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PRIMARY RESEARCH PAPER

Diet as a mechanism of coexistence between intertidal fish species of the U.K.

C. J. Barrett · M. L. Johnson · S. L. Hull

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Abstract While the syntopic nature of many intertidal fish communities suggest that resources such as food are shared, little has been done to assess the importance of diet on the coexistence of intertidal fish of the U.K. In this study, six intertidal fish species (shanny, *Lipophrys pholis,* Blenniidae; long-spined scorpion fish, *Taurulus bubalis,* Cottidae; two-spotted goby, *Gobiusculus flavescens,* Gobiidae; rock goby, *Gobius paganellus,* Gobiidae; plaice, *Pleuronectes platessa,* Pleuronectidae; butterfish, *Pholis gunnellus,* Pholidae) were collected from two sites along the east coast of England (Filey and Thornwick Bay) and two sites around the coast of the Isle of Anglesey, North Wales (Rhosneigr and Penrhos), during summer and winter. A comparison of the diets of those in the highest abundances (*L. pholis, T. bubalis* and *G. flavescens*) found that, in general, prey preferences were dissimilar between species, albeit with some slight overlap, and therefore it could be said that diet acts as an important mechanism of interspecific coexistence.

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C. J. Barrett (✉)
Cefas, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK
e-mail: christopher.barrett@cefas.co.uk

M. L. Johnson · S. L. Hull
CEMS, The University of Hull, Filey Road, Scarborough, North Yorkshire YO11 3AZ, UK

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Introduction

Ecological studies of intertidal fish are important not only in an applied sense, for instance in terms of the fish being biomonitors of ecosystem health (the absence of such fish may indicate high anthropogenic stresses or recent disturbance), but also academically, e.g. in palaeontological research (it is believed that many intertidal fish evolved from deeper, sublittoral species) (Horn et al., 1999). However, the latter seminal overview, though extensive, is based largely on Californian understandings.

Some of the species analysed by Horn et al. (1999), such as the common blenny/shanny, *Lipophrys pholis* (Linnaeus, 1758), are also found in the U.K. It cannot merely be assumed that the ecology of *L. pholis*, or any other reasonably cosmopolitan fish species, is the same between regions, and as far as can be determined from the literature, direct ecological intertidal fish studies around England appear to be lacking. Specifically too, there is little in the literature on U.K. species on how intertidal fish coexist. Published material is available on, *inter alia*, the extent of co-occurrence (Case, 1983; Velasco et al., 2009), morphology (Šimková et al., 2002) and predictors of fish presence (Mason et al., 2008; Pita et al., 2011), and all conclude that such factors may be one of the key factors that influences coexistence. The often synoptic nature of many intertidal fish communities suggests that resources such as food are shared, so acknowledging the Competitive Exclusion Principle of Gause (1934) (that is, the concept that if one or more species are competing for the same resource, their populations cannot remain stable if ecological factors do not change), competition would increase where prey items are scarce. Nevertheless, for the Gulf of Cádiz, Spain, Velasco et al. (2009) reported that a difference in diet can act as a mechanism of coexistence between intertidal fish species where prey items are abundant and variation great, hence reducing competition for resources.

Norton & Cook (1999) concluded, from the results of studies carried out in Chile, South Africa and California, that in temperate waters, despite intertidal fish being relatively abundant, few of them fed on barnacles and that piscivorous and molluscivorous traits were rare. Hence, they felt that such traits were rare in temperate climates and more common in the tropics and subtropics. However, whether this conclusion is true in a temperate climate such as that of the U.K. is unknown. Therefore, the primary aim of this work was to evaluate the dietary traits of some of the U.K.'s common intertidal fish species, within and between two areas, one on the east coast (Yorkshire) and one on the west (Anglesey), and to test the hypothesis that such fish can coexist successfully as a result of differences in dietary preference between species.

Methods

Research sites

Filey Brigg in North Yorkshire (Fig. 1) is a rocky promontory of Middle Calcareous Grit (Hull, 1999) and is a Site of Special Scientific Interest (SSSI), protruding east–west from the north end of Filey Bay. It is approximately 1.5 km long, with its southern side (54°13′00″N 00°15′58″W) sheltered from northerly and westerly prevailing winds and its northern side (54°13′01″N 00°16′17″W) exposed to the prevailing northeasterly winds. The sheltered side features relatively flat bedrock and boulders, with small pools between the base of the cliffs at the extreme upper shore all the way down to the lower shore. In contrast, the exposed side of the Brigg appears to be more homogeneous (Hull et al., 2001) and is a series of stepped platforms with large boulders on the upper shore and similar platforms without the large boulders on the mid- and lower shores.

