

Pike (*Esox lucius*) in Ireland: Developing Knowledge and Tools to Support Policy and Management

IFI/2018/1-4435



Iascach Iníre Éireann
Inland Fisheries Ireland



Inland Fisheries Ireland
Iascach Iníre Éireann



Iascach Iníre Éireann
Inland Fisheries Ireland

National Coarse Fish and Pike Programme

Pike (*Esox lucius*) in Ireland:

Developing Knowledge and Tools to Support Policy and Management

CITATION: McLoone, P., Fitzgerald, C., O' Reilly, S., Shephard, S. and Kelly, F.L. (2018) Pike (*Esox lucius*) in Ireland: Developing Knowledge and Tools to Support Policy and Management. National Research Survey Programme, Inland Fisheries Ireland, 3044 Lake Drive, Citywest Business Campus, Dublin 24.

Cover photo: Pike on Lough Derravaragh © Inland Fisheries Ireland

© Inland Fisheries Ireland 2018



ACKNOWLEDGEMENTS

The authors wish to gratefully acknowledge the help and co-operation of all their colleagues in Inland Fisheries Ireland.

Also we would like to thank the anglers who provided additional pike for the sampling programme.

Thanks also to Dr Keith Farnsworth (Queen's University Belfast) for supervision and expert input in the development of the pike-trout predator-prey model (Chapter 5).

We would also like to thank Dr. Martin O' Grady (RIP) and No. 3 Operational Wing, Irish Air Corps (Aer Chór na hÉireann) for the aerial photographs.

Karen Delanty, Rory Feeney, Kieran Rocks and Martin O'Grady have contributed to scientific papers based upon the work presented here.

The authors would also like to acknowledge the funding provided for the project from the Department of Communications, Climate Action and Environment.

The report includes Ordnance Survey Ireland data reproduced under OSi Copyright Permit No. MP 007508.

Unauthorised reproduction infringes Ordnance Survey Ireland and Government of Ireland copyright.

© Ordnance Survey Ireland, 2018.



Table of ContentsACKNOWLEDGEMENTS	ii
Table of Contents.....	iii
Executive Summary.....	v
1: Introduction	1
1.1 Background	1
1.2 Aims of the project.....	1
2: Seasonal diet of pike in Irish Lakes. An examination of current and historical data sets.....	3
2.1 Introduction	3
2.2 Methods.....	4
2.2.1 Study area	4
2.2.2 Characterising Fish Stocks in Lough Conn and Lough Derravaragh - Fish Stock Assessments & Prey Morphometric Measurements.....	10
2.2.3 Pike sample collection 2016/2017	11
2.2.4 Stomach Content Collection	12
2.2.5 Biosecurity - disinfection and decontamination procedures.....	12
2.2.6 Processing of Stomach Contents in the Laboratory.....	15
2.2.7 Historical Pike Diet Data	15
2.2.8 Inter Era Comparisons of Diet.....	18
2.2.9 Data analysis and indices	19
2.3 Results	24
2.3.1 Whole lake fish stock surveys	24
2.3.2 Description of Current Pike Diet	24
2.3.3 Historical Pike Diet Data	42
2.3.4 Inter Era Comparisons of Diet.....	45
2.4 Discussion.....	50
3: Models of coexistence for pike and trout in Irish lakes.....	53
3.1 Introduction	53
3.2 Methods.....	53
3.2.1 Fish and abiotic data	53
3.2.2 Statistical Models.....	56
3.4 Results.....	57
3.5 Discussion.....	59
4: Potential changes in the effect of pike removal after roach invasion	61
4.1 Introduction	61
4.2 Methods.....	61
4.2.1 Study area	61
4.2.2 Data collection	62
4.2.3 Statistical models	63
4.3 Results.....	65



4.3.1 Fish stocks	65
4.3.2 Chlorophyll a and temperature.....	66
4.3.3 Pike diet	66
4.3.4 Pike removal.....	67
4.4 Discussion.....	69
5: Size-structured population model for the assessment of management options for pike-trout interactions in Irish lakes	70
5.1 Introduction	70
5.2 Methods.....	73
5.2.1 Single-species length-structured model outline	73
5.2.2 Two-species predator-prey model – species interaction	80
5.2.3 Model parameterisation for case study.....	86
5.2.4 Sensitivity analysis	101
5.2.5 Uncertainty analysis and management strategy evaluation	102
5.3 Results and analysis	103
5.3.1 Sensitivity analysis	103
5.3.2 Uncertainty analysis and management strategy evaluation	105
5.4 Discussion.....	108
6. References	110



Executive Summary

This project was initiated to answer some on-going questions related to the dietary preference of pike and to examine pike- trout interactions in lakes in Ireland. These questions are central to the informed management of pike and trout populations. Most pike dietary studies published in Ireland to date were undertaken prior to the expansion of roach in the 1970's. A recent study examined the short term diet of pike in several Irish rivers, lakes and canals and the authors highlighted the need to describe the longer term seasonal diet of Irish pike and also whether the colonisation of roach has influenced pike diet. In response to this, IFI initiated a targeted seasonal diet study on two large lakes, Loughs Conn and Derravaragh, in 2016 to provide an up to date understanding of dietary habits of pike. A size-structured predator-prey model for pike and trout was then developed to integrate this information into a robust framework for evaluation of candidate fisheries management strategies.

The aims of the project were to describe the seasonal diet of pike in two Irish lakes and assess any dietary change since the colonisation of roach, develop statistical models to predict the probability of coexistence between pike and trout, and investigate any changes in the effect of pike control on trout populations after the roach invasion in Lough Sheelin. The final objective was to develop a mathematical modelling tool that could project the likely outcomes of a set of candidate fisheries management strategies, quantify uncertainty and support objective decision making.

Monthly sampling of pike was undertaken on Lough Conn and Lough Derravaragh from August 2016 to July 2017. Standardised electrofishing was the main method used to capture pike. Gastric lavage, a non-lethal method, was used to obtain stomach content samples of pike. Diet information was available from 1481 pike. Additionally whole lake fish stock surveys were conducted on both lakes in August 2016 and July 2017 respectively. Pike diet data was also available from pike captured during the pike stock management undertaken in Lough Conn during spring 2017. Archival IFI pike diet data (prior to the roach invasion) from Loughs Derravaragh and Sheelin was used to explain the impact, if any, that the colonisation of roach has had upon pike diet in Irish lakes. A range of established dietary metrics and prey selectivity indices were calculated. Pike in both lakes examined during the project consumed a wide variety of prey organisms. While invertebrates were common in the diet of pike in both lakes, pike were also found to feed on fish from very early stages in their life history. Roach were the most important fish species consumed by pike in both lakes, including the sample obtained from predator control operations on Lough Conn in March and April 2017. Other fish



species which featured in the diet of pike in both lakes include, perch, stickleback, trout and pike. While representing a relatively small component of fish recorded in pike stomachs, the greatest proportion of trout in the diet occurred in April on Lough Derravaragh and May-June in Lough Conn. This observed peak in trout predation coincides with the period of downstream migration of river trout to lake environments.

Prey selectivity indices (which compare the amount of particular prey consumed with their proportion in the environment) indicated that roach were positively selected by pike and that perch were negatively selected by pike on an annualised basis. This means that there were more roach and less perch in pike stomachs than would have been expected from the relative abundance of these species in the system. All indices for trout tended towards neutrality, i.e., the number in pike stomachs reflected relative abundance in the system.

Comparison of the current data with IFI archival data (1960's and 1970's) indicated a profound shift in the diet of pike in Irish lakes. There was a strongly significant increase between sampling periods in the probability of observing cyprinids in pike stomachs, and corresponding strongly significant decreases in the probability of observing perch or salmonids (mainly trout). Pike in the smaller size class were significantly less likely than large pike to have salmonid (mainly trout) prey in their stomach. Cyprinids, namely rudd and bream were present in both study lakes, but were an insignificant component of the pike diet in the earlier period. However, in the current period roach were the single most important fish prey item for pike in both lakes. Similar changes in pike diet have been observed in Loch Lomond (Scotland) and Lake Windermere (England) following the expansion of ruffe and roach respectively.

Statistical models were developed to endeavour to predict the probability of coexistence between pike and trout across abiotic (e.g. maximum and mean lake depth, altitude, mean temperature, connectivity and lake area) and fish community gradients. The models suggest that relatively large deep lakes with strong stream connectivity offer a greater probability of coexistence for pike and trout in Ireland. However, pike introductions to small low-complexity systems have the potential to be devastating to resident trout populations as observed in recent IFI surveys in counties Donegal and Galway.

Long-term data from Lough Sheelin (fish stock surveys including diet information, pike removal records, and chlorophyll and temperature monitoring) were used to compare pike diet before and after the roach invasion, test for an effect of pike removal on abundance of trout, and to evaluate



whether any pike removal effect changed with roach abundance and environment. The proportion of sampled pike stomachs containing trout was found to decline strongly after the appearance of roach in Lough Sheelin. This observed dietary shift (from trout to roach) was associated with contrasting effects of pike removal on survey abundance of trout in the following year. In years of 'low' roach abundance, pike removal had some positive effect on subsequent trout abundance, but this effect became weakly negative at 'high' roach abundance. These results were significant at a 95% confidence level. The availability of roach seems to have reduced pike predation pressure on trout in Lough Sheelin, and potentially modified the utility of pike removal as a trout conservation tool in the system.

Predicting the results of any fisheries management action is uncertain because ecosystem dynamics are often complex and poorly understood. Operational management strategies for fisheries are typically tested in a modelling framework using management-strategy-evaluation (MSE). This well-developed framework supports the quantification of biological and fishery uncertainty in model inputs, and propagates these through to their effects on fishery performance measures. MSE thus provides a natural framework for incorporating the effects of relatively uncertain factors, e.g., pike recruitment dynamics, into evaluation of management strategies aimed at enhancing trout fisheries in Irish lakes.

It is generally accepted that models tailored for individual species and ecosystems are needed to guide fisheries management policy. A size-based model was developed to express key features in the population dynamics of trout and pike. This model allows for predation by pike on trout and on an alternative size-structured prey spectrum representing other prey species, e.g., roach, perch and invertebrates. The sensitivity of model outputs to changes in biological input parameters was estimated through a sensitivity analysis in order to identify which input parameters exerted the greatest influence on the modelled ecosystem dynamics. The model was particularly sensitive to stock-recruitment parameters for pike and trout, and to the amount of alternative prey available to pike. The model was used in an MSE framework to explore the likely outcome of candidate fisheries management strategies, including different rates of removal for each of pike and trout. A first result is that the likely effect of pike removal on trout populations will change strongly with the abundance of alternative prey. Pike removal may be quite effective in systems where trout are the only available prey for pike, but removal may have little or no effect in systems with abundant alternative prey, e.g., invasive roach.



1: Introduction

1.1 Background

Both brown trout (*Salmo trutta*) (hereafter trout) and pike (*Esox lucius*) are of cultural significance in their own right and support substantial recreational angling fisheries in Ireland, where the estimated annual economic contribution was valued at €148m and €105m respectively in 2014/2015 (IFI, 2015a & b). Several early scientific studies suggested that pike, (particularly large pike) selectively preyed upon trout in preference to other fish species, notably perch (*Perca fluviatilis*), but also the cyprinids such as rudd (*Scardinius erythrophthalmus*) and bream (*Abramis brama*) that were widely available in the environment at that time (e.g. Healy 1956; Toner, 1959; Kennedy, 1969; Bracken, 1973). Concern over the impacts of pike on populations of trout in Irish freshwaters motivated selective management intervention (pike culls and removals) in designated trout fisheries since the 1950s. This practice continues on seven wild trout fisheries in Ireland and is the subject of considerable debate amongst stakeholders (Curtis, 2017). However, most of the early studies were conducted prior to the spread of the invasive fish species roach (*Rutilus rutilus*), and other fish species. In a recent study examining the diet of pike in Ireland Pedreschi *et al.*, (2015) suggested that a certain amount of predation pressure on trout has been alleviated by the invasion of roach throughout Irish freshwaters since the 1970s. However, that study provided only a very short-term snapshot of pike diet in selected waters.

This project was initiated to endeavour to answer some of the on-going questions related to the dietary preference of pike and to pike-trout interactions in large lakes in Ireland. These questions are central to support the informed management of pike and trout populations. A targeted seasonal diet study was initiated on two large lakes to provide an up to date understanding of the dietary habits of pike. A model-based method to integrate this information into a tool that can be used to evaluate management strategies in a structured and robust way was also developed.

1.2 Aims of the project

The primary aim of this project was to address knowledge gaps surrounding the impact of pike predation on fish stocks currently resident in Irish lakes. The project was broken into four work packages with distinct aims:



1. Describe the seasonal diet of pike in two Irish lakes and assess dietary change since the colonisation of roach.
2. Develop statistical models to predict the probability of coexistence between pike and trout across abiotic and fish community gradients.
3. Investigate if the availability of roach has modified interactions between pike and trout in Lough Sheelin.
4. The final objective was to develop a mathematical modelling tool that could project the likely outcomes of a set of candidate fisheries management strategies, quantify uncertainty and support objective decision making.



Plate 1.1: Sunset on Lough Conn (photo taken from western shore)



2: Seasonal diet of pike in Irish Lakes. An examination of current and historical data sets

2.1 Introduction

Resolving the dietary habits of pike is central to informed management of pike and trout populations in Irish waters. Several early scientific studies suggested that pike (particularly large pike) selectively preyed upon trout in preference to other fish species, notably perch, but also the cyprinids such as rudd and bream that were widely available in the environment at that time (e.g. Healy, 1956; Toner, 1959; Kennedy, 1969; Bracken, 1973). This theory is consistent with other studies where pike, which are gape limited predators (Nilsson and Brönmark, 2000), prey upon shallower bodied species (at specific lengths) of fish (Mauck and Coble, 1971; Nilsson *et al.*, 1995, Nilsson and Brönmark, 2000) and select against spiny bodied fish such as perch (Eklöv and Hamrin, 1989). Furthermore, they do not appear to prey significantly upon the deeper bodied cyprinids such as bream or its hybrids in Ireland (Pedreschi *et al.*, 2015).

This understanding had influenced fisheries management practises in Ireland, where management interventions (pike culls and removals) to develop trout angling were widespread from the 1950's (e.g. Fitzmaurice, 1983; Bracken and Champ, 1971), and continue on seven wild trout fisheries. However, most of these studies were conducted prior to the spread of the invasive fish species roach. Roach has spread rapidly throughout Ireland since the 1970's (Fitzmaurice, 1981) and has radically altered fish communities in the watercourses that it inhabits, frequently being the most abundant fish in the lakes that it inhabits and leading to proliferation of hybrids with bream (*Abramis brama*) (Hayden *et al.*, 2014). It has also been suggested that the invasion of roach may alleviate predation pressure by pike on trout in lakes where all three species occur (Pedreschi *et al.*, 2015). That study examined the short term diet of pike in several Irish rivers, lakes and canals and the authors highlighted the need to describe the longer term seasonal diet of Irish pike and also whether the colonisation of roach has influenced pike diet (Pedreschi *et al.*, 2015).

This study describes the current diet of pike in two Irish lakes: Lough Conn in Co. Mayo and Lough Derravaragh in Co. Westmeath. Pike, trout and roach are present in both lakes (Kelly *et al.*, 2017; Connor *et al.*, 2018). Archival pike diet data sets were used to elucidate the impact, if any, that the colonisation of roach has had upon pike diet in Irish lakes. Archive data from the 1960s and 1970s



was available from Lough Derravaragh and Lough Sheelin (Counties Westmeath, Cavan and Meath). Neither lake contained roach at the time that the historical data was collected.

2.2 Methods

2.2.1 Study area

Lough Conn

Lough Conn is located in the River Moy catchment in north County Mayo (Figure 2.1; Plate 2.1). The lake is connected to its immediate neighbour to the south, Lough Cullin, by a narrow channel at Pontoon village (Figure 2.1). The River Deel flows into Lough Conn and exits Lough Cullin at its southern end near Foxford, just before joining the River Moy which discharges into the Atlantic at Killala Bay. The lake has a surface area of 4,704ha and a maximum depth of 37.9m. The lake is categorised as typology class 12 (as designated by the EPA for the Water Framework Directive), i.e. deep (mean depth >4m), greater than 50ha and high alkalinity (>100mg/l CaCO₃). The lake is managed as a wild trout fishery. While annual predator control operations continue on the lake, trout stocks are not currently augmented through stocking of hatchery reared fish. Roach were first recorded in Lough Conn in 2001 (O' Grady and Delanty, 2001a).

Lough Derravaragh

Lough Derravaragh is situated in County Westmeath, north of Mullingar between Castlepollard, Crookedwood and Multyfarnham in the River Inny catchment (Figure 2.1; Plate 2.2a and b). The lake has a surface area of 914ha and a maximum depth of approximately 30m. The lake is categorised as typology class 12 (as designated by the EPA for the Water Framework Directive), i.e. deep (mean depth >4m), greater than 50ha and high alkalinity (>100mg/l CaCO₃). The lake is a mixed fishery with good stocks of trout, pike and coarse fish. Historically, the lake was managed as a trout fishery. Pike and perch were removed annually as predators and competitors of trout respectively (Fitzmaurice, 1983). Furthermore, the wild stocks of trout were augmented by stocking hatchery reared trout. However, fish stocks in the lake are no longer subject to management intervention in the form of fish stocking or removal. Roach were first recorded in fish stock assessments of the lake in 1977 (O' Grady, 1986).



Lough Sheelin

Lough Sheelin is situated in counties Cavan, Meath and Westmeath in the River Inny catchment (Plate 2.3, Figure 2.2). The lake is located north-east of Finnea, Co. Westmeath. It is seven kilometres long and has a surface area of 1,900ha. The River Inny flows through the lake. Lough Sheelin is a relatively shallow lake with a mean depth of 4.4m, a maximum depth of 15m, and 51% of the lake is less than 5m in depth. The geology of the catchment is predominantly Carboniferous limestone, but Silurian/Ordovician formations underlie the western and northern drainage basin. The lake is eutrophic, and is categorised as typology class 12 (as designated by the EPA for the Water Framework Directive), i.e. deep (>4m), greater than 50ha and high alkalinity (>100 mg/l CaCO₃). The lake is managed as a wild trout fishery. While annual predator control operations continue on the lake, stocking of trout ceased in 2011.



Plate 2.1. Lough Conn, aerial view looking NW

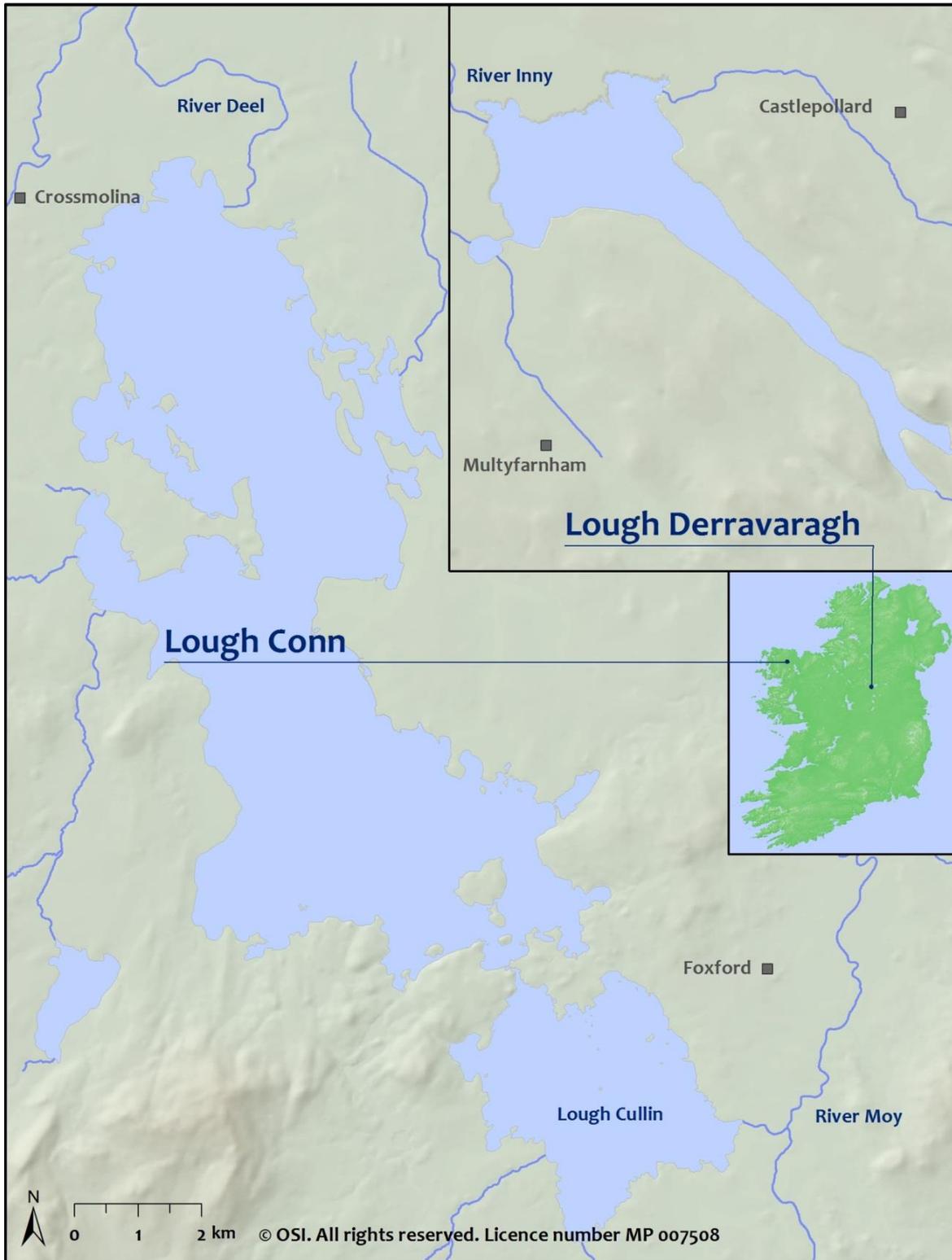


Figure 2.1. Loughs Derravaragh and Conn; lakes where pike dietary data was collected, August 2016 to July 2017.

