966). There was no significant seasonal variation in the proportion of freshwater prey in otter diet; however, the diversity of freshwater prey may have decreased during spring due to the reduced consumption of eel. This could have contributed to the contraction in TNW during this period.

Conclusions and conservation management implications

This study demonstrates that use of the marine environment by otters in Pembrokeshire is more frequent and widespread than previously thought. The current and historical prevalence of marine activity in coastal otter populations may be underestimated, as population monitoring surveys usually target freshwater systems and survey techniques have not been developed for coastal areas. There is, therefore, a dearth of longitudinal data from coastal areas. Marine environments would not have escaped the impacts of chemical bioaccumulation, which are considered to be the principal factor behind otter population declines in the UK (Chanin and Jefferies 1978), but the impact is unlikely to have been as severe as in landlocked freshwater habitats. Coastlines could also function as corridors or routes of dispersal, aiding emigration to new freshwater or coastal systems. Determining the current and historical importance of marine habitats is important to elucidate the function of coastal otter populations as sources or sinks of recruitment at the meta-population scale. The marine environment provided the most important prey resources for coastal otter populations in this study, but the consumption of freshwater and terrestrial prey indicates that access to inland habitats by coastal otters is also required. Marine habitats may provide important prey resources, but inland areas provide access to freshwater crucial for drinking and washing (Kruuk 2006), and may contain more suitable breeding habitat (Beja 1996). Consequently, the conservation management of otters in coastal areas should ensure the protection of both marine and freshwater habitat. In particular, an emphasis on maintaining access between marine and freshwater habitats should be incorporated into management plans.

The impact of human disturbance on biodiversity is currently a priority area of research in ecology (Sutherland 2007). In areas such as Pembrokeshire, there is potential for human leisure and industrial activities to unknowingly cause detrimental disturbance to coastal otter populations. Fishing, water sports, boat trips and coasteering are increasingly popular in many coastal areas of the UK. This study illustrates that otter populations utilise coastal habitats in Pembrokeshire more frequently than previously thought. As coastal sites provide important foraging areas and possible breeding sites (Heggberget and Christensen

1994; Liles 2003b; 2009), the potential for disturbance by increased human access to remote coastal sites may be much greater than previously considered. There has certainly been an increase in the number of otter sightings over recent years throughout the study area, suggesting human–otter contact is more frequent. It may also be that otters can habituate to certain low level disturbance at some sites as a trade-off for utilising a profitable resource (Tüzün and Albayrak 2005). We suggest that the reality is likely to be a combination of the two factors, but research is required to quantify the impact, and if necessary to provide mitigation advice and solutions to conservation managers and statutory conservation bodies.

The trophic diversity of otters on the Pembrokeshire coast demonstrates a broad influence on prey communities. The otter's ability to forage on land and in water enables them to effectively exploit coastlines and estuaries. Many of the marine fish consumed in this study use estuaries and shallow coastal waters as nursery areas (Beck et al. 2001) and as such otters are potentially a key predator influencing their populations. Eels were an important prey resource in this study and widespread declines in eel populations (Feunteun 2002) may pose a significant evolutionary challenge to otters in the UK and Ireland, where they have historically been an important prey item (Carss 1995; Kingston et al. 1999). Amphibians are clearly an important food resource; this is of concern given amphibian population declines (IUCN 2008) and the fact that reliance on this vulnerable prey group commonly coincides with periods of otter breeding activity (Kruuk 2006). Loss of amphibians could lead to declines in otter population fitness and force switching to alternative prey items, resulting in trophic cascade effects in coastal and wetland ecosystems. Therefore, the relationship between amphibian prey and otter reproduction needs to be assessed. There is also increasing evidence of individual trophic partitioning within carnivore populations (Estes et al. 2003; Tinker et al. 2008), which has important consequences for conservation management, and therefore, should be investigated in otters.

Appendix A

Table 6 Studies included in the comparison of total niche width (TNE) of otter populations across Europe

Location	Total niche width Shannon-Wiener (H')	Source
Eire	0.84	Murphy and Fairley 1985
Eire	0.73	Kingston et al. 1999
Norway (Heggberget 1993)	0.78	Heggberget 1993
Norway (Heggberget and Moseid 1994)	0.79	Heggberget and Moseid 1994
Pembrokeshire Wales	0.92	Current study
Portugal	0.70	Beja 1991
Portugal	0.69	Beja 1997
Scotland	0.81	Watson 1978
Scotland	0.80	Watt 1995
Scotland	0.76	Yoxon 1999
Spain	0.76	Clavero et al. 2004
Wales	0.69	Parry *unpub*

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