Thornwick Bay (Fig. 1), also located in Yorkshire but at 54°07′53″N 00°06′51″W, is part of a Special Area of Conservation (SAC), Special Protection Area (SPA) and SSSI, within the Flamborough Head area, designated for its regionally rare intertidal and subtidal chalk reefs, sea caves and sea-cliff vegetation (Solandt & Lightfoot, 2010). It is small, ~0.25 km shore length, and surrounded by chalk cliffs. The upper shore consists of chalk boulders and chalk platforms, with a range of rock pool sizes, depths and shapes. The midshore is relatively flat, with shallow rock pools, and the lower shore consists of a boulder field covered with fucoid algae. A freshwater stream runs onto the Bay from the south cliffs, which may influence local community structure in the immediate vicinity.

The rocky shore at Penrhos in Anglesey (Fig. 1) is located within an SSSI at 53°18′13″N 04°36′45″W. The shore is 0.9 km long, with the busy ferry port of Holyhead 0.4–1.3 km to the northwest. The shore is only exposed to the north, because it is protected by the mainland of Anglesey to the east and south, and by Holyhead and the 2.4-km-long breakwater to the west and northwest, respectively. The shore consists of raised, granite bedrock and slate stones, with *Ulva* pools on the upper shore and fucoids on the mid- and low shore. The upper shore bedrock and rock pools are separated from the mid- and low-shore bedrock and pools by an expanse of mud.

Anglesey's rocky shore of Rhosneigr (Fig. 1) is 0.38 km long, situated at 53°13′06″N 04°30′36″W and is exposed to the west and the south, with limited shelter from the Aberffraw headland to the south, but sheltered by sand dunes on the landward side. Some 0.65 km to the northwest of the shore is the SSSI Rhosneigr Reefs, designated for its rich algal diversity, which includes nationally rare species (Taylor, 2004), which may influence the community structure of the studied rocky shore. The shore consists of raised, granite bedrock surrounded by mixed sand, which provides temporary sediment pools throughout the year.

Sample collection and preservation

Specimen collection from all sites took place over a week of spring tides in August 2010 (summer) and over a week of spring tides in January 2011 (winter).

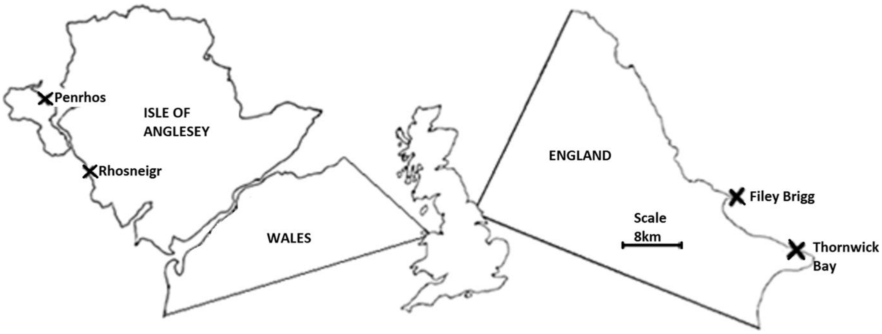

Fig. 1 The location and proximity of the sites sampled along the Yorkshire coast and around the Anglesey coast (adapted from Crisp, 1964; Hull, 1999)

Fish were collected from small pools with the use of handnets, as described by Gibson (1999), and from larger pools using home-made fish traps, made from two-litre plastic bottles, manipulated to function like a minnow trap (see description in Gibson, 1999). Upon capture, the fish were anaesthetised in a solution of clove oil in seawater (Horn et al., 1999), to ensure minimal distress (Griffiths, 2000). Once all obvious activity had ceased, the fish were placed in sample containers with a solution of 4% formalin in seawater (Tucker & Chester, 1984) and taken to the laboratory.

There, specimens were left for 3 days in 4% formalin, then transferred to 70% ethanol for another few days. Once the fixing process was complete, specimens were dried between paper towels to remove excess ethanol and dissected, and the entire digestive tract was removed. Contents of the stomach and the intestine were removed and identified to species level where possible (Hayward & Ryland, 1995) with the exception of most meiofaunal taxa, which were recorded as copepods (calanoids or harpacticoids), ostracods or very small amphipods and isopods, for which identification was unreliable (as in the diet classification of Maze et al. 1999).

Some authors use only stomach contents to examine diet (Dadzie et al., 2000), but this may result in the loss of data if contents have passed through to the intestine. In this case, therefore, both stomach and intestine contents were pooled to yield information on the whole gut contents.