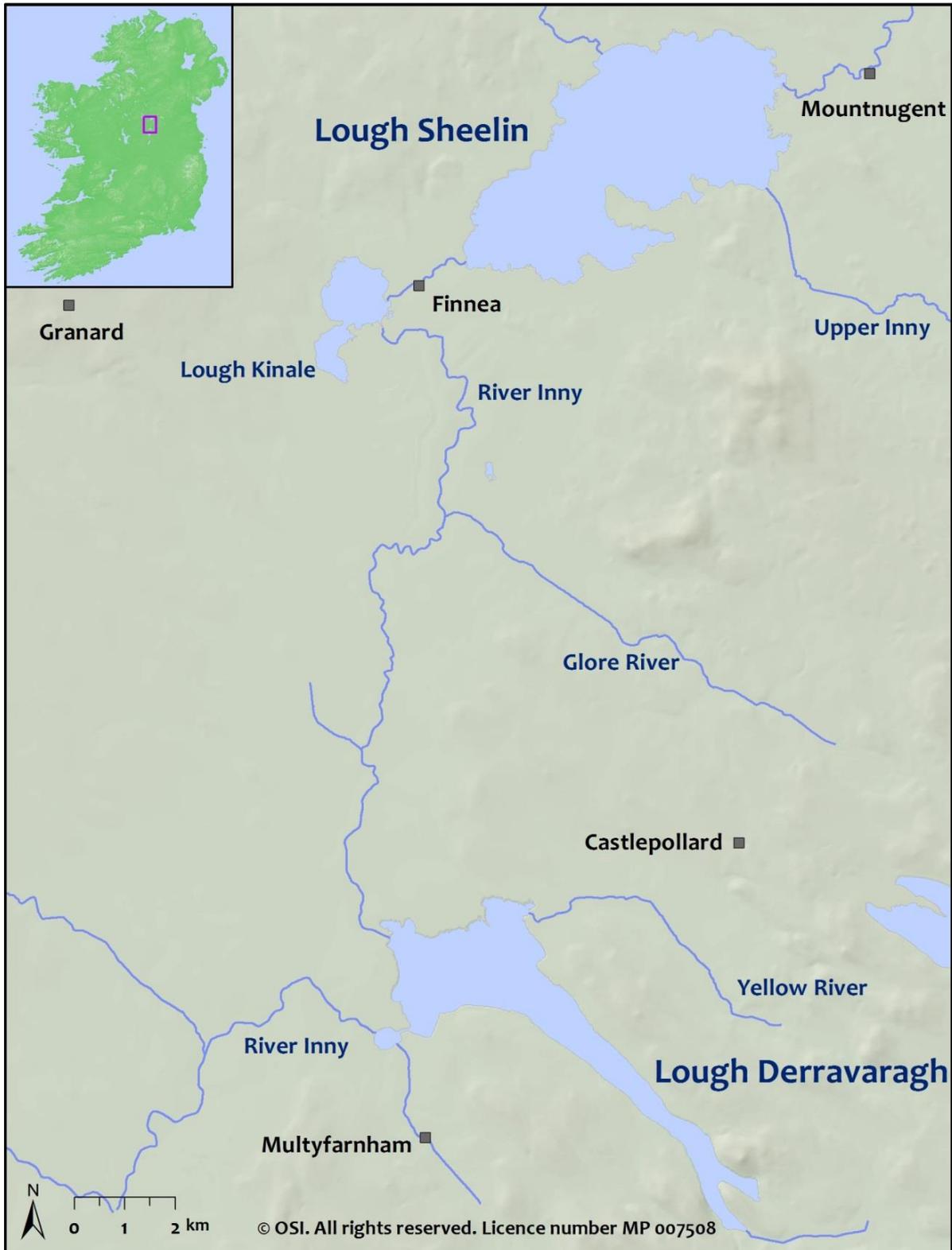


Figure 2.2. Loughs Derravaragh and Sheelin, where historical pike dietary data was analysed from the period 1967-1973



Plate 2.2a. Lough Derravaragh Upper Basin



Plate 2.2b. Lough Derravaragh Lower Basin



Plate 2.3. Aerial view of Lough Sheelin (photo taken looking across the lake in a south-west direction from the northeast shore)



2.2.2 Characterising Fish Stocks in Lough Conn and Lough Derravaragh - Fish Stock Assessments & Prey Morphometric Measurements

Information relating to fish stocks in both study lakes was available from whole lake fish stock surveys of each lake conducted during the study period. They serve as a measure of relative fish prey availability to pike in each lake.

A whole lake fish stock survey was undertaken on Lough Derravaragh over three nights from the 3rd to the 6th of July 2017 (Connor *et al.*, 2018). Lough Conn was surveyed over four nights between the 22nd and the 26th of August 2016 (Kelly *et al.*, 2017). The netting methods that were employed during the surveys are described in Kelly *et al.*, (2017) and Connor *et al.*, (2018). To standardise effort between lakes, only those fish captured using the standardised European survey monofilament gill nets (benthic and pelagic) and fyke nets utilised in Irish lakes is included in the analysis presented here. The proportions of each fish species recorded in Loughs Conn and Derravaragh were calculated as a percentage of the total catch.

Digital vernier callipers were used to measure a suite of morphometric and meristic measurements of fish from Lough Derravaragh that were captured during the fish stock survey in 2017 and from fish captured opportunistically during monthly sampling on both lakes (Table 2.1). Linear models relating to fish fork length were constructed (IFI unpublished data) to aid estimation of digested prey fish length. This data was used to help parameterise the mathematical model used for management strategy evaluations (see chapter 5).

Table 2.1. Morphological and meristic measurements taken from fish (pike and other potential prey) captured in Lough Conn and Lough Derravaragh.

Metric (mm)	Description
Head length	Tip of snout to posterior point on opercular bone
Snout length	Tip of snout to origin of dorsal fin
Body depth	Vertical line from origin of dorsal fin to ventral surface
Caudal peduncle depth	Depth of tail at narrowest point
Dorsal length	Insertion point of anterior of Dorsal fin to centre point origin of mid ray of caudal fin
Caudal peduncle length	End of anal fin (mm) to centre point of the end of caudal peduncle/start of tail fin
Caudal fin length_D	Dorsal ray of caudal fin
Caudal fin length_M	Middle ray of caudal fin



2.2.3 Pike sample collection 2016/2017

With the exception of September 2016, monthly sampling of pike was conducted on Lough Derravaragh and Conn between August 2016 and July 2017.

In order to minimise disturbance to resident fish stocks and also ensure a broad size range of samples, electrofishing was the primary method used to capture pike. This method also allows live release of captured fish. Experience has also shown that the monofilament survey gill nets typically catch relatively few pike, and insufficient numbers to collect an adequate sample for analysis (*per obs.*), while the braided gill net gangs previously used on fish stock surveys in Ireland typically capture fish only greater than 15 or 16cm in length (O' Grady, 1981). Furthermore, use of electrofishing also reduces potential biases, as a result of regurgitation of stomach contents in gill net captured fish (e.g. Sutton *et al.*, 2004; Vinson and Angradi, 2011).

Sites in both lakes were sampled with an electrofishing boom boat (Smith Root 16E) (Plate 2.4). Sites were situated a minimum of 20m apart, and were approached as quietly as possible. At each site, power was activated for a minimum period of 10 seconds. If pike were observed the power was continually activated until fish were captured using landing nets. If no pike were observed the power was turned off after 10 seconds and remained off until the next site was reached. Intermittent fishing was conducted as this was found to be the most effective way of capturing pike as it reduced the possibility of disturbing fish prior to capture.

Electrofishing catches were largely confined to vegetated margins (littoral) in both lakes. While suitable electrofishing sites were targeted during the study, fish capture was typically dependent upon the presence of submerged or emergent weed beds in both lakes. Captured fish were held in the boat mounted live-well through which fresh lake water was regularly flushed. Sampling continued until such time as sufficient fish were retained for efficient processing or when the live well had reached capacity. No fish were held for longer than 30 minutes and, where possible, large fish (> ~60cm) were processed immediately. Angling was used on both lakes to supplement the samples collected by electrofishing. Captured fish were quickly brought to the electrofishing boat where they were handled in the same way as those pike captured during electrofishing.

This data set was further supplemented with seven euthanised pike captured in the whole lake fish stock survey conducted on Lough Conn in August 2016. An additional sample of 110 pike greater



than 50cm in length was obtained from seasonal predator control operations conducted on Lough Conn. These fish were euthanized, frozen and returned to the laboratory for analysis.

2.2.4 Stomach Content Collection

Gastric lavage (or stomach flushing) is a widely utilised, minimally invasive and non-lethal method of recording the stomach contents of fish (Kamler and Pope, 2001 and references therein) and has been used elsewhere for collecting samples of esocid prey (e.g. Wahl and Stein, 1993; Andrews *et al.*, 2018).

The lavage apparatus consists of a small hand pump, to which various sized flexible tubes can be attached (Plates 2.5 and 2.6). Live pike were first anaesthetised in a weak solution of clove oil (~50 mg/l) and deemed unconscious once opercular movement had ceased and balance could no longer be maintained. (See Javahery *et al.*, 2012 for a review of clove oil use as an anaesthetic in fish.)

A suitably sized flexible tube was inserted into the fish's mouth and pushed gently into the stomach. Fresh water was then pumped into the stomach via the pump, using just enough pressure to ensure that any stomach contents were regurgitated. Regurgitated food items (example Plate 2.7) were preserved in alcohol for later examination in the laboratory. Gastric lavage was performed by staff trained in fish welfare and fish handling techniques.

All captured pike were measured (fork length to nearest mm) and weighed (0.1g).

2.2.5 Biosecurity - disinfection and decontamination procedures

Procedures are required for disinfection of equipment in order to prevent dispersal of aquatic invasive species and other organisms to uninfected waters. A standard operating procedure was compiled by Inland Fisheries Ireland for this purpose (Caffrey, 2010) and is followed by the IFI research team when moving between waterbodies.



Plate 2.4. Boom boat electrofishing on Lough Derravaragh, December 2016



Plate 2.5. Gastric lavage equipment



Plate 2.6. Using gastric lavage to remove stomach contents from an anaesthetised pike



Plate 2.7. Example of a bone fragment obtained following gastric lavage of a pike in Lough Derravaragh.



2.2.6 Processing of Stomach Contents in the Laboratory

Fish prey were identified, enumerated and each individual prey item weighed to the nearest 0.001g (blotted wet weight). When possible, undigested body parts such as pharyngeal teeth, bones or scales were identified with reference to identical structures from intact prey, or from reference keys (Wheeler & Jones, 1989). Invertebrate prey were enumerated and assigned to the lowest possible taxonomic level. The combined weight of all invertebrate prey within each group was determined for each stomach (0.001g blotted wet weight). Prey species, numbers of prey and prey weight were thus available for each stomach examined.

2.2.7 Historical Pike Diet Data

Archival stomach data in paper form (see Plates 2.8a and b) was available for monthly predator control operations on Lough Derravaragh and Lough Sheelin for the period 1967-1973 and 1968-1973 respectively. Pike were captured by a variety of methods during these operations. Gillnetting was the dominant method employed in both lakes at that time, but other less common capture methods included otter boards and long lines.

While precise sampling locations are unknown, predator control gill nets were typically located in the shallow vegetated margins of Irish lakes (Roche, IFI, *pers comm*). Thus the habitats sampled are comparable to those sampled using electrofishing during the current period.

In both lakes, monthly pike stomach data were categorised into six main length classes in 5 inch increments. Original length increments were converted to metric size classes (Table 2.2).

In Lough Sheelin, information relating to the total number of empty stomachs in the sample was included for most periods. In Lough Derravaragh, however, only information relating to stomachs which contained food could be accurately captured. Analysis therefore examined the occurrence of dietary items recorded in those pike which contained food items. In the archive, one prey species/group only was recorded for each stomach examined. It was assumed that this was the dominant food type recorded in that stomach. Data was enumerated for input into a digital archive for analysis. Original prey groups are listed in Table 2.3. No distinction between stocked and wild trout was made in the original data.

Met Éireann's meteorological seasonal classification scheme was used to append an additional metric to each monthly sample (Table 2.4) (Met Éireann, 2017).



Table 2.2. Length increments of pike in an archive data set of pike diet from Lough Derravaragh and Lough Sheelin, from the period 1968-1973 and 1967–1973 respectively.

Length (Inches)	Length (cm)
5 - 10	12.7 - 25.4
10 - 15	25.5 - 38.1
15 - 20	38.2 - 50.8
20 - 25	50.9 - 63.5
25 - 30	63.6 - 76.2
> 30	> 76.2

Table 2.3. Prey categories recorded in an archival data set of pike stomach analysis from Lough Sheelin (1967-1973) and Lough Derravaragh (1968-1973).

Fish	Non Fish Vertebrates	Invertebrates	Other
Trout	Frogs, newts	Shrimp & <i>Asellus</i> sp. (freshwater louse)	Other + Unidentified
Trout fingerlings, etc	Birds	Nymph'	
Perch	Mammals	Snails	
Pike	Rat	Mayfly Nymph	
Sticklebacks		Crayfish	
Rudd & bream		Odonata (dragon fly and damsel fly)	
Salmon parr/smolt		Dragon fly	
Salmon adults		<i>Gammarus</i> sp. (Freshwater shrimp)	
Char			
Minnow & gudgeon			
Stoneloach			
Eel			
Lamprey			
Unidentified Fish			



PIKE - STOMACH CONTENTS. LAKE/RIVER Lough Derravaragh YEAR 1969 MONTH April METHOD g.n.

30 +	25-30	20-25	15-20	10-15	5-10	LENGTH (INCHES)
						NO
						EMPTY
						TROUT
						TROUT FINGS ETC.
						SALMON PAR./SMOLT
						SALMON ADULTS
						CHARR
						PIKE
						PERCH
						RUDD + BREAM
						STICKLEBACKS
						MINKON + GUDGEON
						UNIDENT. FISH
						FROGS, NEWTS
						SNAILS
						ODONATA
						BIRDS
						MAMMALS
						OTHER + UNIDENT.

PIKE - STOMACH CONTENTS. LAKE/RIVER Lough Sheelin YEAR 1972 MONTH Jan. METHOD g.n.

30 +	25-30	20-25	15-20	10-15	5-10	LENGTH (INCHES)
						NO
						EMPTY
						TROUT
						TROUT FINGS ETC.
						SALMON PAR./SMOLT
						SALMON ADULTS
						CHARR
						PIKE
						PERCH
						RUDD + BREAM
						STICKLEBACKS
						MINKON + GUDGEON
						UNIDENT. FISH
						FROGS, NEWTS
						SNAILS
						ODONATA
						BIRDS
						MAMMALS
						OTHER + UNIDENT.

Plate 2.8a & b. Example of archive pike stomach data available for Lough Derravaragh (left) and Lough Sheelin (right).

Table 2.4. Meteorological Seasons in Ireland.

Season	Months
Winter	December - February
Spring	March - May
Summer	June - August
Autumn	September - November



2.2.8 Inter Era Comparisons of Diet

For analysis purposes prey categories described in the historical archive were aggregated into appropriate groups (Table 2.5). Incidental prey items (e.g. amphibians), were excluded from the data set. Prey items identified in pike stomachs during the current sampling period were similarly pooled into these groups to facilitate analysis. Likewise, sampled pike in both datasets were aggregated into two categories (Small \leq 50.8cm > Large) and seasons were amalgamated into Winter/Spring and Summer/Autumn. Prey occurrence data (the number of stomachs in which a particular prey item was observed i.e. Frequency Occurrence) was the dietary metric used to compare across eras.

Table 2.5. Aggregated prey categories used for analysis of prey consumption

Prey Category	Description
Salmonid	Trout, trout fingerlings, salmon
Cyprinid	Roach, bream, rudd and their hybrids
Percid	Perch
Esocid	Pike
Gasterosteid	9 and 3-spined Stickleback
Other Fish	All other fish species
Invertebrates	All invertebrate species

A pike diet study was conducted in Lough Sheelin in the early 1980s (i.e. in the period immediately following roach colonisation) (Gargan, 1986). Available data (Gargan, 1986) was not in a format that allowed direct comparison with current and archival data sets. Raw data, which contains information from individual pike, is currently being compiled in a format that will facilitate utilisation of this data set in future studies.



2.2.9 Data analysis and indices

A number of metrics are available to describe dietary importance of prey items of fish and other animals (e.g. Hyslop, 1981). Metrics used in this study were frequency of occurrence (FO), proportion of the total number of prey items (% Number), proportion of total prey biomass (% Biomass) and the index of relative importance (IRI).

Prey selection indices are commonly utilised to provide descriptive metrics of prey selection of preference in predators. Four commonly used prey selection indices are presented here. Each metric compares the number of prey in stomachs with their availability in the environment. In this instance prey availability is defined as the proportion of each respective species captured in the whole lake fish stock surveys (see 2.2.2). Analysis is confined to roach, perch and trout, which together represent in excess of 95% of fish captured in the respective whole lake surveys. Proportions of each species in the diet and the environment are expressed as a fraction of the three species combined. In this way, species such as stickleback, which are represented in the diet but were not recorded in whole lake surveys, are excluded from analysis.

Metrics and indices used in the study are described below.

Frequency Occurrence (FO)

The percentage frequency occurrence (FO) of prey items were calculated to identify key prey items (Amundsen *et al.*, 1996).

$$FO_i = \left(\frac{N_i}{N} \right) * 100$$

Where:

FO_i is the percentage frequency of prey item *i*,

N_i is the number of pike with prey *i* in their stomach,

N is total number of pike with stomach contents.

% Number (% N)

The proportional numeric contribution of individual prey species/groups (*i*) to the overall prey numbers in the diet.

$$\%N_i = \frac{N_i}{(N_i + N_{ii} + N_{iii} \dots)} * 100$$



% Biomass (% W)

The proportional contribution of each prey species'/group's (i) combined weight expressed as a percentage of the total biomass of all prey in the diet.

$$\% W_i = \frac{W_i}{(W_i + W_{ii} + W_{iii} \dots)} * 100$$

Where W_i is the biomass of a particular species in sampled pike stomachs

Index of Relative Importance (IRI) and % IRI

To reduce the potential bias inherent in the use of single dietary metrics, the Index of Relative Importance (IRI) was calculated from each prey item/group by combining %N and %W with FO (Pinkas and Iverson, 1971).

$$IRI_i = (\%N_i + \%W_i) * FO_i$$

To improve the comparison of the importance of different prey types %IRI was calculated for each prey item/group (i) in the diet (Cortés, 1997).

$$\% IRI_i = \frac{IRI_i}{(IRI_i + IRI_{ii} + IRI_{iii} \dots)} * 100$$

Ivlev's Electivity Index (E)

This metric produces values between -1 (complete avoidance) and +1 (complete preference/selection) with values around zero indicating neutral prey selection (Ivlev, 1961).

$$E_i = \frac{(r_i - p_i)}{(r_i + p_i)}$$

Ivlev's Forage Ratio

$$E_i = \frac{r_i}{p_i}$$

Similar to Ivlev's electivity index, larger values are indicative of positive prey selection.



Strauss' Linear ratio (L)

A simple linear ratio derived by subtracting the proportion of available prey from its proportion in the diet.

$$L = r_i - p_i$$

Positive values indicate prey preference/selection. Negative values indicate prey avoidance (Strauss, 1979).

Pearre's Selectivity Index

$$V_i = \frac{(r_i \times p_{iii...}) - (p_i \times r_{iii...})}{\sqrt{(r_i + p_i)(r_{iii...} + p_i)(r_i + p_{iii...})(p_i + p_{iii...})}}$$

This metric also produces values between -1 (complete avoidance) and +1 (complete preference/selection) with values around zero indicating neutral prey selection. This metric allows a chi squared value to be derived (Pearre, 1982).

In all instances:

r_i = is the proportion in diet of prey type i in the diet, and p_i is its proportion in environment.

For Pearre's Selectivity Index: $r_{iii...}$ is the proportion of all other prey in the diet, and $p_{iii...}$ is the proportion of all other prey in the environment.

Graphical Representations of Feeding Strategy

Graphical feeding plots, developed by Costello (1990) as modified by Amundsen *et al.*, (1996) were plotted for pike from both lakes and included the sample derived from predator control operations on Lough Conn in March and April 2017. In this instance the specific abundance of prey (P), is defined as:

$$P_i = (\Sigma S_i / \Sigma S_t) \times 100$$

Where S_i is the weight of prey i , in the analysed stomachs and S_t is the total weight of all stomach contents in those pike containing prey i .



This is plotted two dimensionally against the FO of that specific prey item and can be used to infer prey importance and feeding strategy in predators. In the outputs, the vertical axis is representative of feeding strategy, and items which appear towards the top of the graph have been consumed by specialised predators. Conversely items occurring close to the x-axis have been consumed only occasionally. A hypothetical line intersecting both axes represents the percentage abundance of each prey type, with important prey displayed at the upper end of this line. Unimportant prey are displayed at the bottom. Thus, items occurring close to the intersection of the axis are unimportant. Prey occurring at the top right of the graph would indicate a specialist population of predators (Amundsen *et al.*, 1996)



Plate 2.9 Lough Derravaragh at Donore.



Statistical models

Statistical models were used to explore the proportion of sampled pike stomachs that contained a given prey type in each of two lake sampling periods (1960s-70s and 2016-17). An *a priori* set of 14 models was specified (Table 1), each representing explanatory variables hypothesised to affect the selection and consumption by pike of different prey types. The model set was initially fit using generalized linear mixed models (GLMMs). It was assumed that the number of times that a pike stomach was *Observed* to contain prey *k*, in lake *j* in year *i* of *Sampled*_{ijk} pike stomachs followed a binomial distribution with probability π_{ijk} , as follows:

$$Observed_{ijk} \sim \text{Bin}(\pi_{ijk}, Sampled_{ijk})$$

$$E(Observed_{ijk}) = Sampled_{ijk} \times \pi_{ijk}$$

$$\text{var}(Observed_{ijk}) = Sampled_{ijk} \times \pi_{ijk} \times (1 - \pi_{ijk})$$

A logistic link function was used such that

$$\text{logit}(\pi_{ijk}) = \eta_{ijk}$$

$$\eta_{ijk} = \beta_1 + \beta_2 \times \text{covariates} + Y_{ijk}$$

$$Y_{ijk} \sim N(0, \sigma^2_{\text{Period/Year}})$$

The term Y_{ijk} is a random effect on the intercept of sampling year, nested in sampling period.

These preliminary models showed evidence of over-dispersion, so a modified formulation of the binomial GLMM was applied, including an observation-level random effect (OLRE).

In the OLRE method, each data point receives a unique level of a random effect that can absorb the extra-parametric variation in the data. The statistical formulation is otherwise the same as above. The full set of 14 candidate models was fit using the binomial GLMM with OLRE, using the R package lme4 (Bates *et al.*, 2014). Model selection used Akaike Information Criterion (AIC), with models having $\Delta\text{AIC} < 4$ considered to have similar fit to the data. Model assumptions (linearity and homogeneity of variance) were explored using plots of observed and fitted residuals.



2.3 Results

2.3.1 Whole lake fish stock surveys

The proportions of each fish species recorded in the fish stock surveys on Loughs Conn and Derravaragh in August 2016 and July 2017 respectively are presented in Table 2.6.

Table 2.6. Numbers and proportions of fish captured using standardised European survey monofilament gill nets (benthic and pelagic) and fyke nets during whole lake fish stock surveys of Loughs Conn and Derravaragh in August 2016 and July 2017 respectively.

Species	Lough Conn		Lough Derravaragh	
	Number Captured	Proportion	Number Captured	Proportion
Trout	39	5.69	8	1.63
Perch	300	43.73	334	67.89
*Pike	-	-	4	0.81
Roach	313	45.63	130	26.42
Roach x bream hybrid	-	-	8	1.63
Tench	1	0.15	-	-
European eel	33	4.81	8	1.63

Note: *Live pike captured in nets were released. Gastric lavage was not performed on these fish.

2.3.2 Description of Current Pike Diet

A total of 1481 pike from sampling (electrofishing, angling, predator control and whole lake fish stock surveys) on both lakes were available for stomach analysis (Table 2.7). Locations and method of capture are presented in Figures 2.3 and 2.4.

Table 2.7: Number of pike available for stomach analysis and their methods of capture

Lake	No. pike	Method of capture			
		Electrofishing	Gillnetting (braided multifilament)	Predator control	Angling
Lough Conn	617	500	7	110	0
Lough Derravaragh	864	835	0	N/A	29



Lough Conn 2016/2017

In Lough Conn, a total of 507 pike (including seven pike captured during the fish stock survey) were captured during monthly sampling between August 2016 and July 2017 (Table 2.8 and Figure 2.3). Pike ranged in length from 6.2cm to 94.7cm (Figure 2.5). Food occurred in 394 (77.7%) of the examined stomachs (Table 2.9). The minimum size of piscivorous pike was 7.6cm. The maximum size of invertivorous pike was 42.4cm (March 2017). The latter pike also preyed upon fish.

The combined group representing all invertebrates (principally *Asellus* sp. (freshwater louse) and *Gammarus* sp. (freshwater shrimp)) were an important prey group recorded in stomachs of pike. A total of 806 invertebrate prey items (53.8% N) were recorded in 261 pike stomachs (accounting for 1.4% of all prey biomass. %IRI for the invertebrate prey group was 42.9 (Table 2.9).

Three-spined stickleback (*Gasterosteus aculeatus*) was the most numerous fish prey item recorded in the sampled pike stomachs. A total of 401 three-spined stickleback (26.8% N) were recorded in 131 (33.3% FO) stomachs, accounting for 3.0% of all prey biomass. %IRI for three-spined stickleback was 17.2 (Table 2.9).

Roach was the second most numerous fish prey item recorded in the sampled pike stomachs. A total of 199 prey items (13.3% N) were recorded in 127 (32.2% FO) stomachs, accounting for 47.3% of all prey biomass. The greatest proportion of roach in the diet (expressed as a percentage of all fish prey in stomachs) occurred in February 2017, when roach represented 87.9% (n = 29) of all fish prey recorded in the sampled pike (Figure 2.6). %IRI for roach was 34.0 and was thus the most important fish prey item for pike captured in Lough Conn during the study period (Table 2.9).

A total of 37 (2.5% N) perch were recorded in 36 (9.1% FO) pike stomachs, accounting for 20.5% of all prey biomass. The greatest proportion of perch in the diet (expressed as a percentage of all fish prey in stomachs) occurred in June 2017, when perch represented 20.7% (n = 6) of all fish prey recorded in the sampled pike (Figure 2.6). %IRI for perch was 3.6.

A total of 17 trout (1.1% N) were recorded in 16 (4.1% FO) pike stomachs, accounting for 19.8% of all prey biomass. The greatest proportion of trout in the diet (expressed as a percentage of all fish prey in stomachs) occurred in June 2017, when trout represented 10.3% (n = 7) of all fish prey recorded in the sampled pike (Figure 2.6). %IRI for trout was 1.5.



Lough Conn – Predator Control Samples

An additional sample of 110 pike captured during annual predator control operations on Lough Conn in March and April 2017 were available for analysis (Table 2.8; Figure 2.3). Only large pike ($\geq 50\text{cm}$) were included in this sample. Pike ranged in length from 50.0cm to 91.5cm (Figure 2.5). Food occurred in 67 (60.9%) of the examined stomachs (Table 2.8). The minimum size of piscivorous pike was 51.5cm. The maximum size of invertivorous pike was 62.5cm. That pike also preyed upon fish.

Roach was the most numerous fish prey item recorded in the sampled pike stomachs. A total of 66 prey items (52.0% N) were recorded in 42 (62.7% FO) stomachs, accounting for 74.4% of all prey biomass. % IRI for roach was 95.7 and was thus, by far, the most important prey item for those pike that were captured in the predator control operations conducted on Lough Conn (Table 2.10).

Perch was the second most important fish prey item recorded in pike stomachs. A total of 11 individual prey items (8.7% N) were recorded in 10 (14.9% FO) stomachs, accounting for 9.1% of all prey biomass. % IRI for perch was 3.2 (Table 2.10).

A total of six trout (4.7% N) were recorded in four (6.0% FO) pike stomachs, accounting for 10.2% of all prey biomass. % IRI for trout was 1.1 (Table 2.10).

Amphibians (frogs and newts) were a relatively important prey group for pike caught during the March and April 2017 predator control operations. Together, a total of 15 prey items (11.87% N) were recorded in 12 (17.9% FO) pike stomachs, accounting for 3.2% of all prey biomass. % IRI for amphibians was 3.2 (Table 2.10). Amphibians were not recorded in any of the other pike stomachs in Lough Conn.

The combined invertebrate group (principally *Asellus* sp. (freshwater louse) and *Gammarus* sp. (freshwater shrimp)) were relatively unimportant (compared to the monthly samples) in the stomachs of pike captured during predator control operations, which were all greater than 50cm in length. Together, a total of 27 prey items (21.3% N) were recorded in 8 pike stomachs (13.4% FO), accounting for 3.1% of all prey biomass. % IRI for invertebrates was 3.3 (Table 2.10).



Lough Derravaragh 2016/7

In Lough Derravaragh, a total of 864 pike (including 29 angler caught pike) were captured during monthly sampling between August 2016 and July 2017 (Table 2.11 and Figure 2.4). Pike ranged in length from 8.2cm to 110cm (Figure 2.5). Food occurred in 653 (75.6%) of the examined stomachs. The minimum size of piscivorous pike was 8.2cm (June 2017). That pike had also been feeding on invertebrates. The maximum size of invertivorous pike was 95.9cm (June 2017). That pike had also preyed upon fish.

The combined group representing all invertebrates (principally *Asellus* sp. (freshwater louse) and *Gammarus* sp. (fresh water shrimp)) were an important prey group recorded in stomachs of pike. A total of 5319 prey items (83.2% N) were recorded in 378 (56.4% FO) pike stomachs, accounting for 4% of all prey biomass. % IRI for invertebrates was 66.5 (Table 2.12).

Roach was the most numerous and important fish prey item recorded in the sampled pike stomachs during the study period. A total of 533 prey items (8.3% N) were recorded in 251 (38.4% FO) stomachs, accounting for 44.9% of all prey biomass in the sampled stomachs. The greatest proportion of roach in the diet (expressed as a percentage of all fish prey in stomachs) occurred in January 2017, when roach represented 79.7% (n = 94) of all fish prey recorded in the sampled pike (Figure 2.7). % IRI for roach was 27.7 (Table 2.12).

Perch were the second most important fish prey item recorded in pike stomachs. A total of 255 individual prey items (4.0% N) were recorded in 133 (20.4% FO) stomachs, accounting for 9.6% of all prey biomass. The greatest proportion of perch in the diet (expressed as a percentage of all fish prey in stomachs) occurred in June 2017, when perch represented 76.8% (n = 126) of all fish prey recorded in the sampled pike (Figure 2.7). % IRI for perch was 3.7 (Table 2.12)

A total of 20 (0.3% N) pike were recorded in 20 (2.9% FO) pike stomachs, accounting for 31.7% of all prey biomass. % IRI of pike was 1.3 (Table 2.12).

A total of 14 trout (0.2% N) were recorded in nine (1.4% FO) pike stomachs, accounting for 7.8% of all prey biomass. The greatest proportion of trout in the diet (expressed as a percentage of all fish prey in stomachs) occurred in April 2017, when trout represented 76.8% (n = 4) of all fish prey recorded in the sampled pike (Figure 2.7). % IRI for trout was 0.2% (Table 2.12).



Prey Selection Indices

Common themes were apparent across the various prey selection indices. On an annualised basis, these indicated that roach were positively selected (i.e. that they appeared in pike stomachs more frequently than might be expected based upon their availability in the environment) and that perch were negatively selected (i.e. that they appeared in pike stomachs less frequently than might be expected based upon their availability in the environment). All indices for trout, however, tended towards neutrality (i.e. that they appeared in pike stomachs approximately in proportion to their availability in the environment). The same situation pertains for pike captured during predator control operations in Lough Conn in March and April 2017 albeit the selectivity indices for trout on Lough Conn was slightly higher (but still close to neutral) during this period than the annual index values (Table 2.10, Figure 2.8 and Figure 2.9).

Ivlev's Selectivity Ratio and Pearre's Selectivity Index for the three most important fish prey species (roach, perch and trout) in each lake are presented graphically in Figures 2.8 and 2.9

Feeding Strategy

Analysis of the feeding strategy plots indicates that pike (all fish) in both lakes followed a broadly generalist feeding strategy indicated by the position of the smaller prey items (e.g. *Asellus* sp. (freshwater louse), *Gammarus* sp. (freshwater shrimp) and three-spined stickleback) close to the line intersecting the axes (Amundsen, 1996) in the monthly samples from both lakes (Figure 2.10 and 2.12). There appeared to be a degree of specialisation in the piscivorous pike in both lakes (Figure 2.10 and 2.12) and in the sample from predator control operations (all in the larger size class), with less commonly occurring fish items forming the bulk of the stomach contents of pike that had consumed them. In all three samples, roach was the most abundant or important prey item consumed by pike, clearly segregated from the other points on each plot, having been consumed both in high abundance, and forming a high proportion of the stomach contents (by weight) of the pike that had consumed roach (Figures 2.10, 2.11 and 2.12).

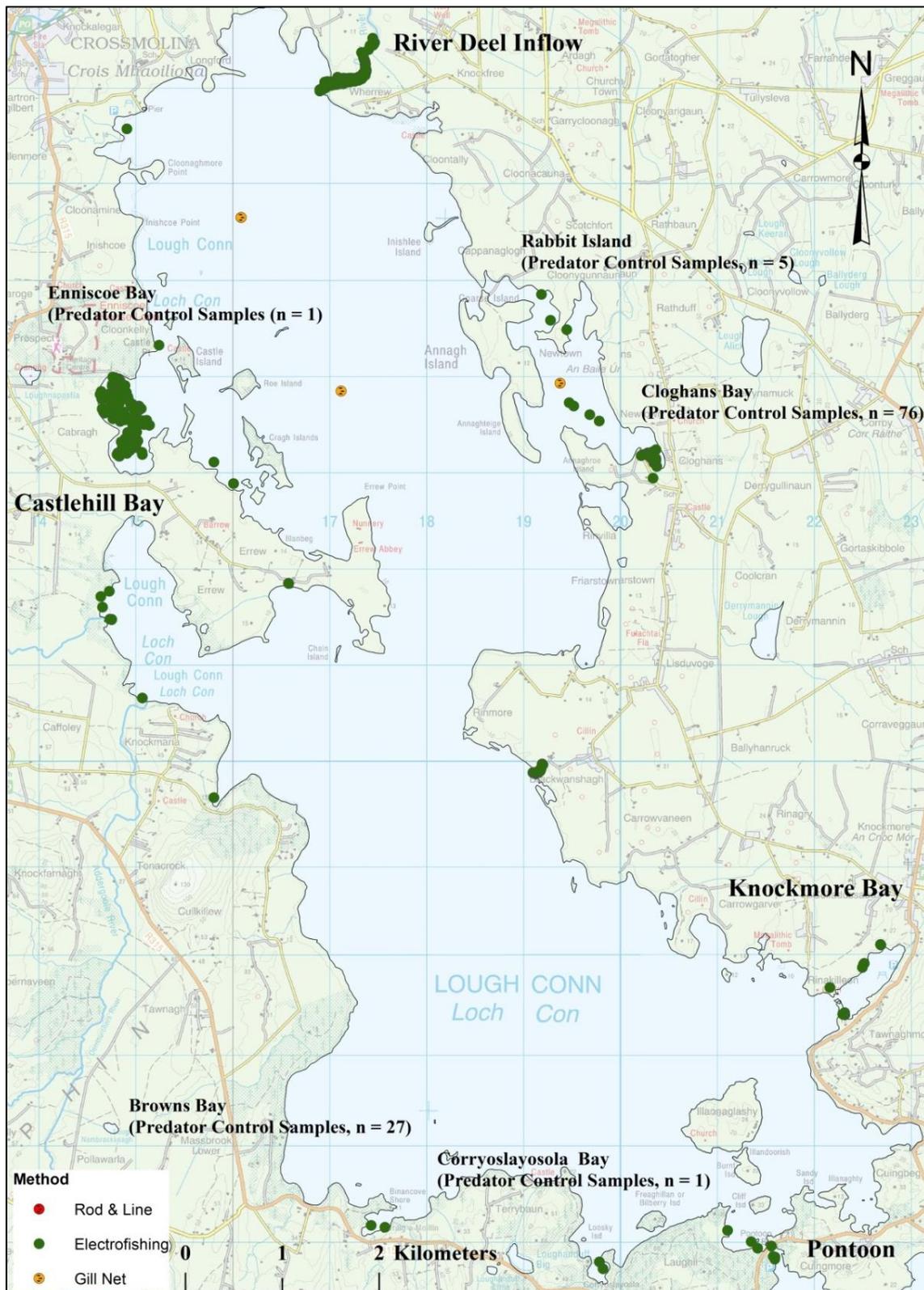


Figure 2.3. Locations of pike captured in Lough Conn between August 2016 and July 2017. The locations of predator control gill nets, and the number of pike included in the sample from each of those locations is indicated.

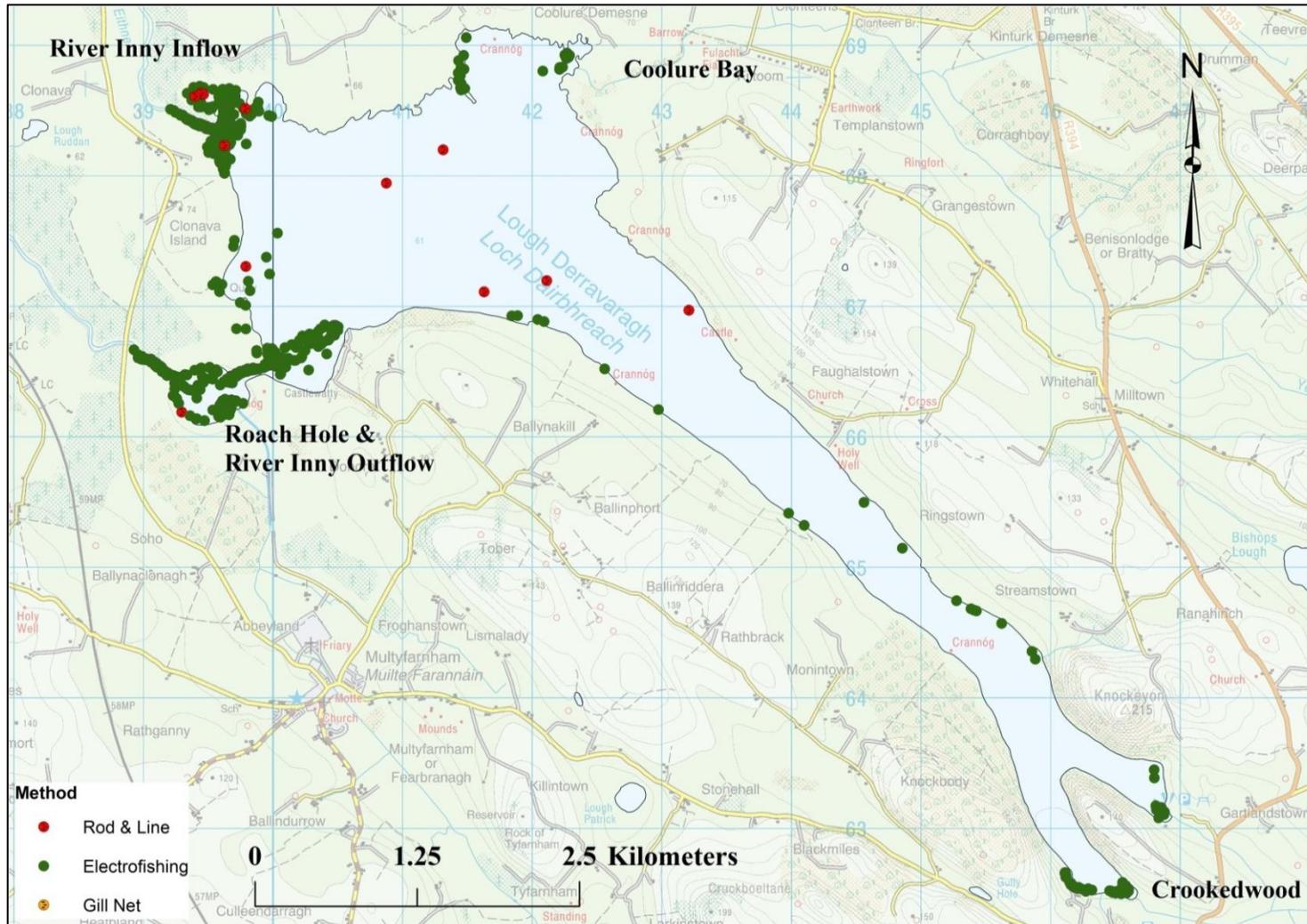


Figure 2.4. Locations of pike captured in Lough Derravaragh between August 2016 and July 2017.

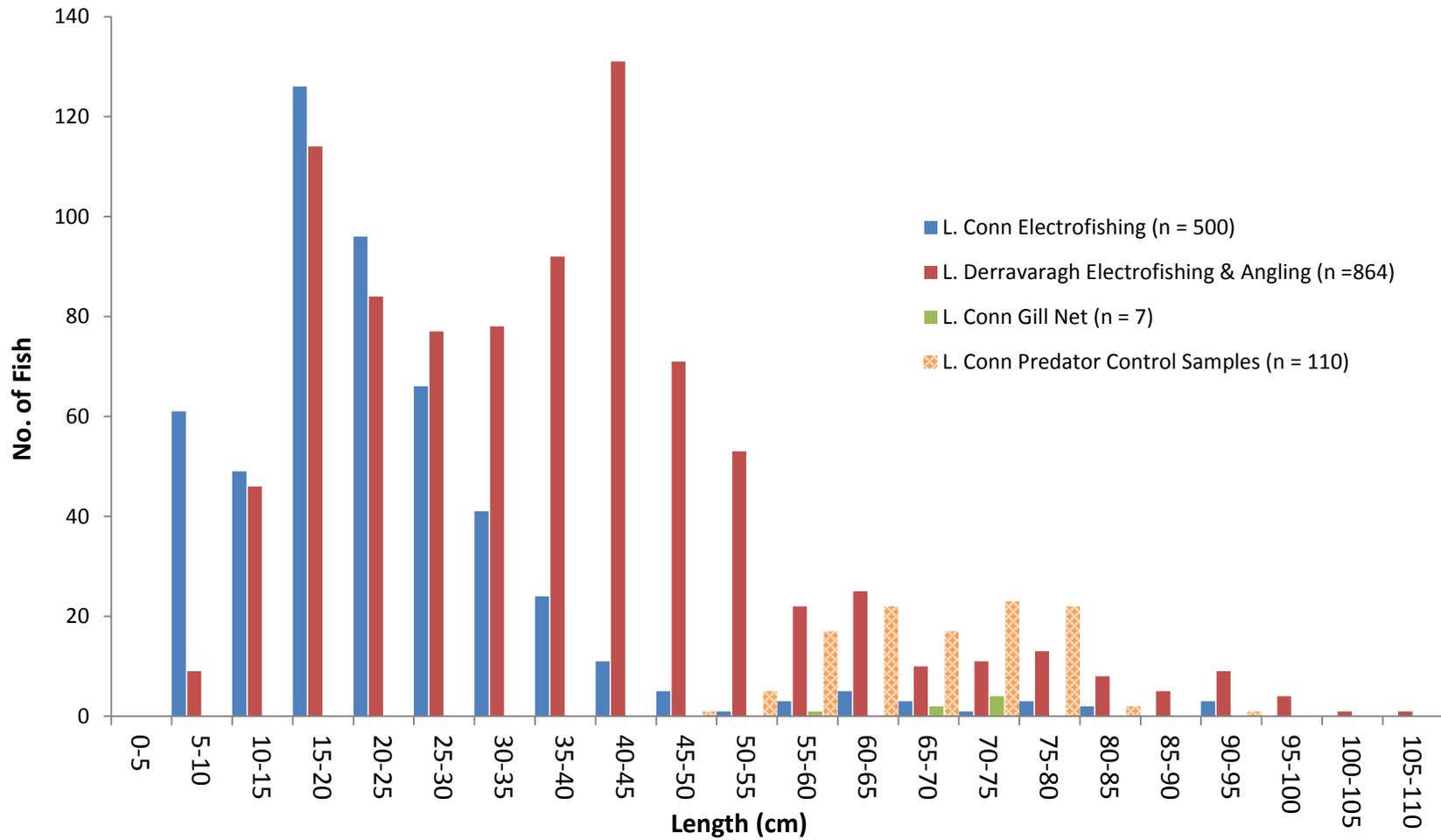


Figure 2.5. Length of pike captured from Loughs Conn and Derravaragh, from which dietary information was collected between August 2016 and July 2017.



Table 2.8. Summary data of pike captured in Lough Conn from which dietary information was collected between August 2016 and July 2017.

Month & Year	n pike	n (with food)	% (with food)	Sex			Length (cm)		
				n (male)	n (female)	n (unknown)	Max	Min	Mean
August 2016	32	26	81.3	10	5	17	57.7	15.5	28.5
October 2016	71	62	87.3	7	14	50	38.8	11.7	21.1
November 2016	21	14	66.7	1	5	15	73.8	14.1	24.4
December 2016	24	12	50.0	3	10	11	59.4	14.2	24.4
January 2017	34	24	70.6	9	6	19	49.1	13.1	22.1
February 2017	40	32	80.0	17	15	8	46.4	13.7	23.5
March 2017	7	4	57.1	4	3	-	91.2	17.5	55.7
April 2017	47	36	76.6	8	8	31	94.7	14.8	27.4
May 2017	50	34	68.0	21	23	6	81.3	14	30.4
June 2017	48	42	87.5	19	11	18	60.5	6.3	19.8
July 2017	126	102	81.0	38	25	63	82.9	6.2	18.9
August 2016 (Braided Survey Gill net)	7	6	85.7	3	4	-	74.5	59.5	69.1
March/April 2017 (Predator Control Sample)	110	67	60.9	49	61	-	91.5	50	65.56
Total	617	461	74.7	189	190	238			



Table 2.9. Summary dietary metrics and indices from pike captured in Lough Conn between August 2016 and July 2017. Data is confined to those fish captured using electrofishing and those caught during the fish stock survey conducted in August 2016. Common names for prey categories are representative of those recorded from pike in both lakes.

Food item	Common name	N (prey item)	% N	n (pike stomachs)	FO	Total Wt (g)	% Wt	IRI	% IRI	Ivlev's Selectivity Ratio	Ivlev's Forage ratio	Strauss' Linear Ratio	Pearre's Selectivity Index
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	401	26.8	131	33.2	40.7	3.0	990.5	17.2	-	-	-	-
<i>Rutilus rutilus</i>	Roach	199	13.3	127	32.2	640.9	47.3	1954.1	34.0	0.25	1.66	31.83	0.30
<i>Perca fluviatilis</i>	Perch	37	2.5	36	9.1	276.9	20.5	209.5	3.6	-0.51	0.32	-31.09	-0.42
Other fish	Unidentified, salmon,	28	1.9	23	5.8	45.7	3.4	30.6	0.5	-	-	-	-
<i>Salmo trutta</i>	Trout	17	1.1	16	4.1	268.5	19.8	85.1	1.5	-0.07	0.88	-0.74	-0.02
<i>Esox lucius</i>	Pike	9	0.6	8	2.0	62.8	4.6	10.6	0.2	-	-	-	-
Invertebrate	All invertebrates	806	53.8	176	44.7	18.7	1.4	2466.8	42.9	-	-	-	-
Total		1497		394		1354.1		5747.2					



Table 2.10. Summary dietary metrics and indices from pike captured during predator control operations on Lough Conn in March and April 2017.
Common names for prey categories are representative of those recorded from pike in both lakes.

Food item	Common name	N (prey item)	% N	n (pike stomachs)	FO	Total Wt (g)	% Wt	IRI	% IRI	Ivlev's Selectivity Ratio	Ivlev's Forage ratio	Strauss' Linear Ratio	Pearre's Selectivity Index
<i>Rutilus rutilus</i>	Roach	66	52.0	42	62.7	2117.1	74.4	7923.7	95.7	0.25	1.66	31.51	0.294
<i>Perca fluviatilis</i>	Perch	11	8.7	10	14.9	259.9	9.1	265.7	3.2	-0.63	0.23	-35.58	-0.51
<i>Salmo trutta</i>	Trout	6	4.7	4	6.0	289.2	10.2	88.9	1.1	0.09	1.21	1.25	0.03
Other fish	Unidentified	2	1.6	2	3.0	0.2	0.0	4.7	0.1				
Amphibia	Common frog, common newt	15	11.8	12	17.9	90.4	3.2	268.5	3.2				
Invertebrates	All invertebrates	27	21.3	9	13.4	87.5	3.1	326.9	3.9				
Total		127		67		2844.4		8278.2					



Table 2.11. Summary data of pike captured in Lough Derravaragh from which dietary information was collected between August 2016 and July 2017.