Data analysis

A total of 207 shanny/common blenny (*Lipophrys pholis*) were captured, with 151 from the east coast (Filey summer = 50, Filey winter = 29, Thornwick summer = 49, Thornwick winter = 23) and the remainder from the west coast (Rhosneigr summer = 32, Rhosneigr winter = 7, Penrhos summer = 11, Penrhos winter = 6). Long-spined scorpion fish (*Taurulus bubalis,* Euphrasén, 1786) were the next most commonly captured species (Filey summer = 28, Filey winter = 7, Thornwick summer = 23, Thornwick winter = 20, Rhosneigr summer = 15 and Penrhos summer = 50), although no specimens were caught from either of the Anglesey sites during winter. 11 plaice (*Pleuronectes platessa,* Linnaeus, 1758) were captured from Rhosneigr's summer, and additionally 17 butterfish (*Pholis gunnellus,* Linnaeus, 1758) (Thornwick summer = 4, Thornwick winter = 8, Rhosneigr summer = 5), 38 two-spotted gobies (*Gobiusculus flavescens,* Fabricius, 1779) (Filey summer = 26, Filey winter = 10, Thornwick summer = 2) and 19 rock gobies (*Gobius paganellus,* Linnaeus, 1758) (Rhosneigr summer = 4, Penrhos winter = 15) were captured. 'Key' fish species were classed as those in numbers >5 in either both seasons and/or at both shores. Considering that fish were trapped by hand or via trap (as opposed to destructive methods such as draining the rock pools via a bilge pump; Griffiths (2002), or commercial species capture methods such as netting and trawling) and considering the Pool Load Capability hypothesis of Monteiro et al. (2005), which believes that, owing to their limited amounts of shelter, rock pools can only accommodate up to a certain amount of fish, the n-numbers were considered adequate for analyses.

Analyses were performed to determine whether the dietary findings of Velasco et al. (2009) are similar in British fish, testing the null hypotheses:

(1) Along the Yorkshire coast, the diet of fish species did not vary between seasons (averaged

across all shores) or between shores (averaged across all seasons).

(2) Along the Anglesey coast, the diet of key fish species did not vary between seasons (averaged across all shores) or between shores (averaged across all seasons).

(3) Between the east and west coasts of the UK, the diet of key fish species did not vary.

(4) There was no overall difference in diet composition between species, irrespective of coast, season and shore.

All diet-related count data were square-root transformed prior to the calculation of Bray–Curtis similarity indices to downweigh the contribution of abundant species. The Bray–Curtis similarity index was chosen for its ease of interpretation and applicability to ecological data, as outlined by Clarke & Gorley (2001).

To test null hypotheses (1) and (2), two-way ANOSIMs (ANalyses Of SIMilarity) were conducted on the Bray–Curtis similarity matrix using the PRIMER (Plymouth Routines In Multivariate Research) 5 software (Clarke & Gorley, 2001), followed by MDS (MultiDimensional Scaling) plots (produced from the Bray–Curtis similarity matrix (Clarke & Warwick, 1994), where significant, to provide a visual representation of the similarities in the data. Then, to test null hypothesis (3), one-way ANOSIMs were conducted, accompanied by MDS plots, where significant. For each prey item, the percentage occurrence (%*F*) in the guts (the number of guts that contained a specific prey item, divided by the total number of guts analysed) and the relative abundance of each prey item (%*N*; the number of specific prey items, divided by the total number of prey items found) were calculated (Velasco et al., 2009) for species in numbers >5 and which were also found on more than one shore or in more than one season. The values from these calculations are tabulated, pooled by coast where shore was not an important factor of diet.

Finally, to test null hypothesis (4), one-way ANOSIMs were conducted, along with an MDS plot. A SIMPER (SIMilarity PERcentage) analysis was carried out to determine the contribution of the most dominant prey taxa to each fish species (Clarke & Gorley, 2001).

Results

Dietary overlap of Yorkshire fish across both sites and between seasons

Lipophrys pholis showed a significant difference in diet similarity between sites (averaged across all seasons) (ANOSIM, Global $R = 0.087$, $P = 0.1\%$) and between seasons of the Yorkshire coast (averaged across all shores) (ANOSIM, Global $R = 0.138$, $P = 0.1\%$). These are shown in Fig. 2, and note that in both panels stress was measured at 0.16, indicating a good representation of the scatter of the samples. A breakdown of food items of this species is provided in Table 1, showing that although the number of taxa was similar, differences could be explained by Filey fish consuming *Hyale*, *Idotea neglecta* (Sars, 1895), *Lasaea rubra* (Montagu, 1803), *Jassa falcata*