Month & Year	n pike	n (with food)	% (with food)	Sex			Length (cm)		
				n (male)	n (female)	n (unknown)	Max	Min	Mean
August 2016	46	34	73.9	6	14	26	82.3	11.4	33.2
October 2016	77	61	79.2	14	27	36	78.1	12.9	34.3
November 2016	57	41	71.9	8	27	22	77.4	13.1	35.0
December 2016	77	57	74.0	11	34	32	93.0	12.3	32.8
January 2017	89	65	73.0	28	35	26	71.5	11.1	32.2
February 2017	74	67	90.5	41	32	1	101.0	16.1	42.5
March 2017	118	88	74.6	60	47	11	99.6	14.3	41.0
April 2017	65	56	86.2	24	27	14	76.6	13.6	38.3
May 2017	81	63	77.8	28	49	4	94.0	13.3	40.0
June 2017	97	67	69.1	24	63	10	110.0	8.2	41.3
July 2017	83	54	65.1	16	56	11	95.6	9.1	36.2
Total	864	653	75.6	260	411	193			



Table 2.12. Summary dietary metrics and indices from pike captured in Lough Derravaragh between August 2016 and July 2017. Common names for prey categories are representative of those recorded from pike in both lakes.

Food item	Common name	n (prey item)	% N	n (pike stomachs)	FO	Total Wt (g)	% Wt	IRI	% IRI	Ivlev's Selectivity Ratio	Ivlev's Forage ratio	Strauss' Linear Ratio	Pearre's Selectivity Index
<i>Rutilus rutilus</i>	Roach	533	8.3	251	38.4	1940.1	44.9	2048.0	27.7	0.41	2.41	38.92	0.44
<i>Perca fluviatilis</i>	Perch	255	4.0	133	20.4	412.7	9.6	276.0	3.7	-0.38	0.45	-38.97	-0.42
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	138	2.2	72	11.0	15.2	0.4	27.7	0.4				
Other fish	Tench, stone loach, Roach x bream, Unidentified fish	71	1.1	54	8.3	10.6	0.2	11.2	0.2				
<i>Esox lucius</i>	Pike	20	0.3	20	3.1	1370.4	31.7	98.2	1.3				
<i>Lampetra sp.</i>	Lamprey sp.	38	0.6	19	2.9	52.7	1.2	5.3	0.1				
<i>Salmo trutta</i>	Trout	14	0.2	9	1.4	338.0	7.8	11.1	0.1	-0.04	0.93	-0.12	-0.007
Amphibia	Common frog, common newt	2	0.0	2	0.3	3.1	0.1	0.0	0.0				
Invertebrates	All invertebrates	5319	83.2	368	56.4	174.2	4.0	4918.4	66.5				
Total		6390		653		4316.9		7395.9					

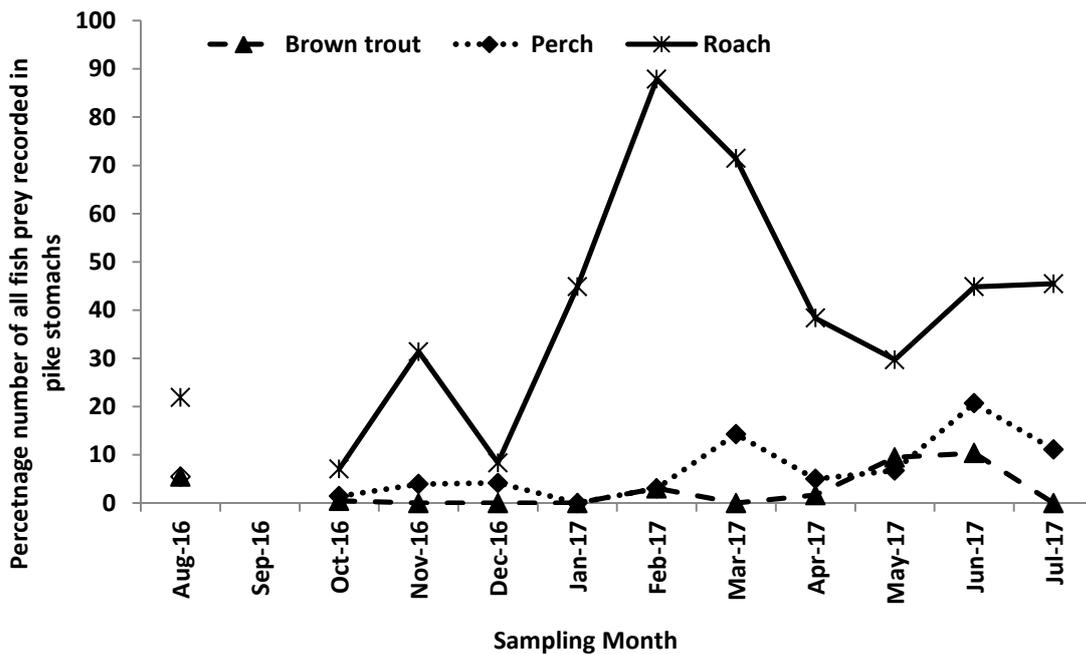


Figure 2.6. Proportional contribution of three fish prey species to the overall fish diet of pike samples monthly from Lough Conn, August 2016 to July 2017. Figures from August 2016 include pike captured during the fish stock survey conducted at that time.

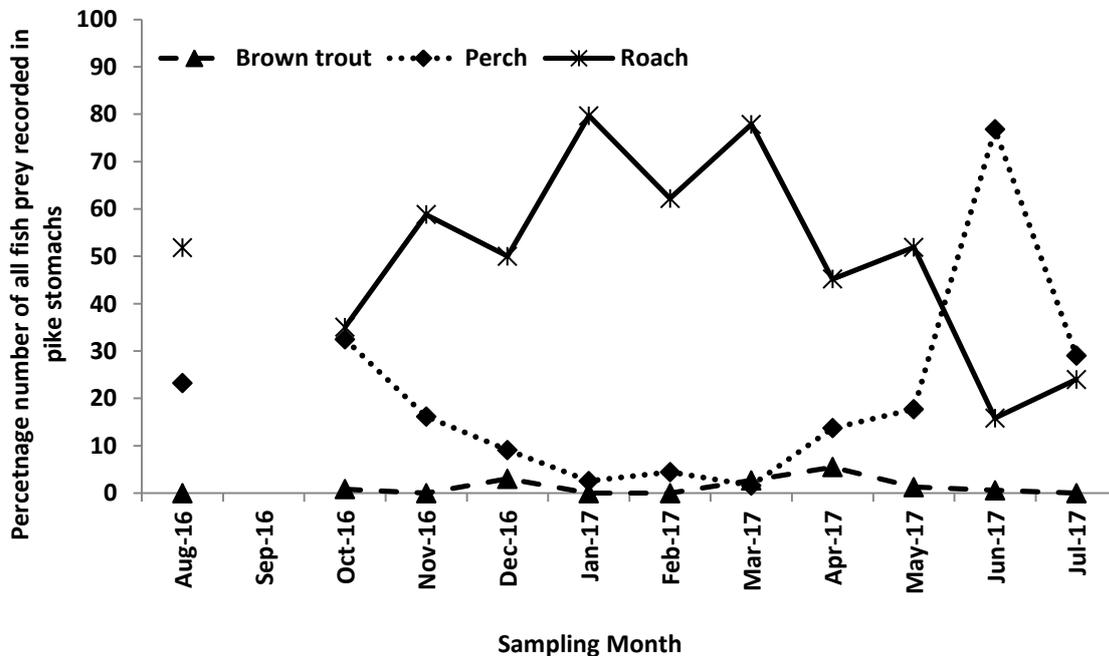


Figure 2.7. Proportional contribution of three fish prey species to the overall fish diet of pike samples monthly from Lough Derravaragh, August 2016 to July 2017.

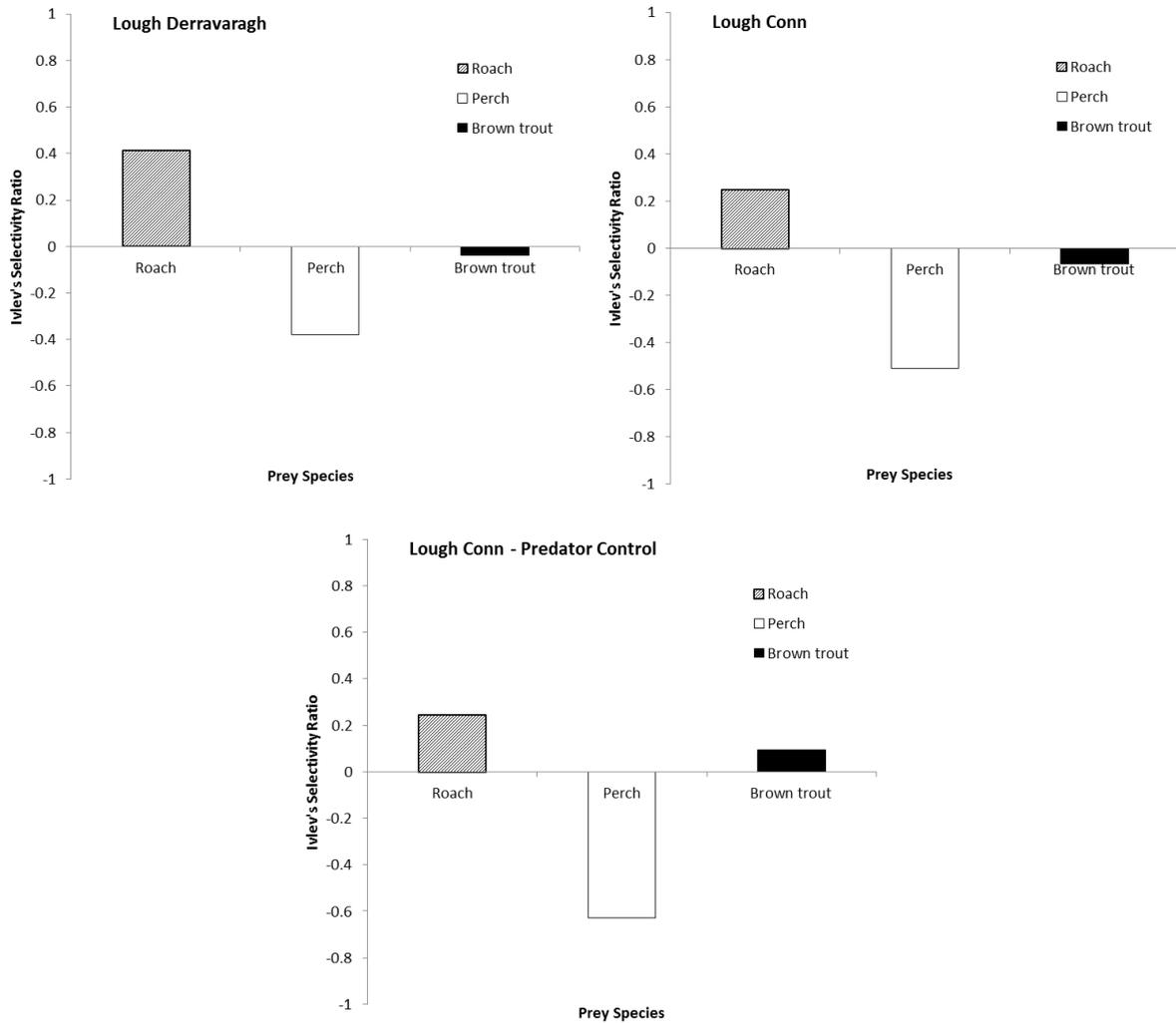


Figure 2.8. Ivlev's Selectivity Ratio for three fish species consumed by pike in Loughs Conn and Derravaragh between August 2016 and July 2017. Values of +1 imply complete selection, while values of -1 imply total avoidance. Prey availability in the environment is based upon relative proportions of the three species captured in European standard survey gill nets (benthic and pelagic) and fyke nets deployed in each lake (Lough Conn, August 2016; Lough Derravaragh, July 2017) during the study period.

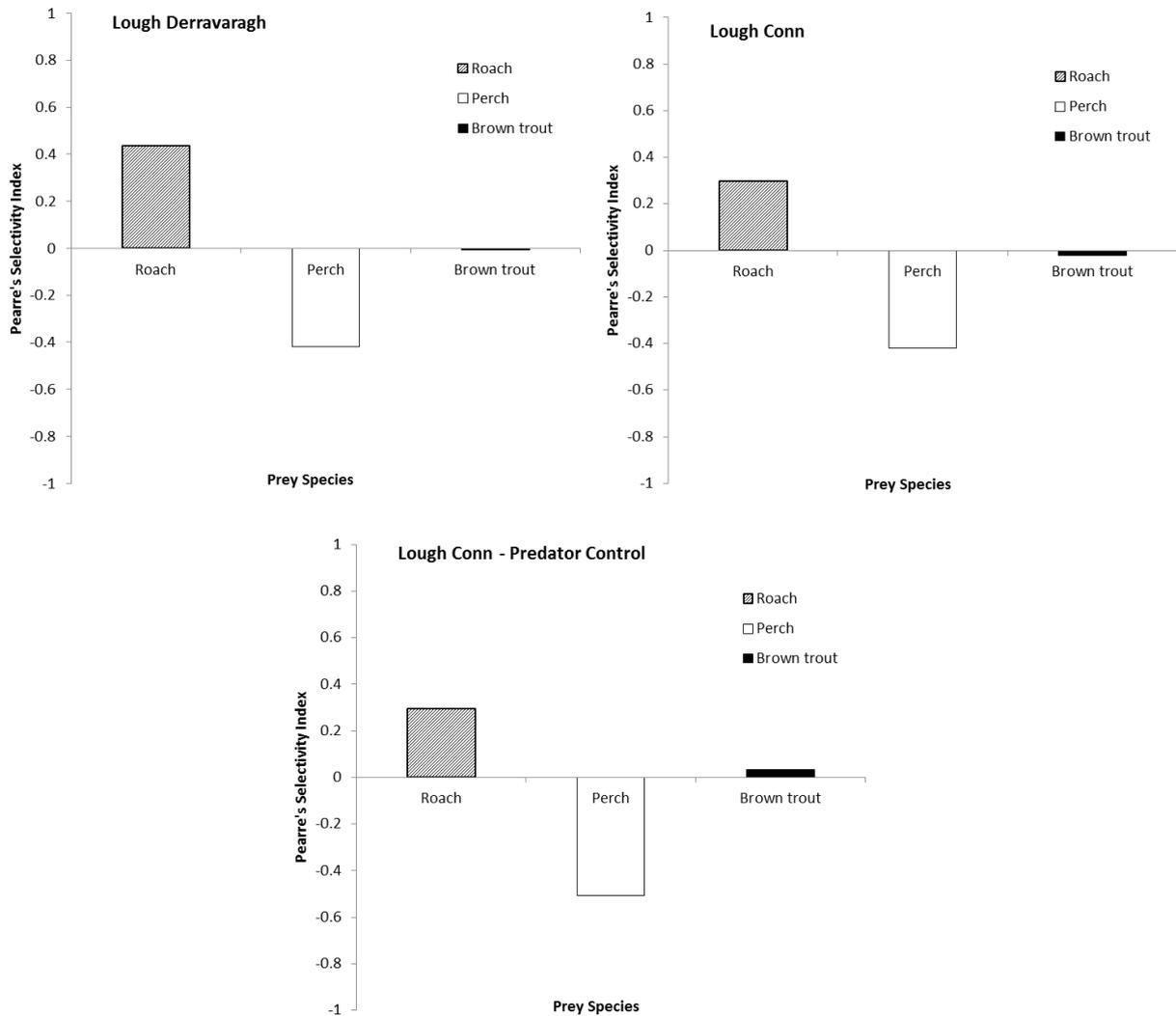


Figure 2.9. Pearre's Selectivity Index for three fish species consumed by pike in Loughs Conn and Derravaragh between August 2016 and July 2017. Values of +1 imply complete selection, while values of -1 imply total avoidance. Prey availability in the environment is based upon relative proportions of the three species captured in European standard survey gill nets (benthic and pelagic) and fyke nets deployed in each lake (Lough Conn, August 2016; Lough Derravaragh, July 2017) during the study period.

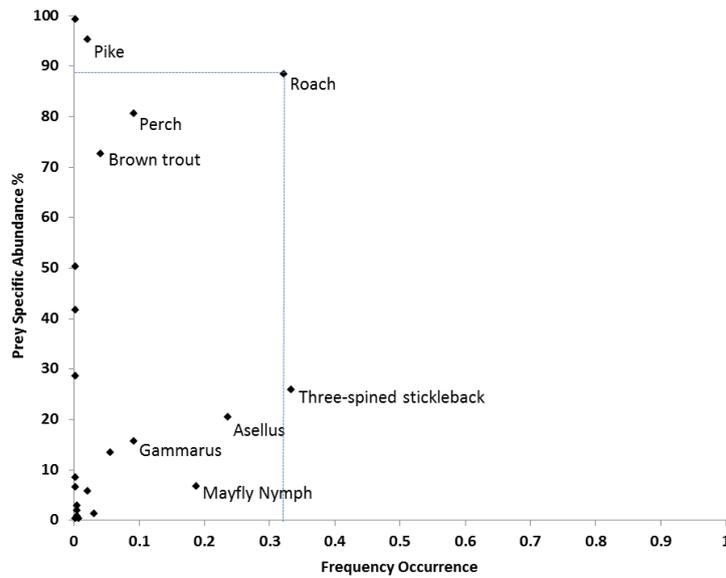


Figure 2.10. Feeding strategy diagram (Amundsen *et al.*, 1996) of pike captured on Lough Conn between August 2017 and July 2016 (n = 394). For each point on the graph prey abundance or importance can be represented by the area within horizontal and vertical lines joining that point to each axis. This is illustrated for roach which is the most important prey item in this instance.

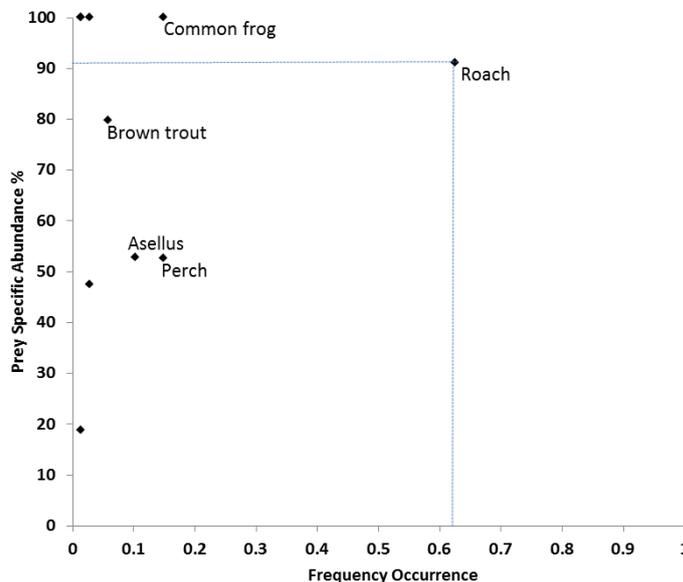


Figure 2.11. Feeding strategy diagram (Amundsen *et al.*, 1996) of pike captured on Lough Conn during predator control operations in March and April 2017 (n = 67). For each point on the graph prey abundance or importance can be represented by the area within horizontal and vertical lines joining that point to each axis. This is illustrated for roach which is the most important prey item in this instance.

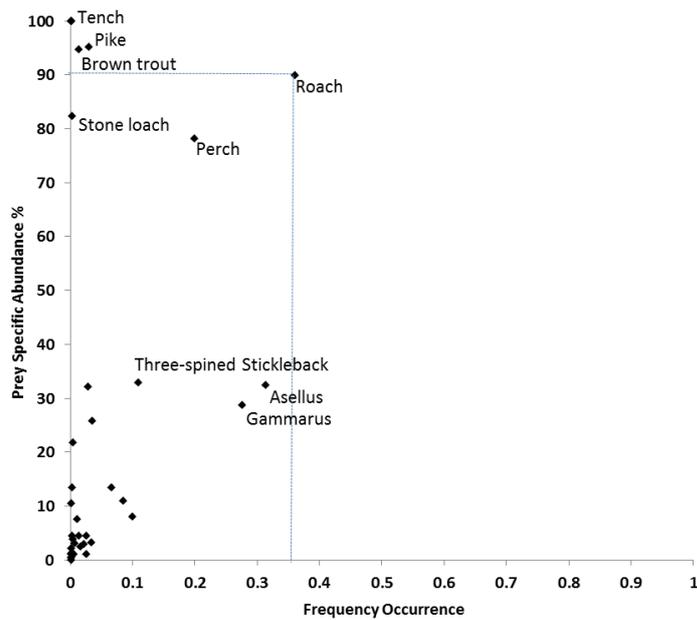


Figure 2.12. Feeding strategy diagram (Amundsen *et al.*, 1996) of pike captured on Lough Derravaragh between August 2016 and July 2017 (n = 653). For each point on the graph prey abundance or importance can be represented by the area within horizontal and vertical lines joining that point to each axis. This is illustrated for roach which is the most important prey item in this instance.



2.3.3 Historical Pike Diet Data

Reliable stomach content data for 3141 and 1538 pike stomachs from predator control operations on Loughs Sheelin (1968-73) and Derravaragh (1967-73) were available for analysis. Length classes of sampled pike are presented in Figures 2.13 and 2.14. Few fish from the smaller two size classes (12.7-25.4cm and 25.4-38.1cm) were captured in either lake, probably due to the selective nature of the gill nets used to capture pike (O' Grady, 1981). Summary data (percentage frequency occurrence of prey items (FO)) is presented both seasonally and by pike size class in Table 2.13.

In both lakes, five prey categories accounted for in excess of 95% of all stomach contents. These were: percid, salmonids, gasterosteids, esocids, cyprinids and invertebrates.

Perch and salmonids (principally trout) dominated the fish diet in both lakes for large and small pike over the early period as a whole (Table 2.13). The latter species was particularly prominent in the stomachs of pike from the larger size class. Cyprinids were a relatively insignificant component of the diet in both lakes at that time. While cyprinids (mainly rudd and bream) were present in both lakes at the time the data was collected, together they represented < 0.1% and c. 1% of all stomachs examined in Loughs Sheelin and Derravaragh respectively (Table 2.13).

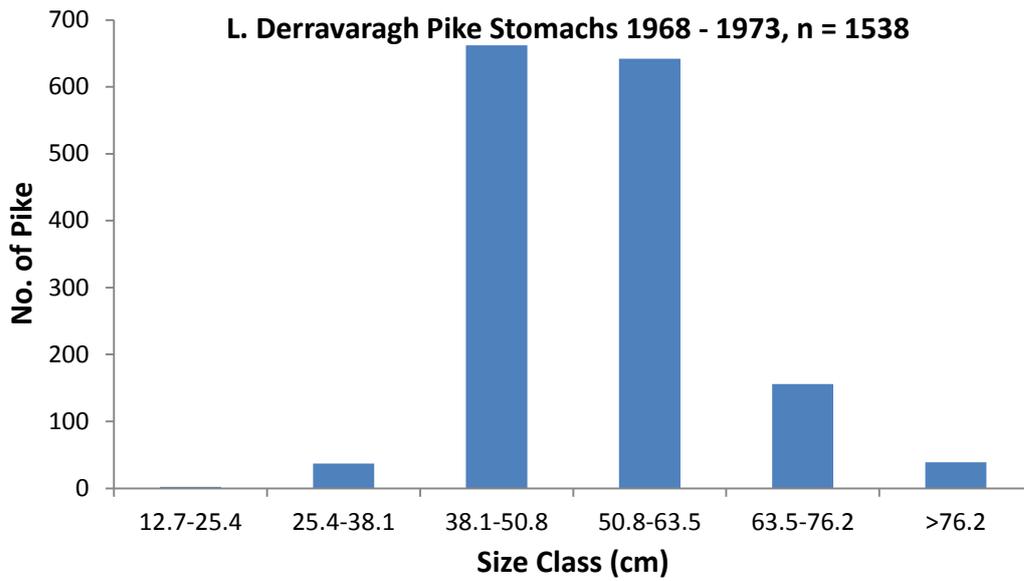


Figure 2.13. Size distribution of pike from Lough Derravaragh from the period 1968-1973 included in a dataset of archival pike diet. Size classes were derived from the archival data set.

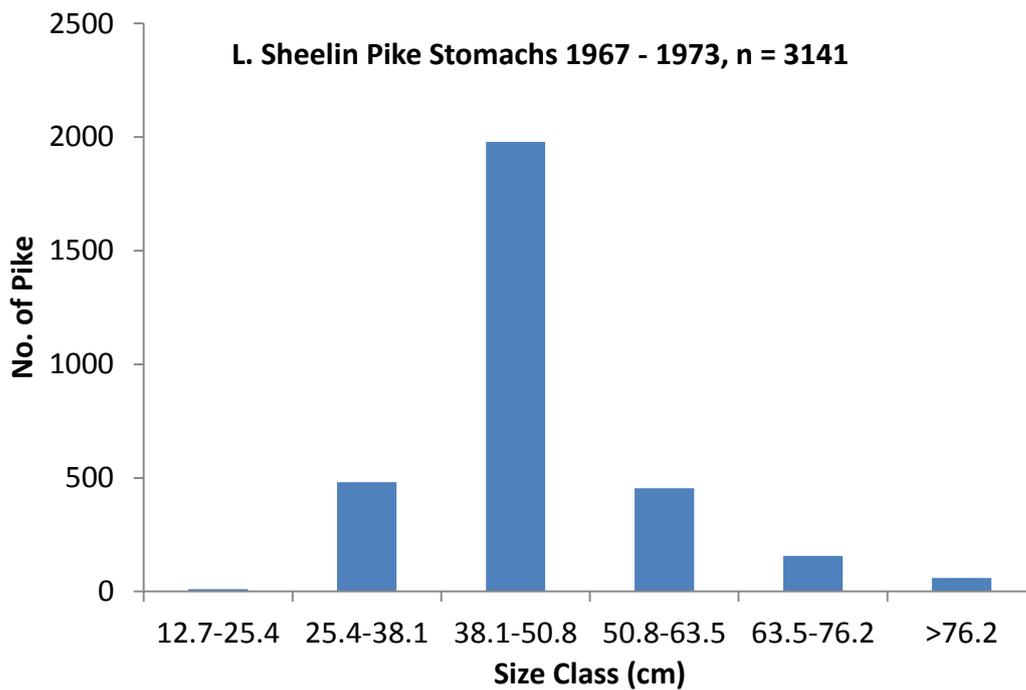


Figure 2.14. Size distribution of pike from Lough Sheelin from the period 1967-1973 included in a dataset of archival pike diet. Size classes were derived from the archival data set.



Table 2.13. Summary percentage frequency occurrence of prey items (FO) obtained from an archival dataset of pike stomach content analysis from Lough Derravaragh (1968-1973) and Lough Sheelin (1967-1973). Data is presented by size class and by season. 'N stomachs' represents the total number of stomachs containing food for each season and/or size class. Insignificant prey groups are not presented.

Lake	L. Derravaragh				L. Sheelin			
Size Category	Small < 50.8cm	Large > 50.8cm	All		Small < 50.8cm	Large > 50.8cm	All	
Season	All		Winter & Spring	Summer & Autumn	All		Winter & Spring	Summer & Autumn
N Stomachs	701	837	1044	494	2470	671	1712	1429
Percid (FO)	52.9	45.9	52.0	42.9	38.1	10.7	50.4	10.5
Salmonid (FO)	32.1	47.9	34.7	53.4	15.5	64.7	28.7	22.7
Gasterosteid (FO)	0.6	0.0	0.3	0.2	26.0	12.1	6.5	42.7
Esocid (FO)	1.7	1.7	1.7	1.6	9.3	5.1	11.0	5.2
Cyprinid (FO)	1.9	0.4	1.1	1.0	0.1	0.1	0.1	0.1
Other Fish (FO)	0.6	0.2	0.3	0.6	0.4	0.4	0.0	1.0
Invertebrate (FO)	9.3	3.3	8.8	0.2	10.1	6.0	2.7	16.9



2.3.4 Inter Era Comparisons of Diet

The selected statistical model (Model 1, see Table 2.14) included interactions between prey type, each sampling period (1960s-70s and 2016-2017), pike size ($\leq 50.8\text{cm}$ $>$) and sampling season (Winter-Spring and Summer-Autumn).

There was a strongly significant increase between sampling periods in the probability of observing cyprinids in pike stomachs, and corresponding strongly significant decreases in the probability of observing perch or salmonids (mainly trout). Pike in the smaller size class were significantly less likely than large pike to have salmonid (mainly trout) prey in their stomach. Pike consumed significantly less perch, salmonids (mainly trout), smaller pike or unidentified fish in the Winter-Spring season than in Summer-Autumn, but there was no seasonal effect on consumption of cyprinids or sticklebacks (Table 2.15 and Figure 2.15).

Graphical representations of the data (FO) used in the models is presented in Figures 2.16 and 2.17. They show broad trends between lakes and across eras and are presented to provide ecological context to the model outputs.

Table 2.14. Candidate statistical models for the presence of a given prey type in pike stomachs sampled from three Irish lakes over two time periods. The best-fitting (lowest AIC) Model 1 (emboldened) was selected.

Number	Model	df	AIC
1	<i>Obs ~ Period × Prey + PikeSize × Prey + Prey × Season + Lake</i>	33	5778
2	<i>Obs ~ Period + PikeSize × Prey + Prey × Season + Lake</i>	27	5833
3	<i>Obs ~ Period × Prey + PikeSize + Prey × Season + Lake</i>	27	5813
4	<i>Obs ~ Period × Prey + PikeSize × Prey + Season + Lake</i>	27	5816
5	<i>Obs ~ Period + PikeSize + Prey × Season + Lake</i>	21	5862
6	<i>Obs ~ Period + PikeSize × Prey + Season + Lake</i>	21	5869
7	<i>Obs ~ Period × Prey + PikeSize + Season + Lake</i>	21	5848
8	<i>Obs ~ Period × Prey + PikeSize × Prey + Lake</i>	26	5824
9	<i>Obs ~ Period × Prey + Prey × Season + Lake</i>	26	5831
10	<i>Obs ~ PikeSize × Prey + Prey × Season + Lake</i>	26	5840
11	<i>Obs ~ Period × Prey + Lake</i>	19	5870
12	<i>Obs ~ PikeSize × Prey + Lake</i>	19	5886
13	<i>Obs ~ Prey × Season + Lake</i>	19	5886
14	<i>Obs ~ Period + PikeSize + Prey + Season + Lake</i>	15	5894



Table 2.15. Results from the selected statistical model (M1, see Table 1) of prey presence in sampled pike stomachs, fit as a binomial GLMM with OLRE.

Covariate	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.534	0.31	-4.947	0
Period-Recent	-0.212	0.198	-1.069	0.285
Prey-Cyprinids	-0.256	0.615	-0.417	0.677
Prey-Small pike	0.438	0.436	1.004	0.315
Prey-Sticklebacks	-0.131	0.45	-0.29	0.771
Prey-Other fish	-0.656	0.824	-0.796	0.426
Prey-Perch	1.781	0.326	5.459	0
Prey-Salmonids	2.648	0.317	8.346	0
PikeSize-Small	-0.085	0.242	-0.349	0.727
Season-Winter/Spring	0.278	0.155	1.797	0.072
Lake-Derravaragh	0.022	0.129	0.17	0.865
Lake-Sheelin	-0.25	0.17	-1.474	0.14
Period-Recent:Prey-Cyprinids	2.35	0.488	4.819	0
Period-Recent:Prey-Pike	0.025	0.417	0.061	0.951
Period-Recent:Prey-Sticklebacks	0.007	0.313	0.023	0.981
Period-Recent:Prey-Other fish	0.655	0.642	1.02	0.308
Period-Recent:Prey-Perch	-1.069	0.27	-3.951	0
Period-Recent:Prey-Salmonids	-1.434	0.394	-3.642	0
Prey-Cyprinids:PikeSize-Small	-0.71	0.457	-1.554	0.12
Prey-Small pike:PikeSize-Small	-0.436	0.407	-1.071	0.284
Prey-Sticklebacks:PikeSize-Small	0.67	0.41	1.633	0.103
Prey-Other fish:PikeSize-Small	-0.128	0.642	-0.2	0.842
Prey-Perch:PikeSize-Small	0.267	0.301	0.888	0.375
Prey-Salmonids:PikeSize-Small	-1.155	0.291	-3.966	0
Prey-Cyprinids:Season-WintSpr	-0.154	0.321	-0.481	0.63
Prey-Small pike:Season-WintSpr	-0.882	0.336	-2.623	0.009
Prey-Sticklebacks:Season-WintSpr	0.521	0.291	1.789	0.074
Prey-Other fish:Season-WintSpr	-0.985	0.45	-2.19	0.029
Prey-Perch:Season-WintSpr	-1.138	0.224	-5.071	0
Prey-Salmonids:Season-WintSpr	-0.889	0.224	-3.967	0

Note: The salmonid category was composed almost entirely of trout (salmon occur in 1 stomach in L. Conn)

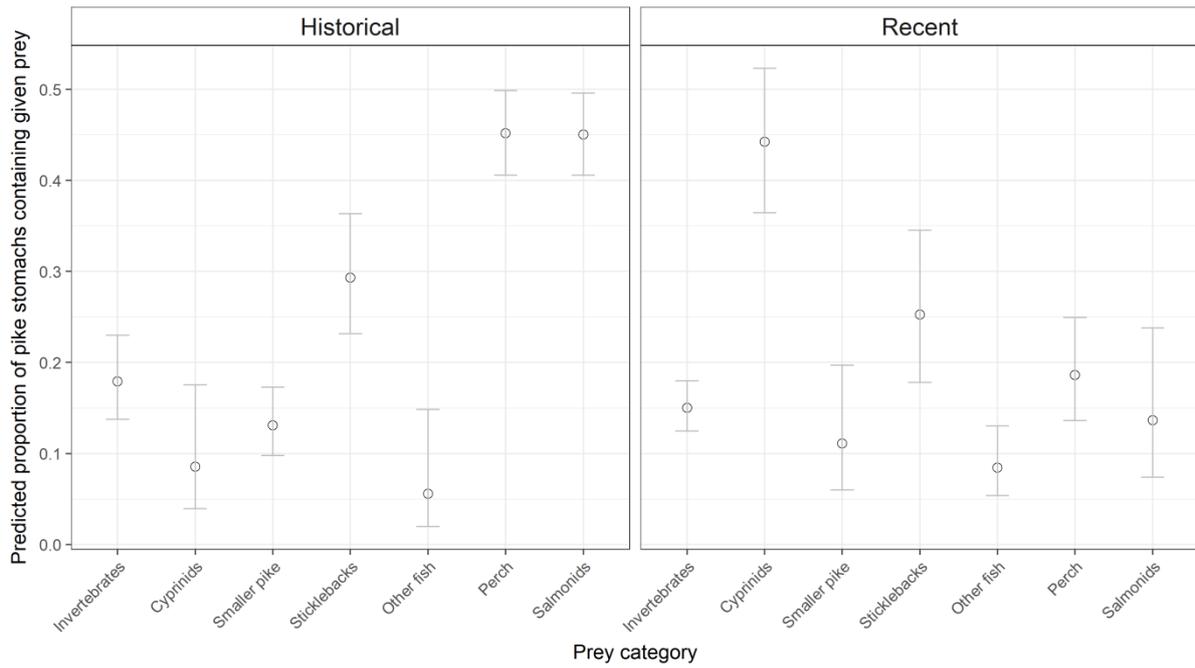


Figure 2.15. The predicted proportion of sampled pike stomachs that will contain a given prey type, for two pike sampling periods (Historical 1960s-70s and Recent 2016-2017). Error bars are 95% confidence intervals. Results were predicted from a binomial GLMM with OLRE (model M1, see Table 2.14).

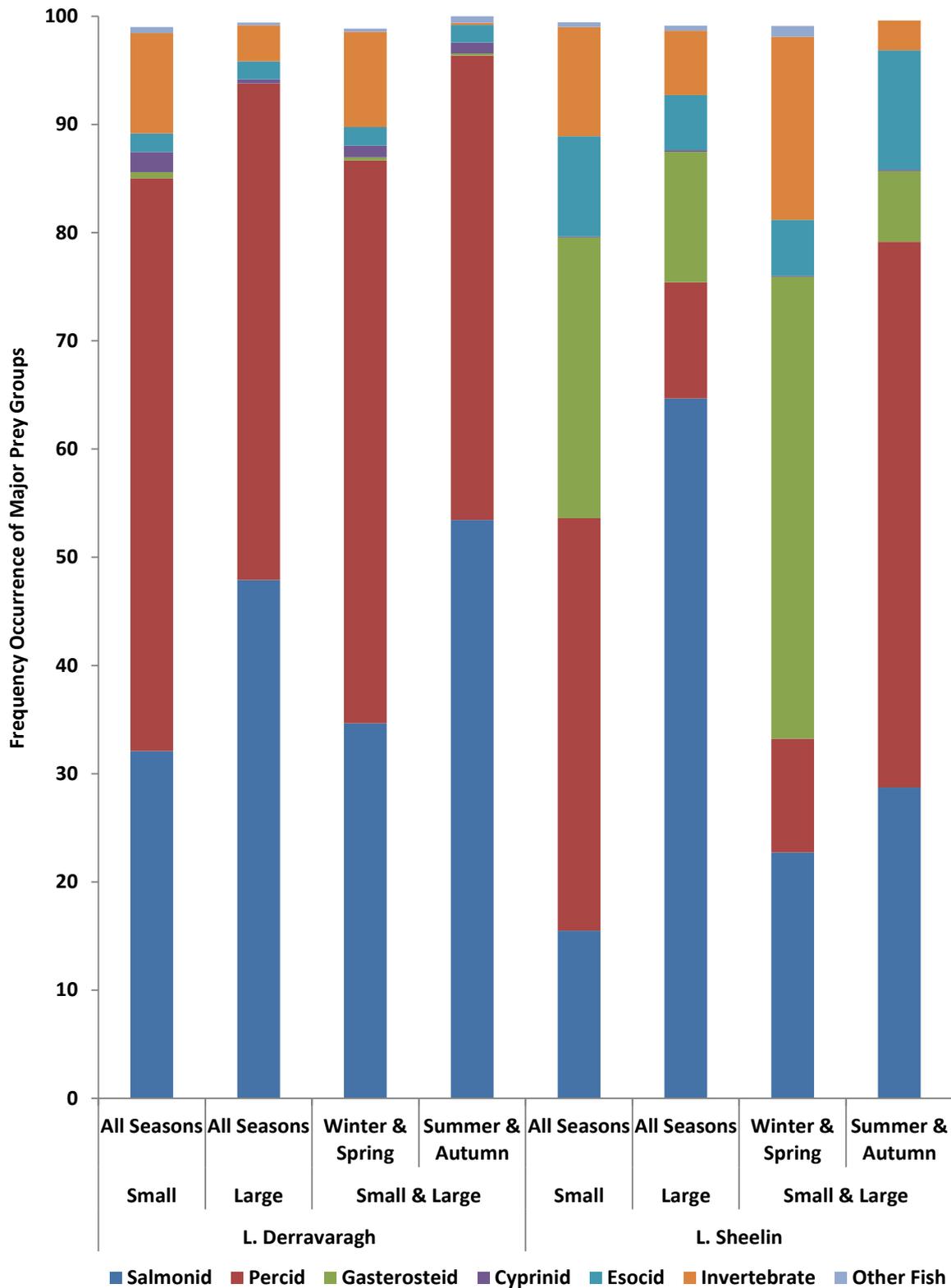


Figure 2.16. Frequency occurrence of prey items (FO) obtained from an archival dataset of pike stomach content analysis from Lough Derravaragh (1968-1973) and Lough Sheelin (1967-1973). Data is presented by size class ($\leq 50.8\text{cm}$ >) and by season.

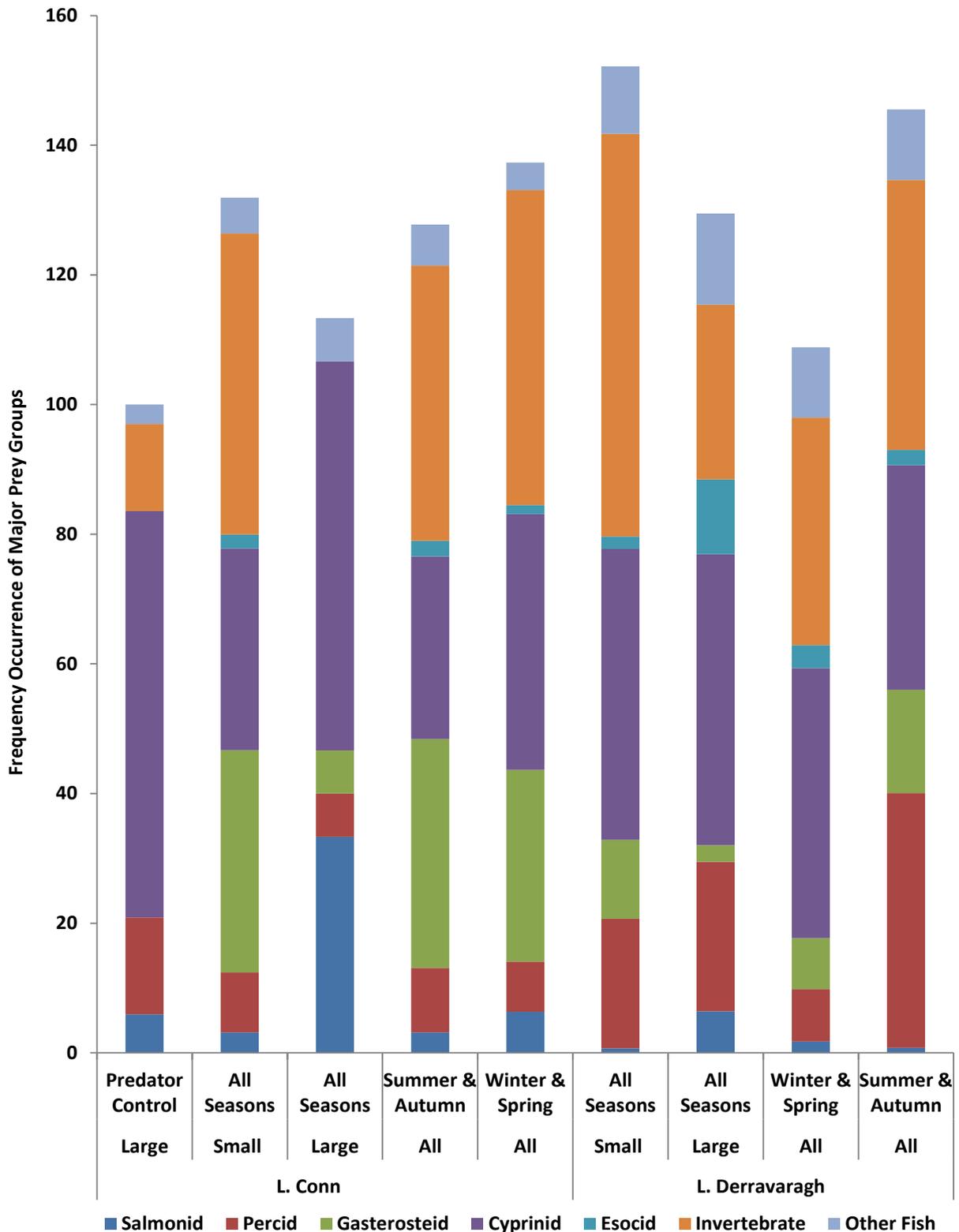


Figure 2.17. Frequency of occurrence of major prey groups recorded in pike stomachs in Loughs Derravaragh and Conn. Samples were collected monthly between August 2016 and July 2017. Data is presented by size class ($\leq 50.8\text{cm}$ >) and by season.



2.4 Discussion

Pike in both lakes examined during the project consumed a wide variety of prey organisms. While invertebrates were common in the diet of pike in both lakes, pike were found to feed on fish from very early stages in their ontogeny. In both lakes the population of pike as a whole were found to adopt a generalist feeding strategy exploiting prey readily available in the environment, a common feature of pike which can display a high degree of dietary flexibility (e.g. Chapman and Mackay, 1990, Beaudoin *et al.*, 1999; Pedreschi *et al.*, 2015).

While the Frequency of Occurrence of invertebrates (principally *Gammarus* sp. (freshwater shrimp) and *Asellus* sp. (freshwater louse) was lower in large pike (>50.8cm) compared to smaller fish (<50.8cm), they were a component of the diet of large pike in both lakes, particularly Lough Derravaragh. While %IRI for invertebrates was high (42.5 and 66.5% in Lough Conn and Derravaragh respectively) in the monthly samples from both lakes, it should be noted that such compound metrics, where species are combined, may inflate these values (Hansson, 1998).

Although very few pike less than 10cm were captured, early piscivory is consistent with findings elsewhere where piscivory is common in young of year pike (Mittelbach and Persson, 1998) and increases in frequency with length (Skov *et al.*, 2003). Previous Irish studies suggested that Irish pike became predominantly piscivorous only at length > 55-60cm with an apparent preference for trout in some lakes (e.g. Healy, 1956). Although fish were recorded in stomachs of smaller pike in that study, small Irish pike were believed to be largely invertivorous, with more recent studies also indicating that Irish pike become primarily piscivorous only when they have attained large sizes (Pedreschi *et al.*, 2015). While analysis of the current pike diet in both lakes does indicate increased piscivory in the larger fish, pike in the smaller size class do feed on fish in both lakes, where they occurred in a large proportion (> 50%) of those stomachs which contained food. Fish also formed a large component of the diet of small pike during the historical period in both lakes, where perch and trout combined occurred in greater than 50% of the stomachs of pike in both lakes. Trout were found in the stomachs of c.65% of large pike in Lough Sheelin during the earlier period, supporting the conclusions of the early research that larger, piscivorous pike preyed predominantly upon trout (e.g. Toner, 1959) even in lakes where other prey was available (Healy, 1956; Fitzmaurice, 1983). The cyprinids, namely rudd and bream were present in both study lakes, but were an insignificant component of the pike diet. This is consistent with other studies where pike, which are gape limited predators (Nilsson and Brönmark, 2000), prey upon shallower bodied species (at specific lengths) of fish (Mauck and Coble, 1971; Nilsson *et al.*, 1995, Nilsson and Brönmark, 2000) and select against



spiny bodied fish such as perch (Eklöv and Hamrin, 1989). This was not the case in Lough Derravaragh, however, where perch and trout occurred in similarly high proportions, possibly due to differences in fish stocks at that time.