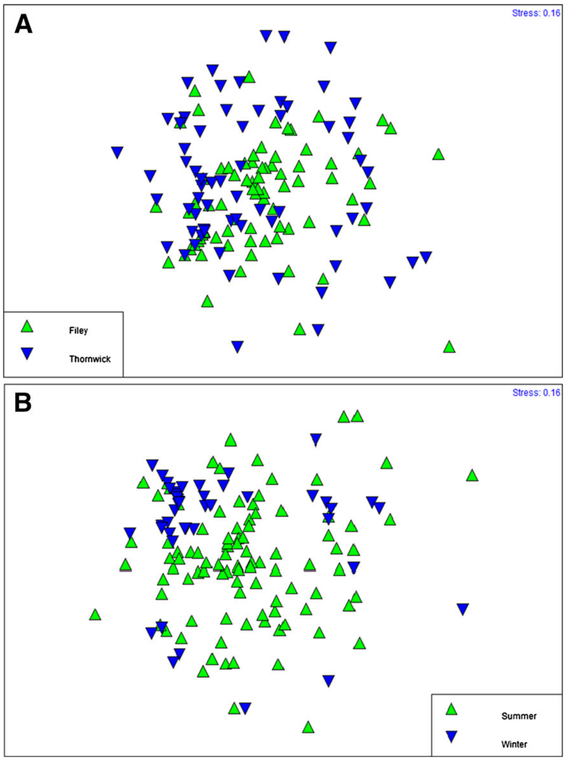

Fig. 2 Results of an MDS analysis on a Bray–Curtis similarity matrix for diet of *L. pholis* between two shores (**A**) and two seasons (**B**) along the Yorkshire coast. It appears as though diet is varied between the variables, albeit dissimilar, with some overlap

Table 1 Diet of *L. pholis,* by shore and season

	Filey summer (*n* = 50)		Filey winter (*n* = 29)		Thornwick summer (*n* = 49)		Thornwick winter (*n* = 23)		Anglesey summer (*n* = 43)		Anglesey winter (*n* = 13)	
	%F	*%N*	*%F*	*%N*	*%F*	*%N*	*%F*	*%N*	*%F*	*%N*	*%F*	*%N*
Calanoid copepod	14	6.65			6.12	3.41			2.38	0.68		
Harpacticoid copepod									7.14	2.89		
Hyale	6	1.74					4.35	0.9	11.9	1.19		
Amphipod (indet)	8	1.02			4.08	0.4			2.38	1.17		
Mytilus edulis	52	10.74			10.2	2.4	4.35	0.9	54.76	47.45	66.66	29.69
Semibalanus balanoides	72	36.3	68.97	72.67	38.78	21.84	56.52	72.97	33.33	17.86	66.66	43.75
Littorina neglecta	48	4.91	13.79	4.07	8.16	1.2	4.35	0.9	2.38	0.34		
Littorina littorea	52	7.98	6.9	1.74	44.9	21.04	13.04	2.7	23.81	2.55		
Littorina obtusata	50	4.19	13.79	4.07	24.5	8.42	21.74	10.81	23.81	2.72	11.11	3.125
Littorina saxatilis	24	2.15	10.34	8.14	14.29	5	4.35	0.9				
Carcinus maenas	25	2.05	6.9	1.74	18.37	2			11.9	1.7		
Patella vulgata	26	4.7	13.79	5.81	28.57	12.63	13.04	4.5	23.81	4.59		
Lacuna vincta	12	1.02			2.04	0.2			2.38	1.36		
Lacuna pallidula	6	0.41	6.9	1.74	2.04	0.2	4.35	1.8				
Idotea granulosa	34	4.7			6.12	1	8.7	1.8	14.29	1.7		
Idotea emarginata									4.76	2.04		
Idotea neglecta	2	0.1										
Lasaea rubra	8	0.82										
Jassa falcata	6	0.41										
Isopod (indet)	18	3.07			10.2	1.4			2.38	0.17		
Chironomid larvae	28	3.99			14.29	6.61			21.43	3.06		
Rissoa parva	4	0.2										
Urothoe marina									2.38	0.68		
Crangon crangon									2.38	0.17		
Rissoella diaphana	12	0.82										
Aporrhais pespelecani									2.38	0.17		
Otolith									4.76	0.34		
Galathea strigosa									2.38	0.34	11.11	1.56
Ascidia									2.38	0.17		
Oribatida									7.14	0.51		
Eggs (*Nucella lapillus*)									100	7.14		
Skeneopsis planorbis	6	0.41										
Eupagurus bernhardus	12	0.82			2.04	0.2						
Crangon crangon	2	0.1			2.04	0.2	4.35	0.9				
Chiton	2	0.1			2.04	0.2						
Hydrobia	8	0.6			4.08	1.6	4.35	0.9			11.11	21.875
Ulva sp.	√	√			√	√			√	√		
Osmundea pinnatifida	√	√							√	√		
Oyster					2.04	0.8						
Nucella lapillus					12.25	8.22						

(Montagu, 1808), *Rissoa parva* (da Costa, 1778), *Rissoella diaphana* (Alder, 1848), *Skeneopsis planorbis* (Fabricius, 1780) and *Osmundea pinnatifida* (Stackhouse, 1809), which the Thornwick fish did not, and Thornwick fish consuming oyster and *Nucella lapillus* (Linnaeus, 1758), which the Filey fish did not. Further, fish from both of the Yorkshire shores consumed primarily *Semibalanus balanoides* (Linnaeus, 1767), littorinids, *Mytilus edulis* (Linnaeus, 1758), *Carcinus maenas* (Linnaeus, 1758) and *Patella vulgata* (Linnaeus, 1758) among others.