While some differences were apparent between lakes, roach were the most important component of the diet of pike in both lakes assessed in 2016/7. Although three-spined stickleback were numerically the most abundant fish recorded in stomachs of pike sampled monthly in Lough Conn, roach were the most abundant fish prey in stomachs of pike in Lough Derravaragh. In both lakes roach were recorded in >30% of pike stomachs. Roach also accounted for the highest proportion of all consumed biomass (>40%) in both Lough Conn and Derravaragh. This dominance was more pronounced in the sample of larger pike obtained during predator control operations on Lough Conn.

Preferences (as indicated by prey selectivity indices) for consuming roach and an avoidance of perch were observed in samples from both lakes, perhaps because of an avoidance for spiny bodied fish such as perch (Eklöv and Hamrin, 1989). However, selectivity of the survey gill nets used may bias this estimate seasonally towards perch (Prchalová *et al.*, 2009). Trout were recorded in the stomachs of pike from both lakes, but generally in small numbers. In Lough Conn, trout were recorded in 4.1 % (16) of stomachs which contained food in monthly samples and in 6.0 % (4) of stomachs which contained food in pike obtained from predator control operations in March and April 2017. In Lough Derravaragh, trout were recorded in 1.4% (9) of pike stomachs which contained food. Their occurrence in stomachs was typically similar to the proportion recorded in surveys of both lakes and does not indicate a selection preference for this species, as indicated by the various prey selection indices presented. Likewise, in a recent study in North America, the closely related esocid (Muskellunge *Esox masquinongy*) predated predominantly upon the widely available river herrings (Alewife and blue backed herring) and not downstream migrating Atlantic salmon smolts, as was commonly assumed (Andrews *et al.*, 2018). However, the apparent peak in trout predation observed in the current era during spring/early summer coincides with the period of downstream migration of river trout to lake environments, and many of the trout were small (< 15cm) individuals. Lake entry is believed to be a pike predation bottleneck for salmonids in natural lakes with hydropower barriers (Kennedy *et al.*, 2018) and reservoirs (Jepsen *et al.*, 1998).

Comparison with an equivalent data set obtained from pike in Lough Derravaragh and Lough Sheelin from the 1960's and 1970s indicates a profound shift in the diet of pike in Irish lakes, where roach have been introduced. The earlier period predates the colonisation of roach in many waterbodies



(Fitzmaurice, 1981) and many of the other major anthropogenic changes that have occurred in Irish lakes, such as eutrophication (Champ, 1998) and the colonisation of invasive species such as zebra mussels (Millane *et al.*, 2008). The presence of large numbers of roach fry and juveniles in Loughs Conn and Derravaragh also now represents a widely available and easily exploitable food resource for pike in those lakes. Furthermore, trout were stocked to, and perch removed from, both lakes at the time that the earlier data was collected, although the impact of this practise on the diet of pike at that time is unclear.

Interestingly, a study conducted in Lough Sheelin in the early 1980's when roach were available to pike, did not find that roach were a significant component of pike diet (Gargan, 1986). At that time, perch fry, and trout were the dominant fish prey recorded in pike stomachs. The latter species dominated the diet of larger pike (Gargan, 1986). The capacity of predators to quickly adapt to non-native or introduced prey has been described, with apparent lags in prey utilisation (e.g. Carlsson, *et al.*, 2009) or differences in prey use by individual predators (Pintor and Byers, 2015) reported. It is possible, therefore, that at that time, pike in Lough Sheelin had not yet adapted to the new prey resource that had become available. A study of fish diet in Lough Sheelin following colonisation by zebra mussels, conducted in the mid 2000's indicated a greater degree of predation upon roach in that lake (Millane, 2008) compared to the earlier period.

In the most recent period, roach were the most important fish prey consumed by pike in both Lough Conn and Lough Derravaragh. A similar dietary shift following an expansion of a roach population in Lough Windermere has also been noted (Winfield *et al.*, 2012). Changes in pike diet have been recorded following the colonisation of ruffe (*Gymnocephalus cernua*) in Loch Lomond possibly alleviating predation pressure on native fish stocks (Adams, 1991).



3: Models of coexistence for pike and trout in Irish lakes

3.1 Introduction

Pike is an apex (opportunistic, but predominantly piscivorous) predator (Craig, 2008) that can rapidly shape fish community structure (DeBates *et al.*, 2003). Pike demonstrate a large degree of dietary flexibility both individually and at population level (Chapman and Mackay, 1990; Beaudoin *et al.*, 1999; Pedreschi *et al.*, 2015). The ability of pike to reduce or even extirpate resident fish species has been described across Europe (e.g. Hesthagen *et al.*, 2015) and North America (Patankar, 2006; Sepulveda *et al.*, 2013; Nicholson *et al.*, 2015) where pike have expanded outside of their native range. The potential of salmonids to coexist with pike has been examined by a number of authors (e.g. Byström *et al.*, 2007; Spens and Ball, 2008; Hein *et al.*, 2014). While no coexistence was recorded in a total of 1029 boreal lakes in Sweden, where pike and salmonids were found to be mutually exclusive (Spens and Ball, 2008) other authors have shown that abiotic variables including lake area and air temperature influence coexistence (Hein *et al.*, 2014).

The aim of this study was to develop statistical models to predict the probability of coexistence between pike and trout across abiotic and fish community gradients to inform future lake management strategies.

3.2 Methods

3.2.1 Fish and abiotic data

The study mainly used data from an IFI database that includes records of 26 fish species collected between 1951 and 2015 from 891 lakes across the island of Ireland. A total of 522 lakes with current and/or historical records of pike were included in the analysis (Figure 3.1). Only waterbodies having some current and/or historical record of pike presence were included in analysis. It was assumed that trout have been extirpated from systems currently having only pike. Fish data for each lake recorded whether or not pike and trout coexisted successfully, and if alternative prey fish species were present, with presence and absence recorded as 1 and 0 respectively.

Six abiotic variables were chosen for inclusion in candidate models (Table 3.1). Geographic information system (GIS) software – ESRI's ArcGIS 10.3.1 – was used to derive lake area (ha) and elevation (m) for all 522 lakes from national lake polygon and digital terrain model datasets. Mean air temperature (°C) served as a surrogate for water temperature (McCombie, 1959) and was



derived by joining an ArcGIS polygon of each lake with the nearest point in a 1km grid of modelled 30-year average values for mean air temperature, available from Met Éireann (Walsh, 2012). Connectivity, a measure of the total wetted width (m) of inflowing streams at the point where they enter each lake was calculated in ArcGIS for 439 lakes, and served as a measure of stream size/habitat quantity and of the potential recruitment of trout to each lake. It also provides a measure of pike dispersal potential, both downstream and upstream where gradients are suitable (Spens *et al.*, 2007; Hein *et al.*, 2011).

Statistical models were used to identify important abiotic factors explaining the coexistence of pike and trout in Irish lakes. A Bayesian framework was applied using the R package “INLA” (Rue *et al.*, 2017), which can model spatial autocorrelation among sampling locations.

Table 3.1. Median (minimum and maximum) values of abiotic variables, and the ‘alternative prey’ variable included in the tested statistical models.

Variable	Value	No Lakes
Area (ha)	11.16 (0.09 - 11650.5)	522
Maximum depth (m)	7 (0.46 - 57)	477
Mean depth (m)	3.05 (0.15 - 15.57)	449
Elevation (m)	48.09 (0.71 - 195)	522
Mean air temperature (°C)	9.5 (8.4 - 11)	522
Connectivity (m)	3.4 (0.8 - 258.3)	438
Alternative Prey	0 or 1	522

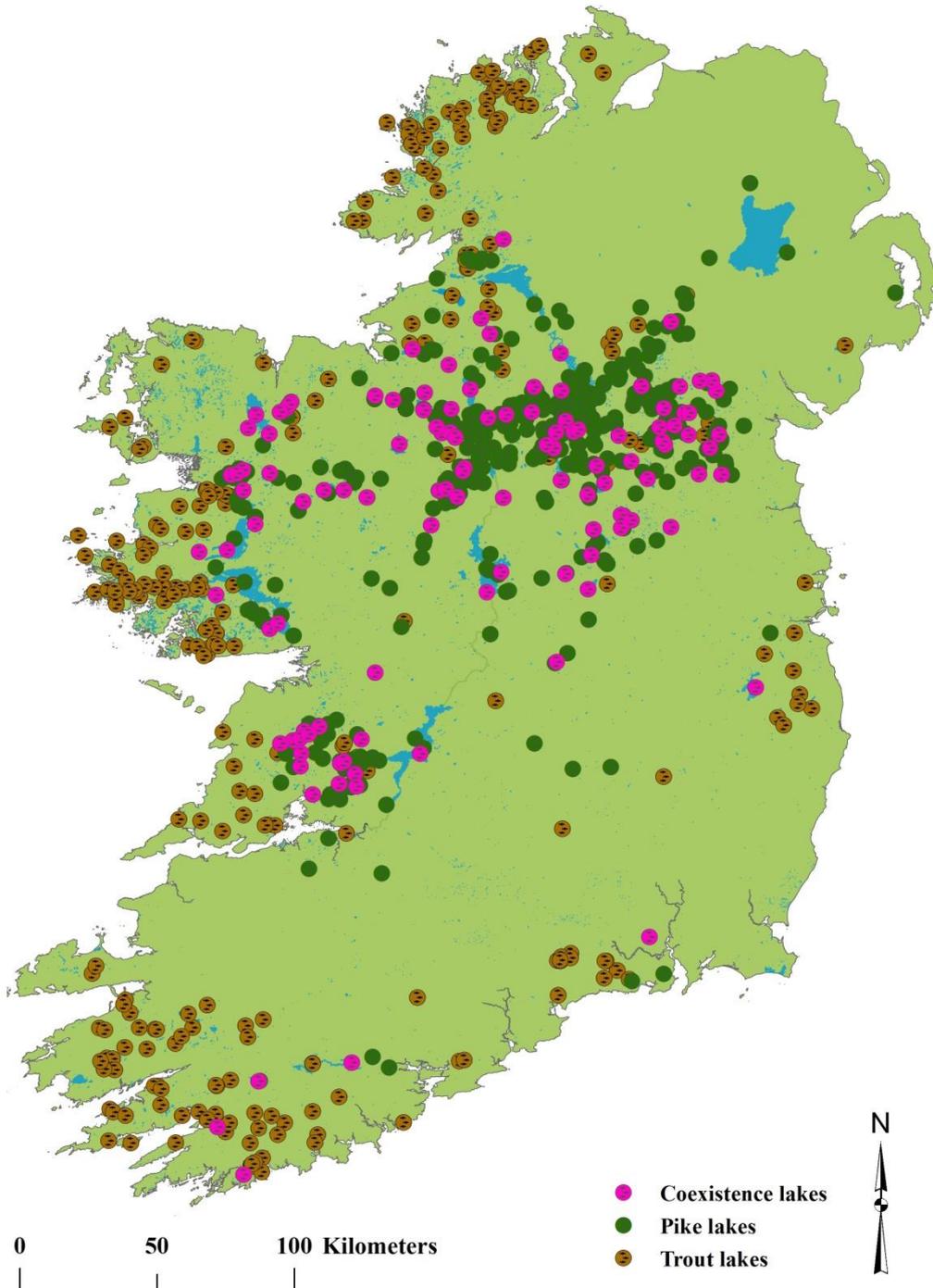


Figure 3.1. Distribution of lakes in the IFI database. Only those lakes where there have been positive records of pike were used in the analysis. 'Coexistence lakes' contain records for both species. 'Pike lakes' have records for pike but not trout. 'Trout lakes' have records for trout, not pike.



3.2.2 Statistical Models

Twelve candidate models (Table 3.2) were specified. Each model represented an *a priori* hypothesis about the likely set of factors explaining the coexistence of pike and trout in Irish lake *i*. In some models, given covariates were included as random smoothing terms. All models were formulated as follows:

$$\begin{aligned} \text{Coexist}_i &\sim \text{Bernoulli}(\pi_i) \\ E(Y_i) &= \pi_i \text{ and } \text{var}(Y_i) = \pi_i \times (1 - \pi_i) \\ \text{logit}(\pi_i) &= \beta_1 + \beta_n \times \text{Covariate}_i \end{aligned}$$

Models were compared using the Watanabe Akaike Information Criterion (WAIC). Further analysis was performed on two models that had strongly lower ΔWAIC (Table 3.2).

Examination of the residuals of these two selected models showed evidence of positive spatial autocorrelation up to about 100km, i.e. proximate lakes were more likely to have a similar coexistence response than lakes further apart. A version of each selected model was then fit with a random term for spatial dependency as follows:

$$\begin{aligned} \text{Coexist}_i &\sim \text{Bernoulli}(\pi_i) \\ E(Y_i) &= \pi_i \text{ and } \text{var}(Y_i) = \pi_i \times (1 - \pi_i) \\ \text{logit}(\pi_i) &= \beta_1 + \beta_2 \times \text{Covariate}_i + u_i \\ u_i &\sim \text{GMRF}(0, \Sigma) \end{aligned}$$

The term u_i is a spatially correlated random intercept, which models dependence in the coexistence response among proximate lakes. The u_i are assumed to be normally distributed as a continuous Gaussian field, represented in the model as a Gaussian Markovian Random Field (GMRF). The GMRF modelled spatial dependence on a triangulation of the study domain (Ireland and Irish lakes); the triangulation mesh was specified to avoid boundary effects and comprised 2850 vertices with a maximum edge of 10km. This spatial random intercept represents the effect of latent (unquantified) spatial factors, not included in the fixed part of the model, which impact the probability of pike - trout coexistence across Ireland. Drivers of coexistence in Irish lakes were inferred from the two models with the spatially correlated random intercept.



3.4 Results

Pike were recorded in 522 Irish lakes. Of these, 425 currently contain pike, but not trout. Pike and trout coexist in 97 lakes (Figure 3.1). Statistical models, accounting for spatial non-independence among lakes, suggested that large deep lakes with strong stream connectivity show a greater probability of pike-trout coexistence (Table 3.3). There were strong positive values for the spatial random term u_i (expressing latent effects on coexistence) in two patches in the west of Ireland, where pike have only been recorded recently. These patches may be consistent with the assumption that this term partly expresses a latent effect of period since pike introduction. In contrast, the Irish midlands showed areas of coexistence ‘cold-spots’ where coexistence between the two species is lower than predicted by the fixed effects in the models.

However the results are highly uncertain, with large ranges of possible probabilities with the 95% credible intervals. This uncertainty suggests that it may be difficult to predict the probability of coexistence between pike and trout in a given lake in Ireland. Only the largest (Figure 3.2) and deepest lakes with strong connectivity can be confidently assumed to have a high probability of coexistence. Neither of the two selected models included presence of alternative (non-trout) prey.

Table 3.2. Candidate statistical models of pike-trout coexistence in Irish lakes. The term s represents a smoothing function. Selected models are highlighted in bold.

Number	Model	Effective pars	WAIC
1	Coexist ~ Max depth + Mean temperature	3.34	397.02
2	Coexist ~ Lake area + Mean temperature	4.14	401.05
3	Coexist ~ Max depth + Mean temperature + Prey	3.35	402.40
4	Coexist ~ Max depth + Elevation	3.58	397.66
5	Coexist ~ Max depth	2.38	396.92
6	Coexist ~ Max depth + s (Mean temperature)	2.40	396.91
7	Coexist ~ Max depth + s (Elevation)	2.40	396.91
8	Coexist ~ Area + s (Max depth)	8.74	356.71
9	Coexist ~ Area + s (Mean depth)	8.20	403.33
10	Coexist ~ Connectivity + factorDepth	4.48	356.22
11	Coexist ~ Max depth + factorConnectivity	4.50	381.00
12	Coexist ~ Max depth * Connectivity	7.37	385.14



Table 3.3. Parameters of selected statistical models of pike and trout coexistence in Irish lakes (see Table 3.2 above). Values are the mean, and the 2.5th and 97.5th percentiles of the posterior distribution of each parameter.

Variable	Mean	0.025quant	0.975quant
Model 8			
Intercept	-0.854	-4.088	2.248
Area	7.424	4.233	11.27
Model 10			
Intercept	-2.067	-4.572	0.207
Connectivity	1.774	1.275	2.319
factor Depth Deep	1.757	0.675	3.001
factor Depth mid-Deep	0.784	-0.269	2.006
factor Depth mid-Shallow	-0.62	-1.851	0.724
factor Depth Shallow	-2.904	-5.805	-0.629

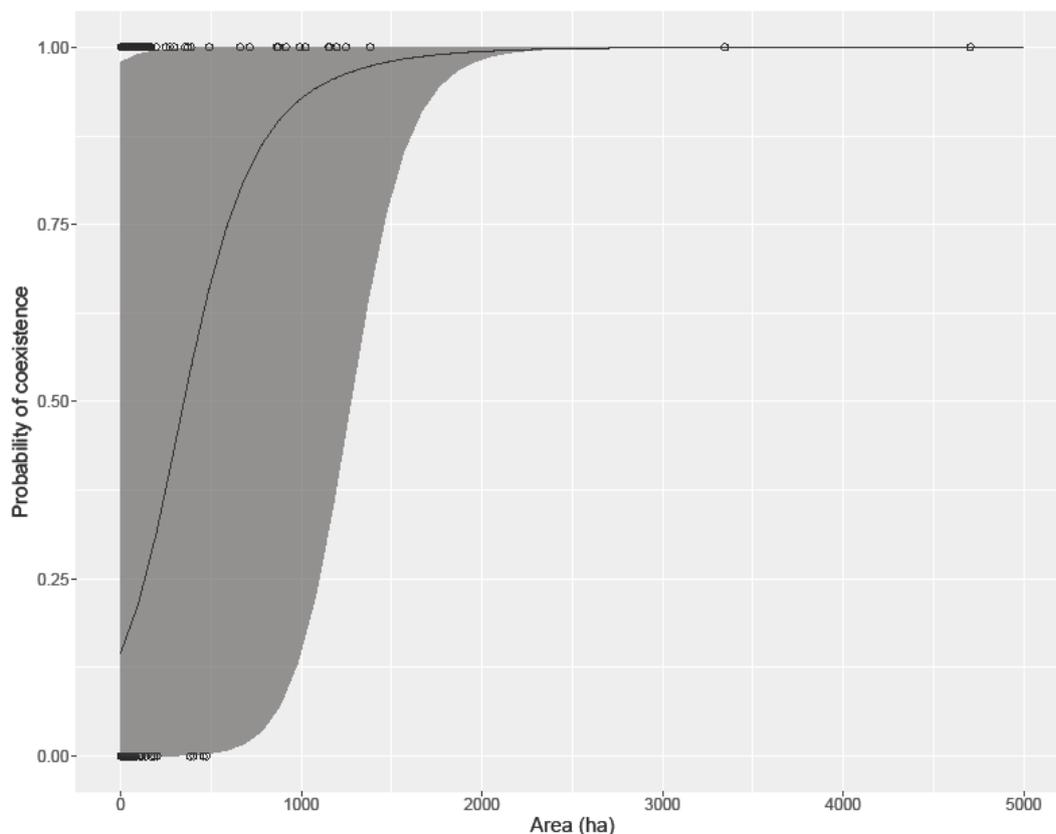


Figure 3.2. Predicted probability (from Model 8) of pike-trout coexistence across a gradient of total area (ha) in Irish lakes. The dark grey shaded area is a 95% credible interval.



3.5 Discussion

Statistical models suggested that relatively large deep lakes with strong stream connectivity offer a greater probability of coexistence for pike and trout in Ireland.

Lake size (area) and temperature can determine coexistence potential thresholds for pike and trout in Swedish lakes (Hein *et al.*, 2014). We showed that there is a strong positive effect of lake size in determining the probability of coexistence of trout and pike in individual Irish lakes. The median size of lakes used in the models was 11.18ha, and thus trout populations in the majority of Irish lakes (which are predominantly relatively small) may be vulnerable to pike introduction. All study lakes exceeding 600ha currently support coexisting pike and trout stocks. Large lakes provide a diversity of habitats and are therefore likely to reduce the impacts of predation *via* reduced encounter rates between trout and pike (e.g. Whitehead and Walde, 1992). Large and deep lakes may also provide a thermal refuge to predation by conferring on trout some physiological resistance to predation at temperatures lower than 11°C (Öhlund *et al.*, 2014).

Lake connectivity (width of inflowing streams) provides an approximate measure of potential trout recruitment to lakes from natal streams, and had an important positive effect on coexistence potential in Irish lakes. Trout persisted in streams flowing into a Norwegian lake where pike colonisation had led to their extirpation (Hesthagen *et al.*, 2015). On the contrary, the ability of pike to enter a waterbody naturally influences the distribution of fish communities in boreal lakes in Sweden (Spens *et al.*, 2007; Hein *et al.*, 2011), where stream slopes in excess of 6.6% (Spens *et al.* 2007) and 7% (Hein *et al.*, 2011) are natural dispersion barriers to pike. Lakes isolated from pike are dominated by salmonids whilst those connected to pike lakes are dominated by species such as perch and roach (Spens and Ball, 2008). In Ireland, those lakes in central lowland areas, most of which contain pike, are also characterised by mixed fish stocks (e.g. cyprinids and perch) where historical distributions of pike and potential fish prey species overlap (Kennedy and Fitzmaurice, 1968; Kennedy and Fitzmaurice, 1974; Went, 1978). If these coexistence 'cold-spots' correspond to earlier arrival of pike, it is possible that fish communities in these lakes have been structured by pike over a longer period. Genetic evidence for relatively new populations of pike in Ireland (Pedreschi *et al.*, 2014), corresponds to the strongest patches of positive u_i in our models.

Habitat morphology can influence resistance to predation by pike on three-spined stickleback (Haight and Von Hippel, 2011) and salmonids (Sepulveda *et al.*, 2013), while the amount of littoral



(Pierce and Tomcko, 2005) and vegetated (Grimm, 1981) habitat may also mediate coexistence potential.

Lake morphology, specifically the amount of littoral (<5m deep) habitat was an important factor determining pike density and biomass in small (800ha) lakes (Pierce and Tomcko, 2005; Haught and Von Hippel, 2011; Sepulveda *et al.*, 2013). The availability of vegetated habitat can be an important factor driving recruitment success in young of year pike (Grimm, 1981) and possibly mediates coexistence potential. Many Irish lakes have undergone strong ecological change in recent decades (Champ, 1998), including the introduction of roach as an abundant new prey species (Pedreschi *et al.*, 2015). Invasive species (i.e. zebra mussel *Dreissena polymorpha*) have also altered lake ecosystems (Millane *et al.*, 2008). Associated and potentially compounding impacts of these factors on littoral habitats and water clarity which have been reviewed by Jacobsen and Engström-Öst (2018) are also likely to influence competitive interactions between the two species.

Most of Ireland's wild trout fisheries that contain pike are large and well-connected lakes with deep areas. Acknowledging the statistical uncertainty surrounding our model outputs, it is likely that pike and trout would be able to coexist in such systems. Pike introductions to small low-complexity systems could, however, be devastating to resident trout populations as observed in recent IFI surveys in counties Donegal and Galway (IFI unpublished data; IFI, 2018). Fish stocks in Irish lakes have important cultural and economic value (Campbell and Hutchinson, 2007) and management should focus on preventing the transfer of fish species outside of their current range (Caffrey *et al.*, 2014).



4: Potential changes in the effect of pike removal after roach invasion

4.1 Introduction

The Inland Fisheries Trust Inc. (IFT) was formed in 1951, and took over the management of many Irish lakes with the objective of developing trout angling and monitoring pike populations (Fitzmaurice, 1983). The IFT commenced pike removal on Lough Sheelin in about 1952. In the early 1970s, Lough Sheelin had a healthy trout stock and was considered one of Ireland's foremost trout fisheries (Allott *et al.*, 1998). The lake has subsequently experienced the effects of eutrophication (since the 1970s, Champ, 1977), introductions of the cyprinid roach (late 1970s, Fitzmaurice, 1981) and zebra mussel invasion (late 1990s, Millane *et al.*, 2008). These anthropogenic factors have interacted, with a strong effect of zebra mussels on chlorophyll *a* concentration (Higgins *et al.*, 2008). There have been boom-and-bust cycles in the abundance of roach in Lough Sheelin, and this fish has become an important prey species for pike (Pedreschi *et al.*, 2015). Trout populations showed a long-term decline since the 1970s, with some recent recovery.