Seasonal differences (Fig. 2B; Table 1) reveal 30 prey items during summer, but just 15 during winter, with the differences being accounted for by isopods, chironomid larvae, *Eupagurus bernhardus* (Linnaeus, 1758), chitons and *Ulva* being consumed during summer, but not during winter. In contrast, there were no food items consumed during winter but not summer. In general, Table 1 reveals that *L. pholis* are omnivores (although they did not consume algae during winter) and that prey diversity is greater during summer. The species also shows strong molluscivorous traits throughout both seasons, across both Yorkshire shores.

Taurulus bubalis yielded a significant difference in diet similarity between seasons (averaged across all shores) (ANOSIM, Global $R = 0.406$, $P = 0.1\%$) but not between Yorkshire coast sites (averaged across all seasons) (ANOSIM, Global $R = -0.003$, $P = 48\%$). Seasonal difference is portrayed in Fig. 3 and Table 2.

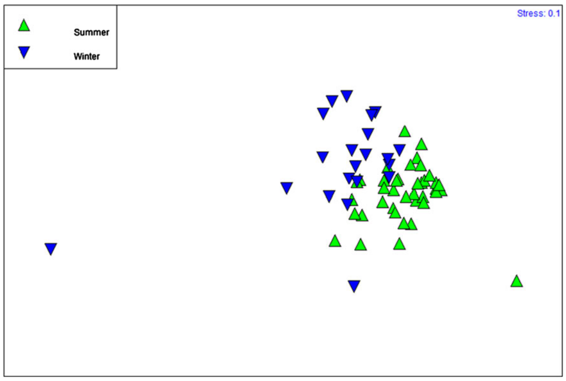

Fig. 3 Results of an MDS analysis on a Bray–Curtis similarity matrix for diet of *T. bubalis* between two seasons along the Yorkshire coast. It can be seen that diet is dissimilar between the seasons, with very little overlap. Stress was 0.1, indicating a very good representation of the scatter of the samples

Table 2 shows that at Filey, *T. bubalis* consumed 15 prey taxa during summer, but only eight during winter. In contrast, at Thornwick Bay, *T. bubalis* consumed more prey taxa during winter (15) than during summer (12). Table 2 also shows that *T. bubalis* are piscivorous (predating on *L. pholis* and also confirmed by the presence of unsourced otoliths). Figure 3 can be explained by the tendency of the species to consume *L. pholis* more in winter than in summer, as well as their tendency to eat *Mytilus edulis* and *Littorina saxatilis* (Olivi, 1792) during summer only, and *Idotea neglecta* (Sara, 1897) and *Crangon crangon* (Linnaeus, 1758) during winter only. The species also tended to consume algae, with *Laminaria* being eaten in winter, at Thornwick Bay.

Similarly, *Gobiusculus flavescens* showed a significant difference in diet similarity between seasons along the Yorkshire coast (ANOSIM, Global $R = 0.583$, $P = 0.1\%$), as shown in Fig. 4 and Table 3.

From Table 3, it is clear that *G. flavescens* are more specialised than both *L. pholis* and *T. bubalis*, with the targeted prey diversity less during winter (three taxa) than summer (five taxa). *G. flavescens* additionally targeted amphipods (indeterminate) and ostracods.

Dietary overlap of Anglesey fish across both sites and between seasons

Between Anglesey sites averaged across both seasons (ANOSIM, Global $R = -0.006$, $P = 48.9\%$) and seasons averaged across both sites (ANOSIM, Global $R = -0.131$, $P = 99.2\%$), *L. pholis* showed no significant difference in diet similarity. During seasons (Table 1), *Mytilus edulis* and *Semibalanus balanoides* made the greatest contributions to diet, followed by *Littorina obtusata* (Linnaeus, 1758). Although 26 prey items were identified during summer and just five during winter, those prey items that were consumed only during summer were of relatively minor importance.