Several early studies (e.g. Healy, 1956; Kennedy, 1969; Gargan and O'Grady, 1992) indicated trout as a preferred food source for pike in Lough Sheelin, but most associated sampling was conducted prior to the establishment of invasive roach. The subsequent availability of this cyprinid fish as an abundant alternative prey species may have alleviated pike predation pressure on trout (Winfield *et al.*, 2012; Pedreschi *et al.*, 2015). This putative dietary shift could change the efficacy of pike removal as a salmonid conservation tool. Annual fish stock surveys were conducted in Lough Sheelin from 1981-2015 (e.g. O'Grady and Delanty, 2001b), and pike removal records were available from 1980-2014. These long-term data-sets were used here to (1) compare pike diet (stomach contents) before and after the roach invasion, (2) test for an effect of pike removal on abundance of trout in Lough Sheelin, and (3) evaluate whether any pike removal effect changed across a threshold of roach abundance and with temperature and chlorophyll *a* concentration.

4.2 Methods

4.2.1 Study area

Lough Sheelin is a relatively shallow (mean depth 4.4 m, maximum depth 15.0 m) and highly productive hard-water lake in the upper Shannon catchment; it has a surface area of 18.1 km² and catchment area of 256 km². The lake supports populations of trout, pike and roach, as well as perch, hybrids of bream, roach and other fishes.



4.2.2 Data collection

Fish sampling

Fish were sampled in Lough Sheelin during March annually from 1981-2015 (excluding 1997 and 1998). Sampling used 7-panel (2 inch to 5 inch at 0.5 inch intervals) benthic braided survey gill nets designed to capture trout in excess of 19.8cm (O' Grady, 1981). 80 survey gill nets per year (nets y^{-1}) were set from 1981-1987, being reduced to 60 nets y^{-1} in 1988, 40 nets y^{-1} from 1989-1996 and 30 nets y^{-1} in subsequent years. Fish catch was recorded as number of individuals per net by species and year. Annual number of fish caught by species per 10 survey nets ($\frac{\text{Number of fish}}{\text{Number of nets}/10}$) was used for the current analysis. This metric accounted for survey effort while retaining the Poisson (count) distribution of the data; number per net resulted in some non-integer values. Three missing values for roach and trout catch (years when no survey occurred) were each estimated as the average of the two closest proximate values.

Pike diet

Pike diet was analysed in 17 years, with good coverage of the overall Lough Sheelin survey history. Annual number of stomachs sampled varied from $n = 9$ to 130 (mean = 49 stomachs). Stomach contents were identified to species for all fish, and to family or genus for invertebrate and other groups. The number of empty stomachs was recorded. Stomachs were separated into two pike length classes for analysis ($< 51\text{cm} \geq$) as this length has historically been thought to represent an ontogenetic shift to piscivory for Irish pike.

Pike removal

Inland Fisheries Ireland maintained an annual pike removal programme in Lough Sheelin during the spring prior to pike spawning. The primary methods used were gill nets, long lines and wire traps and more recently electric fishing. Records of the number of pike removed from the lake as part of this formal programme were available for 1980-2014. A missing value for 2010 was estimated as the average of the two proximate records.



Chlorophyll a

Chlorophyll a was measured in Lough Sheelin once a month from 1976-2015 by Inland Fisheries Ireland (e.g. Kerins *et al.*, 2007). Annual mean values for chlorophyll a concentration ($\mu\text{g l}^{-1}$) were calculated.

Temperature

Seasonal temperature regime for Lough Sheelin was derived from a nationwide 1km grid of average summer (JJA) air temperature ($^{\circ}\text{C}$) modelled by Met Éireann. Fish sampling occurred in March, so summer air temperature was lagged by 1-year for the analysis to capture the most recent period of assumed maximum fish feeding activity.

4.2.3 Statistical models

Pike Diet

A generalized linear mixed model (GLMM) with a binomial distribution was used to test for a change in the annual proportion of sampled Lough Sheelin pike stomachs containing a given prey species, in years before and after the appearance of introduced non-native roach in the diet. It was assumed that the number of pike stomachs *observed* to contain a given prey species (or being empty) in pike length class k (small and large individuals: $< 51\text{cm} \geq$) in year j (see above) nested in period i (up to and including the first year that roach were observed in pike stomachs, and subsequently: $< 1983 \geq$) of total pike stomachs *sampled* follows a binomial distribution with probability π_{ijk} as follows.

$$\text{Observed}_{ijk} \sim \text{Bin}(\pi_{ijk}, \text{Sampled}_{ijk})$$

$$E(\text{Observed}_{ijk}) = \text{Sampled}_{ijk} \times \pi_{ijk}$$

$$\text{Var}(\text{Observed}_{ijk}) = \text{Sampled}_{ijk} \times \pi_{ijk} \times (1 - \pi_{ijk})$$

The probability that a sampled stomach contained a given prey species (or is empty) was specified in the tested model as follows.

$$\text{logit}(\pi_{ijk}) = \eta_{ijk}$$

$$\eta_{ijk} = \theta_1 + \theta_2 \text{Prey}_{ijk} \times \theta_3 \text{Period}_i + \theta_4 \text{LengthClass}_k + y_j + \varepsilon_{ijk}$$

$$y_j \sim N(0, \sigma_{\text{year}}^2)$$

$$\varepsilon_{ijk} \sim N(0, \sigma_{\varepsilon}^2)$$



Pike removal

The annual survey catch (number of fish 10nets⁻¹, see above) of trout in Lough Sheelin was modelled in the Bayesian statistical framework using the R package 'INLA' (Rue *et al.*, 2017). The aim was to evaluate whether the effect of pike removal (year_{*t-1*}) on trout survey abundance (year_{*t*}) changed with abundance of roach (year_{*t-1*}), hence an interaction between annual number of pike removed and the roach survey catch (number of fish 10nets⁻¹) was included as the fixed part of the model. A smoother was used to model a temporally auto-correlated year effect (capturing inter-annual fluctuations in trout abundance that are not explained by the model covariates). Additional smoothers on temperature and chlorophyll *a* concentration were also tested, as these factors are likely to be important underlying ecological drivers in Lough Sheelin. This approach defined four candidate models: (1) including smoothers on temperature and chlorophyll *a*, (2) including a smoother only on chlorophyll *a*, (3) including a smoother only on temperature, and (4) including neither additional smoother. Model comparison was conducted using the deviance information criterion (DIC). The four candidate models had similar DIC (Δ DIC = 1.76), acceptable residuals and no evidence of over-dispersion. The simplest model (Model 4) was thus selected:

$$\text{Trout}_t \sim \text{Poisson}(\mu_t)$$

$$E(\text{Trout}_t) = \mu_t \text{ and } \text{var}(\text{Trout}_t) = \mu_t$$

$$\log(\mu_t) = \text{Intercept} + f_1(\text{Year}_t) + \text{PikeRemoval}_{t-1} \times \text{RoachLevel}_{t-1}$$

Where Trout_t is the number of trout caught per 10 survey nets on Lough Sheelin in year *t*. $f_1(\text{Year}_t)$ is a random walk smoother on year (continuous variable). PikeRemoval_{t-1} is the number of pike removed from Lough Sheelin in year *t-1* as part of the pike management programme in designated trout lakes. RoachLevel_{t-1} is a categorical variable with two levels (Low, High) that expresses roach abundance as less or greater than the 50th percentile of observed roach abundance (< 37 fish per 10 survey nets >) in Lough Sheelin in year *t-1*. Model validation used residual plots to check that models fulfilled the assumptions of linearity and homogeneity of residuals. The predicted effect of pike removal on trout survey catch at each level of survey roach abundance was plotted for the start, middle and end of the tested time period (1981, 2000, and 2014).



4.3 Results

4.3.1 Fish stocks

The trout population showed a sustained decline in Lough Sheelin, with evidence of recovery in the early 1990s and in the most recent five years (Figure 4.1). 'Low' roach abundance (< 50th percentile) occurred in 16 survey years, while 'high' roach abundance (> 50th percentile) occurred in 18 survey years. Numbers of pike removed fluctuated during the study period and peaked between 1995 and 2000 (Figure 4.1).

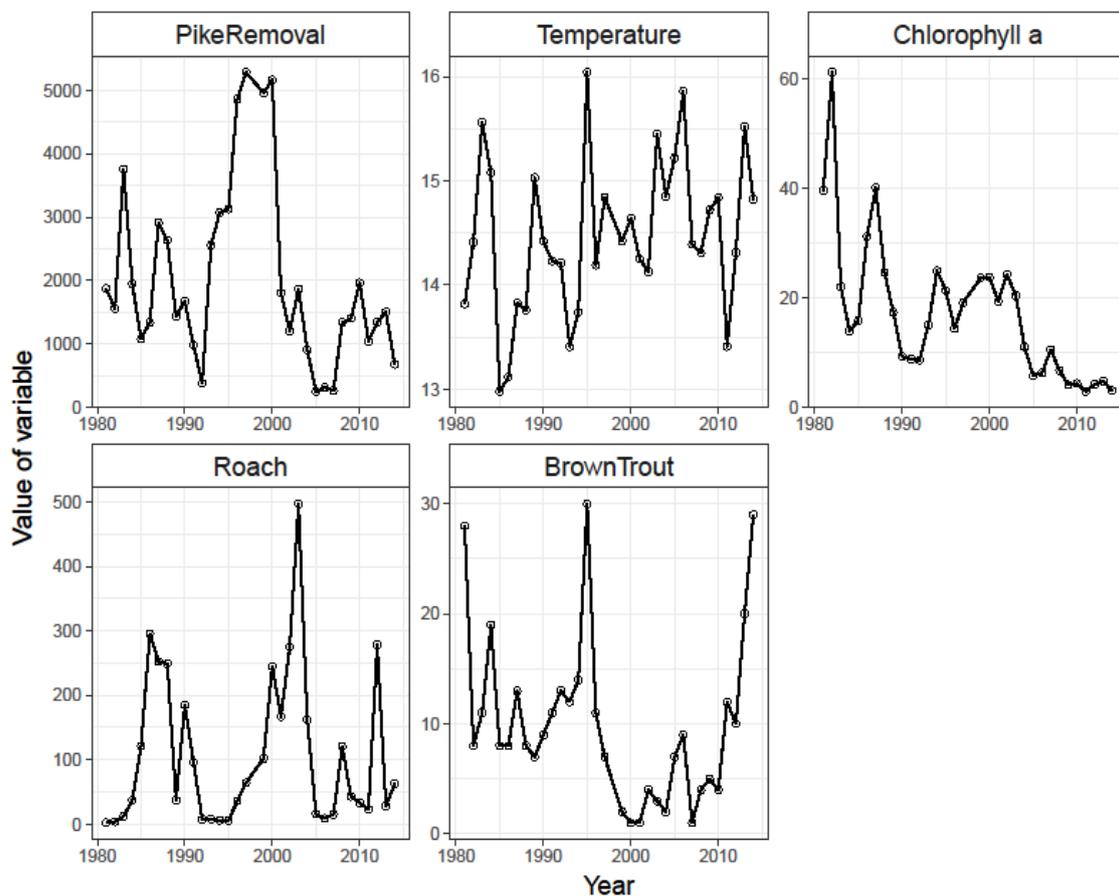


Figure 4.1. Time series of annual number of pike removed from Lough Sheelin as part of a predator control programme, environmental variables (mean summer (JJA) temperature °C and mean annual chlorophyll $a \mu\text{g l}^{-1}$), and abundance of trout and roach (number fish caught per 10 survey nets).



4.3.2 Chlorophyll *a* and temperature

There was a significant decrease in mean annual chlorophyll *a* values after the early 1980s. Mean annual values were at an all-time low during the period 2008 to 2014 (Figure 4.1). Mean summer (JJA) air temperature (°C) in the Lough Sheelin catchment generally increased over the study period (Figure 4.1). Model selection (Table 4.1) suggested that the inclusion of temperature and chlorophyll *a* did not add important additional information in tested models of trout survey catch.

4.3.3 Pike diet

There were important changes in the diet of Lough Sheelin pike following the first appearance of roach in sampled stomachs in 1983 (Figure 4.2). Statistical analysis suggested that the proportion of sampled stomachs containing trout declined strongly, with weaker declines in perch and three-spined stickleback, in favour of a strong increase in the proportion containing roach (Table 4.2). The proportion of stomachs containing prey did not differ significantly between pike length classes or sampling periods (Table 4.1).

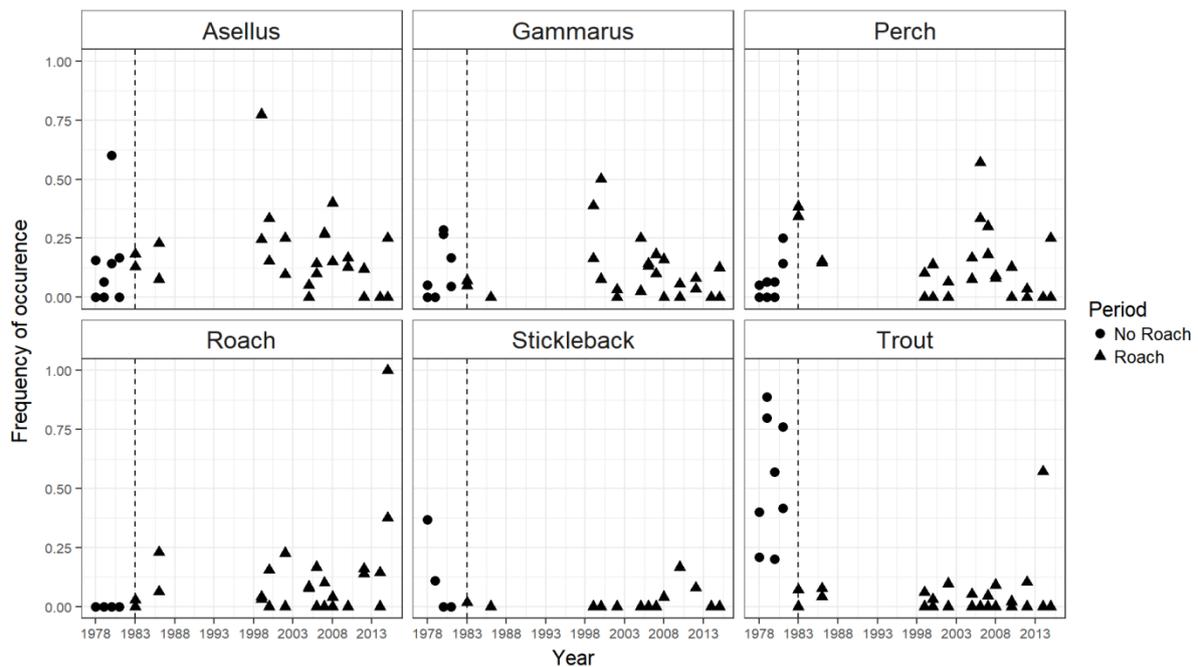


Figure 4.2. The proportion of sampled pike stomachs containing given prey items in periods before and after the first detection of roach in the diet (dashed vertical line in 1983).



Table 4.1. Results of a statistical model describing change in the annual proportion of sampled Lough Sheelin pike stomachs containing a given prey species, in periods before and after the appearance of introduced roach in the diet. Each level (species) of the prey variable is compared to the occurrence of the commonly-consumed invertebrate *Asellus sp.* (freshwater louse) 'Empty' is empty stomachs. 'Fish' is unidentified fish remains.

Variable	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.699	0.186	-9.149	0
Period	0.278	0.209	1.334	0.182
Length Class	-0.001	0.08	-0.01	0.992
Empty	0.477	0.239	1.993	0.046
Fish	-2.64	0.609	-4.337	0
Gammarus	-0.781	0.305	-2.559	0.011
Perch	0.549	0.237	2.312	0.021
Roach	-3.05	0.733	-4.161	0
Stickleback	-0.767	0.394	-1.948	0.051
Trout	0.618	0.236	2.623	0.009
Period:Empty	0.609	0.273	2.229	0.026
Period:Fish	1.629	0.635	2.565	0.01
Period:Gammarus	-0.008	0.349	-0.022	0.982
Period:Perch	-1.117	0.287	-3.891	0
Period:Roach	2.165	0.753	2.873	0.004
Period:Stickleback	-1.391	0.579	-2.402	0.016
Period:Trout	-2.303	0.326	-7.066	0

4.3.4 Pike removal

The selected model (Model 4) of trout survey catch in Lough Sheelin showed important effects of pike removal and roach abundance (Table 4.2). There was also an important interaction between these variables, showing that the effect of pike removal changed between low and high roach abundance in the lake. During periods of low roach abundance, the predicted number of trout in year t increased with increasing levels of pike removal in year $t-1$. During periods of high roach abundance, the predicted number of trout in the lake decreased with increasing levels of pike removal (Figure 4.3).



Table 4.2. Posterior means, standard deviations and 95% credible intervals for parameters of the selected model of trout survey catch in Lough Sheelin. Note that the 95% credible intervals of the covariates do not contain zero and hence may be considered important.

Parameter	Mean	Standard deviation	2.5% Quantile	97.5% Quantile
(Intercept)	1.89303	0.183	1.52	2.24658
Pike removal	0.00026	0.00009	0.00008	0.00044
Roach abundance	0.50929	0.236	0.0452	0.97369
Pike removal:Roach abundance	-0.00044	0.00011	-0.00066	-0.00022

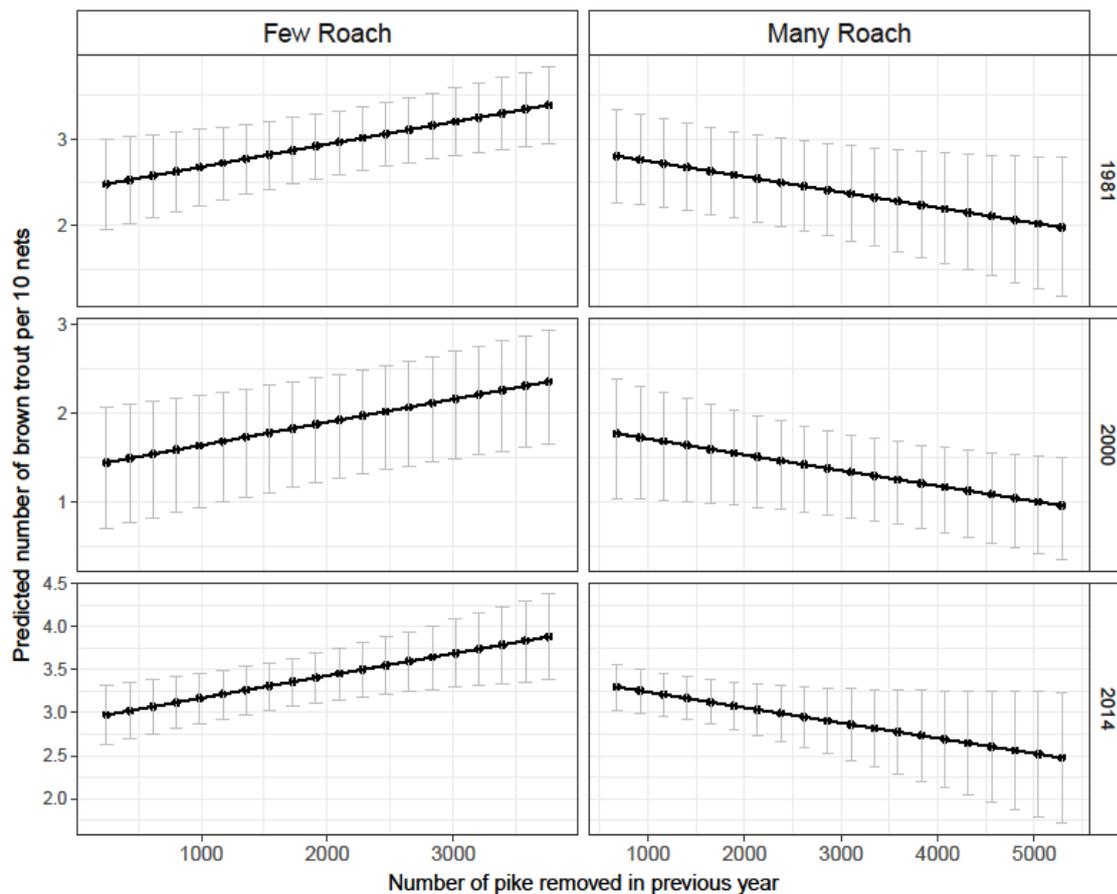


Figure 4.3. The predicted effect of pike removal in year $t-1$ on trout survey catch in year t at two levels of roach abundance ($< 50^{\text{th}}$ percentile $>$) and three time periods in Lough Sheelin. Error bars are 95% credible intervals from the Bayesian statistical model.



4.4 Discussion

Pike removal is an established procedure on certain Irish lakes managed as wild trout fisheries. Many of these lakes have shown strong ecological changes in recent decades (Champ, 1998), including the introduction of roach as an abundant new prey species (Pedreschi *et al.*, 2015). This study in Lough Sheelin found that the proportion of sampled pike stomachs containing trout declined strongly after the appearance of roach. A similar effect on pike diet has been recorded in Lake Windermere, where eutrophication and warming are associated with increased cyprinid populations (Winfield *et al.*, 2012). The observed dietary shift in Lough Sheelin pike was associated with contrasting effects of pike removal on survey abundance of trout in the following year. In years of 'low' roach abundance, pike removal had some positive effect on subsequent trout abundance, but this effect became weakly negative at 'high' roach abundance. The availability of roach seems to have reduced pike predation pressure on trout in Lough Sheelin, and modified the potential utility of pike removal as a trout conservation tool in the system. Removing top predators may have unanticipated and potentially negative effects on target fish stocks in systems experiencing multiple anthropogenic pressures.



5: Size-structured population model for the assessment of management options for pike-trout interactions in Irish lakes

5.1 Introduction

A number of large Irish lakes were designated in the late 1950s as trout fisheries. Various management actions have subsequently been undertaken in order to improve trout stocks in these systems. Key actions include trout stock enhancement with hatchery-reared fish, nursery stream enhancement programmes, competitor or predator species removals (see IFT reports from 1960s) and the introduction of angling minimum size limits. Such policies comprise an implicit ecosystem-based approach to fisheries management, which has been defined in a marine context as “developing ecosystem-level goals that are multispecies focused and that consider multiple kinds of human activities that are tied to healthy marine ecosystems” (NRC, 2006; Pine III *et al.*, 2009). The ecosystem approach acknowledges the complexity of exploited aquatic systems, but it is difficult to assess the impacts of such ecosystem-based management strategies without careful, continual monitoring of the response of target species. Appropriate monitoring programmes can be resource intensive and expensive, particularly in respect to freshwater fisheries. For this reason, and to add value to data collected from monitoring programmes, modelling methods have been widely adopted by fisheries managers in other jurisdictions to explore and assess proposed management policies and their effect on target species and the wider ecosystem.

The ‘traditional’ modelling approach to evaluating marine fisheries involves stock-assessments based on single-species population models and management strategy evaluations for different total allowable catches (TACs) or other input regulations (Karagiannakos, 1996). Precautionary catch advice for the management of Atlantic salmon on Irish rivers is provided using this approach (Ó Maoiléidigh *et al.*, 2004). Such a single-species modelling process is appropriate where the primary interaction in the fishery ecosystem occurs between the target species and the fishery. However, the ecosystem-based approach to fisheries management recognises that target species interact with other species and are influenced by other (environmental/ecological) drivers in the ecosystem. This ecosystem approach is now considered best practice for management of inland fisheries systems (Beard *et al.*, 2011; Lapointe *et al.*, 2014). Informed management of pike and trout populations in Irish lake fisheries requires an approach that can integrate the potential influence of other species and ecological interactions on the target species.