Taurulus bubalis also showed no significant difference in diet similarity between sites (ANOSIM, Global $R = 0$, $P = 40.8\%$). A summary of their diet is given in Table 2, which shows that in Anglesey, *T. bubalis* consumed nine prey taxa, with *Carcinus maenas* being the most common, followed by *Idotea granulosa* (Rathke, 1843) and *Littorina obtusata.*

Table 2 Diet of *T. bubalis*, by shore and season

	Filey summer ($n = 28$)		Filey winter ($n = 7$)		Thornwick summer ($n = 23$)		Thornwick winter ($n = 20$)		Anglesey summer ($n = 25$)	
	%*F*	%*N*	%*F*	%*N*	%*F*	%*N*	%*F*	%*N*	%*F*	%*N*
Calanoid copepod					8.7	12.8				
Harpacticoid copepod									4	30
Hyale	25	8.45					10	9.87		
Amphipod (indet)	14.29	4.23			4.35	0.8	5	1.64		
Mytilus edulis	14.29	4.93			21.74	5.6			8	1.43
Semibalanus balanoides	7.14	1.41			8.7	2.4	5	3.28		
Littorina neglecta			14.29	24.14					12	3.57
Littorina littorea	3.57	0.7			17.39	5.6	5	1.64	4	2.14
Littorina obtusata	7.14	1.41	14.29	3.45	13.04	2.4			20	5
Littorina saxatilis	10.71	2.82			8.7	4				
Carcinus maenas	75	32.39	28.57	6.9	78.26	44.8	10	3.29	72	34.29
Lacuna vincta							10	4.92		
Lacuna pallidula							5	4.92		
Idotea granulosa	21.43	9.15	42.86	10.34	39.13	17.6	45	29.5	48	20
Idotea neglecta			14.29	6.9			25	18.03		
Isopod (indet)	3.57	1.41			4.35	0.8				
Chironomid larvae	3.57	2.11								
Crangon crangon			57.14	13.79			25	8.2	4	1.43
Urothoe marina									4	2.14
Chiton										
Hydrobia	3.57	0.7					5	3.28		
Stenothoe	7.14	1.41								
Lipophrys pholis	3.57	0.7	57.14	17.24	13.04	2.4	15	4.92		
Ascidia	3.57	27.46								
Eggs (*Nucella lapillus*)			14.29	17.24						
Amphipholis					4.35	0.8				
Otolith							10	3.28		
Scolelepis squamata							10	3.28		
Laminaria							√	√		

Dietary overlap of fish between east (Yorkshire) and west (Anglesey) coasts

Taurulus bubalis showed no significant difference in diet similarity between coasts (ANOSIM, Global $R = -0.081$, $P = 96.9\%$), whereas there was a significant difference in diet similarity between coasts for *L. pholis* (ANOSIM, Global $R = 0.131$, $P = 0.1\%$). Stress for the *L. pholis* analysis was 0.16, indicating a good representation of the scatter of the samples (Fig. 5).

Whereas the diversity of prey items of *L. Pholis* consumed at each coast was similar (30 on the east coast, 27 on the west coast), prey items were notably different. For example, on the east coast, 12 prey taxa were consumed which were not eaten on the west coast (*Littorina saxatilis, Lacuna pallidula* (da Costa, 1778)*, Idotea neglecta, Lasaea rubra, Jassa falcata, Rissoa parva, Rissoella diaphana, Skeneopsis planorbis, Eupagurus bernhardus,* chiton, oyster and *Nucella lapillus*). Conversely, on the west coast, nine prey taxa were consumed (harpacticoid copepod, *Idotea*

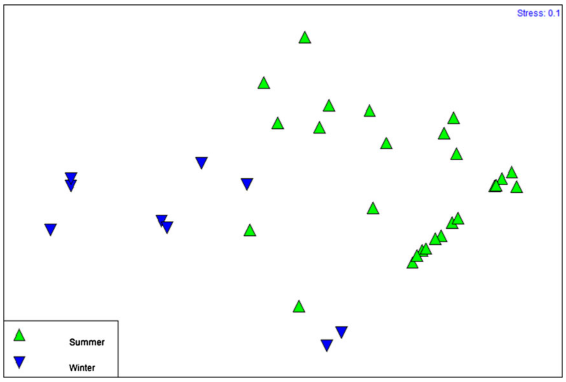

Fig. 4 Results of an MDS analysis on a Bray–Curtis similarity matrix for diet of *G. flavescens* between two seasons along the Yorkshire coast. It can be seen that diet is dissimilar between the seasons and more varied during summer

Table 3 Diet of *G. flavescens,* by shore and season

	Filey summer ($n = 26$)		Filey winter ($n = 10$)	
	%*F*	%*N*	%*F*	%*N*
Harpacticoid copepod	30.77	3.06	70	61.4
Calanoid copepod	100	84.39	20	33.33
Hyale	42.3	11.02	20	5.26
Amphipod (indet)	11.54	1.22		
Ostracod	3.85	0.31		

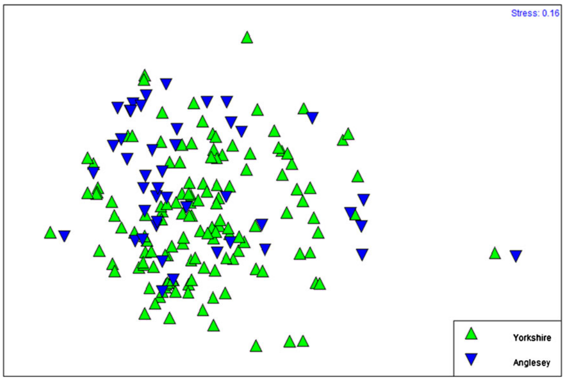

Fig. 5 Results of an MDS analysis on a Bray–Curtis similarity matrix for diet of *L. pholis* between the two coasts. It can be seen while overlap exists, diet is varied

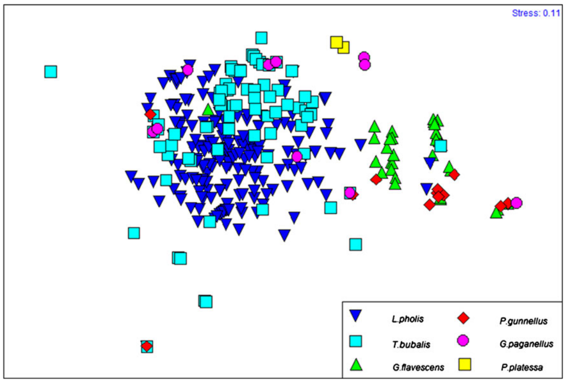

Fig. 6 Results of an MDS analysis on a Bray–Curtis similarity matrix for diet of six fish species. It can be seen that diet is dissimilar, albeit with some overlap

emarginata (Fabricius, 1793)*, Urothoe marina* (Bate, 1857)*, Aporrhais pespelecani* (Linnaeus, 1758), otoliths, *Galathea strigose* (Linnaeus, 1767), ascidia, oribatida and eggs of *Nucella lapillus* (rather than the actual specimen themselves), which were not consumed on the east coast.

Dietary overlap of all species across all sites (east and west coasts)

There was a significant difference in overall diet similarity between the different species of fish sampled from all sites (ANOSIM, Global $R = 0.401$, $P = 0.1\%$). In all cases, pairwise comparisons of diet similarity were significant ($P \leq 0.6\%$) indicating little overlap in the diet of the different species across sites. This is displayed in Fig. 6, which shows that *L. Pholis* and *T. Bubalis* had wide ranges in prey preference with slight overlap, but that *P. Platessa* showed no overlap and a small dietary range. *G. flavescens* also appeared to show little overlap with the other species, *P. Gunnellus* diet was quite different from that of *T. Bubalis* and *L. Pholis*, and *G. Paganellus* data displayed a wide distribution of points, reflecting a wide range of diet, although many points overlapped with *T. Bubalis.* The stress value of the analysis was 0.11, indicating good representation of the scatter of the samples.

The distribution of points in Fig. 6 shows that the dominant taxa for each fish species were different, with the exception of *T. bubalis* and *G. paganellus,* which both targeted *C. maenas* (providing the noticeable points overlap). In the former species, this prey item contributed to 71.18% of their diet and in the latter, 71.76%). *G. flavescens* and *P. gunnellus* both targeted copepods, but consumed different types of copepod (calanoids for the former (83.52% contribution of diet), harpacticoids for the latter (52.1%)). *P. platessa* consumed only amphipods, and *L. pholis* primarily acorn barnacles (60.4%).

Discussion

The research documented here recognises that, overall, species diet is independent of coast (west or east), except for *L. pholis*. More specifically, on the Yorkshire coast, the diet of key species (*L. pholis* and *T. bubalis*) differed between seasons, whereas this was not the case on the Anglesey coast. Additionally, the diet of *L. pholis* differed between sites along the Yorkshire coast, but not between the two sites on the Anglesey coast. This may mean that the *L. pholis* in Wales target prey that is abundant in both seasons, so they do not need to search for the different prey items seasonally. Further, *L. pholis* diet may have varied between Yorkshire sites because of the geological differences between the two shores, which could influence prey availability. Whereas *L. pholis* consumed acorn barnacles at Thornwick, that prey was present only at low frequency, unlike at Filey, where acorn barnacles were dominant. This could perhaps be explained by the chalk bedrock of Thornwick Bay deterring acorn barnacles to the extent that none were found on intertidal bedrock or boulders. Instead, at Thornwick, *L. littorea* was the main contributor to the diet of *L. pholis* during summer, although acorn barnacles were eaten, perhaps indicating that intertidal fish migrate out of their pools at high water to forage farther offshore (perhaps even specifically for acorn barnacles), before returning back to their pools on the ebb tide.

These findings imply that diet might be responsible for maintaining the coexistence of fish in two ways. Conforming to the coexistence theory of Denny & Gaines (2007) (three types of mechanisms were described where the coexistence of potential competitors may be promoted: those mechanisms that operate when competition is low and resources are constant; mechanisms that occur when disturbance or predation is reduced; and mechanisms which occur when competitive intensity is reduced by variability in the recruitment of resources and competitors, temporally and/or spatially) and the findings of Velasco et al. (2009) from the Mediterranean, the differences between prey selectivity of the species investigated here suggests that coexistence is obtained by (i) the limited competition at sites on both coasts, with high variability of resources, and (ii) a difference in the most targeted prey items between fish species, despite some overlap in prey items consumed. Mechanism (i) may explain why *L. pholis* and *T. bubalis*, the two most common species in this study, can coexist, despite *T. bubalis* being a predator of *L. pholis*. According to Optimal Foraging Theory (OFT; Irons et al., 1986), search time is a key variable, and as a cryptic, mobile species, *L. pholis* may be a difficult prey item to target (in relation to energy expenditure and search time) than other prey items taken (such as the slower gastropods or the sessile mussels) which also contributed greatly to the diet of *T. bubalis*.

The results of this study contradict the findings of Norton & Cook (1999), who stated that few intertidal fish species (and even fewer in temperate waters than in tropical waters) are piscivorous or molluscivorous and that few feed on barnacles. In the current study, *T. bubalis* did feed extensively on fish, and the presence of otoliths in the guts of *L. pholis* from Anglesey's summer samples indicates that *L. pholis* does too. The otoliths were not identified to species, but may have been those of *L. pholis,* because it is believed that the species does resort to cannibalism of its offspring when food availability is scarce, or to provide energy to other offspring during nesting (Smith, 1991). As the otoliths were found in *L. pholis* only during summer, when prey availability was seemingly good, the latter explanation is deemed to be more appropriate. Further, all of *L. pholis*, *T. bubalis* and *G. paganellus* consumed molluscs in this study, so, considering the statement of Norton & Cook (1999), it may be that the molluscs are being consumed incidentally, particularly given that small snails are often found in or between barnacles (Johnson et al., 2000). Indeed, one reason for the selection of *S. balanoides* might be that they are easier to find and capture than mobile species, are very abundant and may provide good energy source to species such as *L. pholis* despite the effort needed to prise them from the bedrock (Monteiro et al., 2005). Without evaluating search time, removal time and energy expenditure/gain, however, this explanation remains an open question.

If rock pools are utilised primarily for shelter, one would expect a trade-off between protection and prey availability (as has been found with *G. flavescens*; Utne et al., 1993). Here, two-spotted gobies distribute themselves according to the concept of an Ideal Free Distribution (distributing themselves in proportion to the amounts of resources available) and would spend more time in the presence of a predator (when food was readily available) if shelter was also accessible, influencing the condition of a fish. This issue is worth focusing on in future, in an attempt to determine whether fish condition does vary between sites and coasts.

Seasonally, the shore crab *C. maenas* was consumed by both *L. pholis* and *T. bubalis*, and in both species the contribution of *C. maenas* to the diet was always greater in summer than in winter. This may be because *C. maenas* recruits appear along the shore during summer (Vinuesa, 2007), and such small crabs would certainly be of a size suitable for capture by *L. pholis* and *T. bubalis*. However, as the crabs grow, they may quickly become too big (by winter) to be consumed easily by the fish predators and, on attaining a certain size, might themselves become predators on the fish species (pers. obs.). Future work could therefore also beneficially focus on these intertidal fish and prey size, to examine the tool usage maximisation hypothesis suggested by Monteiro et al. (2005). Those authors proposed that when fish reach a certain size, it would be more profitable to consume larger, benthic species than smaller, pelagic (or more mobile) ones. Such a study would determine whether intraspecific coexistence is maintained by a difference in diet between different sizes of a species. Additionally, confirmatory studies could be carried out throughout all four seasons and over consecutive years to determine whether dietary findings are similar to those found in the current study, building on what has been learned thus far. The studies could also include macro-fauna analysis (one method could be to hand-remove clumps of algae from random pools of the upper, mid- and lower shores from the various sites. Sieving the samples in a laboratory can then identify which macro-fauna are present at the different sites) to test whether dietary specimens are similar between sites/seasons. Findings from these future works could be added to the conceptual model of intertidal fish coexistence created by Barrett et al. (2014).

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