Predicting the results of any fisheries management action is very uncertain because the dynamics of ecosystems are complex and poorly understood. Operational management strategies for fisheries are typically tested in a modelling framework using management-strategy-evaluation (MSE). These methods rely on simulation testing of the whole management process using performance measures derived from operational objectives (Bunnefeld *et al.*, 2011; Sainsbury *et al.*, 2000). The MSE approach involves selecting candidate management tools, specifying performance measures, and evaluating these using numeric simulations. The framework emphasizes the quantification of uncertainties, and propagates these through to their effects on the performance measures (Sainsbury *et al.*, 2000).

Plagányi (2007) presents a review of ecosystem-based modelling methods developed for fisheries management. Emphasis is placed on multi-species population dynamic aspects of ecological interactions within ecosystems; although it is acknowledged that environmental influences may also have significant effects of ecosystem behaviour. Despite focusing on marine fisheries, it is recognised that this discussion is also relevant to freshwater fisheries. Freshwater fisheries present unique challenges compared to marine fisheries, such as greater habitat diversity and ecological sensitivity to environmental drivers, and relative paucity in fisheries data (Lynch *et al.*, 2016). Nevertheless, the principles of fisheries ecology overlap substantially between marine and inland systems (Cooke *et al.*, 2014), and there are no conceptual difficulties in applying similar population modelling concepts across these environments.

Ecosystem-based approaches to fisheries management encompass a broad range of models of various complexities (Plagányi, 2007) including:

- Minimally Realistic Models (MRMs) representing the interactions of a small subset of species within the fish community and their effect on the (target) species of primary interest. Such models are also known as dynamic multi-species models;
- Models of Intermediate Complexity for Ecosystem assessments (MICE, see Plagányi *et al.*, 2014) which are similar to MRMs but explicitly assess ecosystem impacts, i.e. the effects of interactions on each species;
- Dynamic System Models which include both top-down (fisheries) and bottom-up (primary production) forces interacting in an ecosystem;
- Whole Ecosystem Models which seek to model all trophic levels of an ecosystem in a balanced way;



We developed a ‘minimally realistic’ size-based model that captures key features in the population dynamics of trout and pike, and allows for predation by pike on trout and on an alternative size-structured prey spectrum. The model is used in an MSE framework to explore the likely outcome of certain candidate fisheries management strategies such as angling size limits and different rates of removal for each species.

We adopted the minimally realistic modelling approach for several reasons. First, as model complexity increases data requirements for model parameterisation also increase and, compared to commercial marine fisheries, Ireland’s recreational wild trout lake fisheries may be considered “data poor” (Fitzgerald *et al.*, 2018). Extensive and valuable data on fish populations in these systems have been collected through on-going systematic scientific monitoring of Irish waterbodies (see wfdfish.ie for details of the WFD fish sampling programme) and historical sampling programmes (cf. e.g. O’Grady and Delanty, 2001a). However, data to support models of fish community interactions with linkages to lower trophic levels, such as length- or age-structured fishing removals, long-term stock-recruitment data, fecundity and maturation data and absolute abundance indices, are currently unavailable. Secondly, the primary management tools for the wild trout fisheries (apart from stream and fisheries enhancement) are pike removal operations and wild trout angling regulations. Management questions thus pertain largely to two species from the fish community, and so it seems reasonable to configure the model around the corresponding predator-prey pike-trout interaction. Lastly, increasing model complexity can increase scientific uncertainty because of lack of understanding of biological and ecological mechanisms and how they affect population dynamics (Link *et al.*, 2012). The quantification of uncertainty is a key strength of MSE, and provides managers with a realistic understanding of the strength of their management tools’ and the likelihood of attaining specified management objectives (Harwood and Stokes, 2003).

The pike-trout model draws on recent concepts in fish community modelling, and this report focuses on the model construction and parameterisation. Attention has been given to examining model sensitivity to underlying biological assumptions, and to assessing their importance for potential management advice (Patterson *et al.*, 2001). A simple MSE demonstration is presented and potential difficulties with extending the MSE to a broader suite of management actions are highlighted. The modelling has been developed in the context of important empirical research also reported here, including analyses of unique long-term data series from large Irish trout lakes. In this best-practice context, it is important to recognize that ‘projections’ from the model can only



describe likely future events subject to a specified set of assumptions, all of which have some associated uncertainty (Brander *et al.*, 2013).

5.2 Methods

The development of a size-based model of population-level interactions between pike and trout in an ecosystem incorporating other prey and fishery removals is presented. The model captures key features in the population dynamics of trout and pike, and allows for predation by pike on trout and on a size-structured 'ecosystem' prey spectrum representing other unspecified prey species and organisms. Principal model mechanisms are examined in some detail. Thereafter, the parameterisation of the model based on available data is described for a particular case study.

Length-structured stock-assessment models were first developed as an alternative to age-structured models for marine species that are hard to age, such as tropical fish (cf. e.g. Sullivan *et al.*, 1990) and crustacean or mollusc species (e.g. Punt and Kennedy, 1997; Chen *et al.*, 2005). Caswell (2001) provides a broader treatment of the theory of size-structured matrix population models beyond applications to fish stock-assessments. Quinn II and Deriso (1999) identified several reasons why length- or size-structured models are increasingly popular even for easily aged fish species, including how length data are the primary information collected when sampling a fish population and the stronger dependence of fishing and biological processes on length rather than age. The lengths of predator and prey are particularly strong determinants of predation mortality for prey of a particular size for a highly size-selective, gape-limited predator such as pike (e.g. bigger pike can consume bigger prey and some prey reach a size where they are safe from predation) (Hyvärinen & Vehanen, 2004). Therefore, the population interactions of trout and pike in size-regulated wild trout lake fisheries are most naturally represented in a primarily length-based model framework.

5.2.1 Single-species length-structured model outline

A length-structured population analysis assigns individuals in the population into discrete length classes. Growth and survival rates may vary between length classes but are identical for individuals within each length class, i.e. differences in lengths for individuals within each length class are assumed to have no effect on the growth or survival probability of those individuals. Length classes are typically equal in width, although other configurations have been adopted (Drouineau *et al.*, 2008), and the particular choice of length class boundaries is fishery- or species-dependent. Length-class abundances are updated at discrete time intervals according to growth, natural mortality,



removals mortality (e.g. fishing) and population renewal through juvenile recruitment. Time intervals in marine fishery stock-assessment models are often seasonal owing to quarterly sampling regimes; however for freshwater fisheries, where quarterly fish surveys are rare, it is more reasonable to adopt time intervals of one year corresponding to the length of the reproductive cycle for both species.

A single-species, length-structured matrix population model was formulated in mathematical terms using the matrix equation

$$\mathbf{N}_{t+1} = \mathbf{PSN}_t + \mathbf{R}_{t+1} \quad (1)$$

where \mathbf{N}_t is a vector of length-class abundances at time t , \mathbf{P} is growth transition matrix, \mathbf{S} is a survival matrix, and \mathbf{R}_{t+1} is the vector of juvenile recruits to each length class.

The matrix formulation provides a compact mathematical representation of the length-structured population dynamics and is straightforward to implement for computational purposes. The goal of the analysis is to project the population forward in time based on assumed vital rates for fish in each length class. The vector of length-class abundances \mathbf{N}_t comprises the numbers-at-length ($N_{1,t}, N_{2,t}, \dots, N_{L,t}$) for all length classes where $N_{i,t}$ represents the number of individuals in length class i at time and L is the number of length classes. The growth transition matrix is

$$\mathbf{P} = \begin{pmatrix} P_{1,1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ P_{L,1} & \dots & P_{L,L} \end{pmatrix}, \quad (2)$$

where $P_{i,j}$ is the probability of transitioning from length class j to length class i . The survival matrix \mathbf{S} has the diagonal form

$$\mathbf{S} = \begin{pmatrix} S_{1,1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & S_{L,L} \end{pmatrix}, \quad (3)$$

where $S_{i,i}$ is the survival probability for individuals in length class i . The recruitment vector is

$$\mathbf{R}_{t+1} = \begin{pmatrix} R_{1,t+1} \\ \vdots \\ R_{L,t+1} \end{pmatrix} \quad (4)$$

and the majority of juvenile recruits would be expected to enter length class 1.



Several assumptions – additional to those already introduced when discretising the population and time – are implicit in the model. The annual survival fraction for fish in length class i depends on total instantaneous mortality Z_i which is assumed to comprise natural M_i and fishing/removals mortality F_i . Both are assumed to act continuously and concurrently throughout the year so that $S_{i,i} = \exp(-Z_i)$. Thus, of the $N_{i,t}$ fish in length class i at year t , only $S_{i,i}N_{i,t}$ remain at the end of year t . Only the surviving fish grow and this growth is assumed to act instantaneously at the end of the year. The proportion of fish remaining in length class i is $P_{i,i}(S_{i,i}N_{i,t})$ and the fraction that grows to length class j is $P_{j,i}(S_{i,i}N_{i,t})$ where $j > i$. No shrinkage in fish length is allowed so that $P_{j,i} = 0$ for $j < i$ and fish must move to some length class $\sum_j P_{j,i} = 1$ (all growth proportions sum to 1 for each length class i). Lastly, juveniles recruit to the population at the start of year $t + 1$. This annual population renewal process, represented mathematically in (1), is most easily understood in diagrammatical form as shown in Figure 5.1. Details of length-based representations of growth, mortality, and reproduction are discussed next.

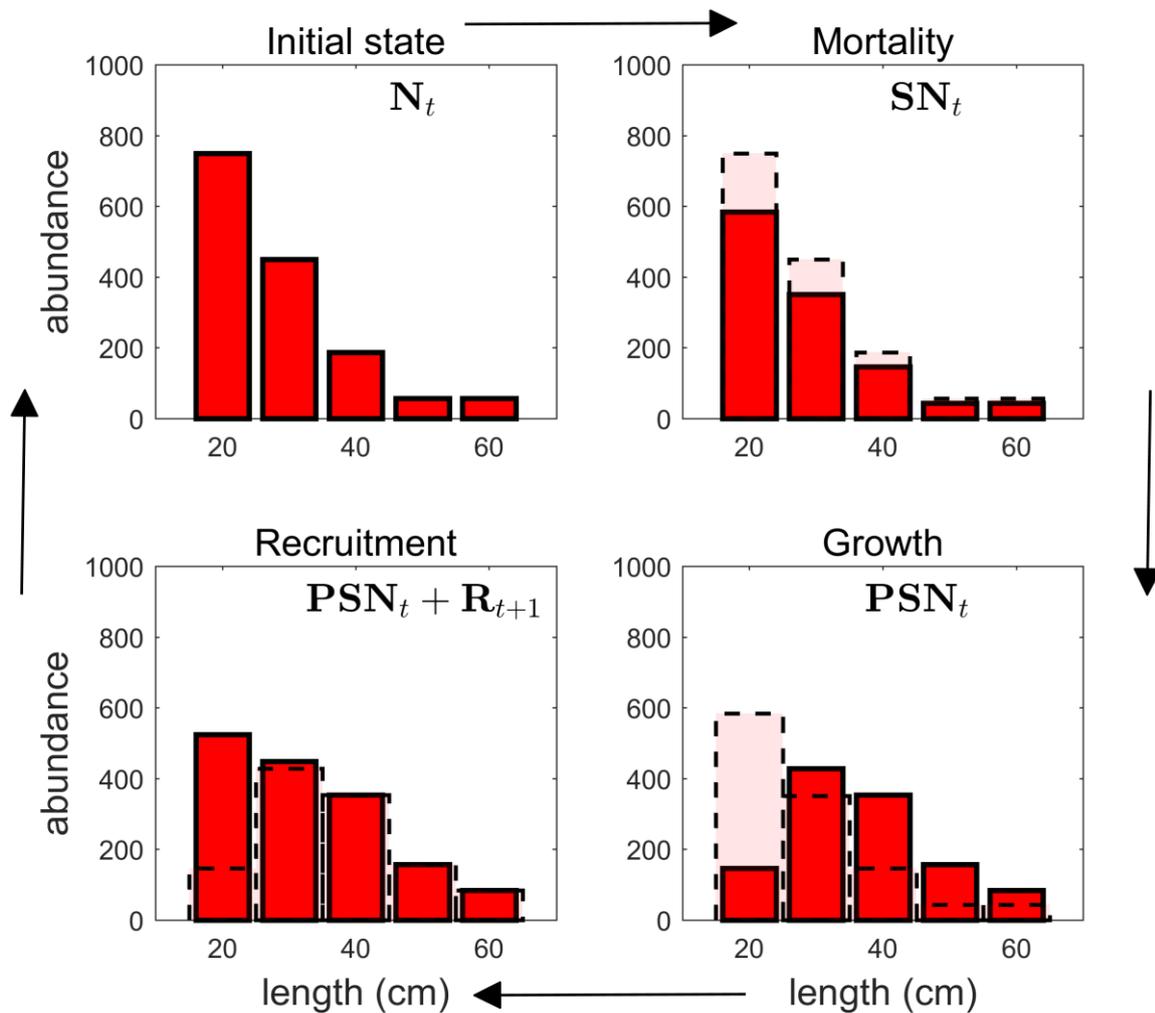


Figure 5.1. Annual population renewal in length structured model featuring reduction by survival fraction (top right), growth redistribution of population (lower right) and recruitment (lower left).

Mortality

Natural mortality represents population losses to disease, starvation, predation and senescence. In the coupled length-structured predator-prey model presented here, only the prey species may suffer predation mortality - the predation sub-model to estimate this mortality is discussed separately in Section 5.2.2. Therefore, natural mortality is decomposed into a predation component M^P and a residual term M^R . Residual natural mortality is assumed to be constant in time and uniform across length classes. The size-dependence of natural mortality has been extensively studied in fish population dynamics literature, cf. e.g. Beyer (1989), but much of the size-dependence can be attributed to the influence of predation. Predation mortality may vary in time and across length classes so the total natural mortality is expressed as



$$M_{i,t} = M^R + M_{i,t}^P. \quad (5)$$

Fishing mortality is separated into a possibly time-dependent fully-selective fishing term F_t and a length-dependent gear selectivity term s_i and is written as

$$F_{i,t} = F_t s_i. \quad (6)$$

Gear selectivity s_i can take a maximum value of 1 and will depend on the definitions of the length class and size regulations in place. For example, if angling is regulated with a minimum length limit, then length classes above the limit will have selectivity of 1 whereas those below the limit will have selectivity of 0 (assuming the limiting length corresponds to the end of one length class and the beginning of another).

Mortality is expressed in terms of an instantaneous rate, i.e. numbers per year, which are translated to an annual survival fraction through the relationship $S = \exp(-Z)$ assuming constant mortality over the duration in question (see Caswell (2001), Quinn II and Deriso (1999) or any other population modelling text). For example, natural mortality is expected to take a value between 0.2 yr^{-1} and 0.5 yr^{-1} for adult fish, and in the absence of fishery harvest the corresponding survival fractions are approximately 82% and 61%, respectively.

Growth

Growth is represented as a stochastic process, so that each individual in a length class has a certain probability of transitioning to a larger length class or remaining in the same length class over the course of a year. At the population level, this translates to certain proportions of individuals transitioning from or remaining in the current length class. Transition proportions depend on the initial length class and growth rates.

Following Sullivan *et al.*, (1990), we used a stochastic LVB growth model to obtain the growth transition matrix \mathbf{P} . In brief, the growth increment is represented by a probability distribution that can be parameterised by its mean and variance. The mean corresponds to the expected growth increment of an individual in the population and the variance represents the individual variability about the population mean. The deterministic LVB growth model (von Bertalanffy, 1938) predicts the expected length of an individual in the population as

$$L(t) = L_\infty(1 - \exp(-\kappa(t - t_0))) \quad (7)$$



where $L(t)$ is the length of fish at age t , L_∞ is the asymptotic length of a fish in the population, κ is the Brody growth constant, and t_0 is the age at length zero. Thus, the growth increment for a fish of length $L(t)$ is

$$\Delta l = L(t + 1) - L(t) = (L_\infty - L(t))(1 - \exp(-\kappa)). \quad (8)$$

Similarly, the expected growth increment for fish in length class i with a mid-point length $l_i^* = (l_i^l + l_i^u)/2$, where the l and u subscripts denote the upper and lower bound of the length class, is approximated as

$$\overline{\Delta l_i} = (L_\infty - l_i^*)(1 - \exp(-\kappa)). \quad (9)$$

A gamma distribution is chosen to represent individual variability in the growth increment about the mean. Drouineau *et al.* (2008) noted that the gamma distribution promotes robustness and parsimony in a length-structured modelling framework. The variance is proportional to the mean and requires the specification of a so-called shape parameter which is typically fixed at a standard value (see Chapter 9, Quinn II and Deriso, 1999, or Sullivan *et al.*, 1990). The mean and variance, which depend on the growth parameter κ and asymptotic length L_∞ alone, uniquely determine the proportion of individuals transitioning from one class to another. Exact details of the growth transition probability computations are omitted in favour of a brief example.

Consider a hypothetical fish species with an asymptotic length $L_\infty = 70\text{cm}$, categorised into four equally spaced length classes spanning (20cm, 80cm) and having two possible growth constants $\kappa = 0.25 \text{ yr}^{-1}$ or $\kappa = 0.5 \text{ yr}^{-1}$. The growth transition matrices for the fish population with slow growth ($\kappa = 0.25 \text{ yr}^{-1}$) and fast growth ($\kappa = 0.5 \text{ yr}^{-1}$) are

$$\mathbf{P}_{\text{slow}} = \begin{pmatrix} 0.44 & 0 & 0 & 0 \\ 0.48 & 0.59 & 0 & 0 \\ 0.07 & 0.36 & 0.73 & 0 \\ 0.01 & 0.05 & 0.27 & 1 \end{pmatrix} \text{ and } \mathbf{P}_{\text{fast}} = \begin{pmatrix} 0.16 & 0 & 0 & 0 \\ 0.58 & 0.41 & 0 & 0 \\ 0.23 & 0.47 & 0.68 & 0 \\ 0.02 & 0.12 & 0.32 & 1 \end{pmatrix}, \quad (10)$$

respectively. A comparison of the growth of fish in length class 1 (column 1 of the matrices) shows that the proportion of fish remaining in length class 1 $P_{1,1}$ is 44% for the slow growth case but only 16% for the fast growth case. Similarly, 58% and 48% of fish in the fast growth case and the slow growth case, respectively, transition to length class 2 from length class 1 ($P_{2,1}$). Similar deductions



for transition probabilities to and from larger length classes can be made by further examining these matrices.

Population regeneration is modelled through a spawner-recruitment relationship or 'stock-recruitment' (SR) relationship as it is commonly referred to in a fisheries context. Stock-recruitment models seek to represent the dependence of juvenile recruitment on adult spawning stock in a mathematical form and are of fundamental importance in long-term population dynamics projections. However, juvenile recruitment shows extreme natural variability as a result of environmental influences. In fact, debate still exists as to whether the dominant factor in determining recruitment success is spawning stock abundance or environment conditions. Nevertheless, we assume that intrinsic population mechanisms and not extrinsic environmental determinants drive recruitment success and that SR follows a simple functional relationship.

Two classical stock-recruitment theories from the field of fish population dynamics were derived by (Beverton and Holt, 1957) and (Ricker, 1954). Each model elaborates on simple density-independent recruitment (where the ratio of recruitment to spawning stock is constant) by including a form of density dependence. The Beverton-Holt stock-recruitment model is formulated as

$$R = \frac{\alpha S}{1 + \beta S}, \quad (11)$$

where S is a measure of spawning stock, R measures the abundance of recruits, α is the recruits per unit spawning-stock at low density and β is a parameter determining the strength of density dependence. Beverton-Holt SR theory predicts a monotonic increase in recruitment towards an asymptotic maximum as spawning stock size increases representing purely compensatory density dependence. Ricker's SR theory predicts that recruitment increases to a maximum at an optimal spawning stock value before decreasing as the spawning stock continues to increase corresponding to a dome-shaped curve. The corresponding mathematical formulation of the Ricker model is

$$R = aS \exp -bS \quad (12)$$

and it describes over compensation in density dependence. Beverton-Holt and Ricker SR curves are shown in Figure 5.2. Spawning stock S may be measured in terms of egg deposition, spawner biomass, spawner abundance or total adult abundance depending on the sampling process or convention adopted. If age at recruitment is denoted a_r , then the total annual recruitment in year



$t + 1$ will have a functional dependence on the spawning stock (and hence length-structure abundance) in year $t + 1 - a_r$ so that

$$R_{t+1} = f(S(N_{t+1-a_r})) \quad (13)$$

where $f(S)$ describes the stock-recruitment relationship and $S(N_{t+1-a_r})$ indicates that spawning stock depends on the numbers in each length class. A stochastic form of the stock-recruitment model allows random variation about these deterministic curves to represent environmental influences; such error terms are necessary when fitting to empirical data.

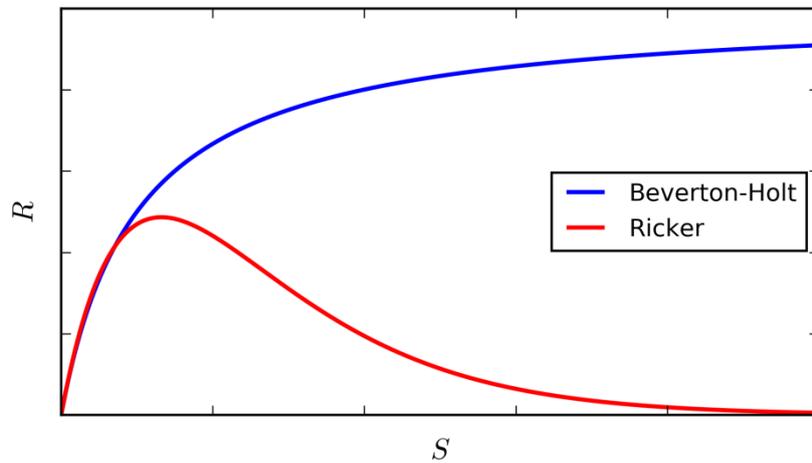


Figure 5.2. Examples of asymptotic (Beverton-Holt) and dome-shaped (Ricker) stock-recruitment curves.

In length-structured models, recruitment is modelled as the product of annual juvenile recruitment and the proportion of annual recruits entering each length class (Punt *et al.*, 2013). The proportion of recruitment in each length class will depend on the length-classes and recruitment age and is assumed to be constant in time. Therefore, the recruitment vector in Equation (1) is expressed as

$$\mathbf{R}_{t+1} = \mathbf{r}R_{t+1} \quad (14)$$

where \mathbf{r} is a constant vector of length-specific recruitment proportions which distributes the total number of recruits across the length classes.

5.2.2 Two-species predator-prey model – species interaction

A two-species predator-prey length-structured model was constructed by coupling two single-species length-structured models as formulated in Equation (1) through a prey species mortality term which depends on both predator and prey populations. A schematic of this model structure



featuring a one-way linkage between the predator and prey is shown in Figure.5.3. Implicit in this one-way predator-prey coupling is the assumption that predator abundance may affect prey abundance but not vice versa. That is, it is assumed that the predator always meets its daily ration irrespective of the target prey species abundance and so the model corresponds to the “Efficient Predator” (Plagányi, 2007) class of Minimally Realistic Models. This restricts the model application to ecosystems where the predator is not food-limited.

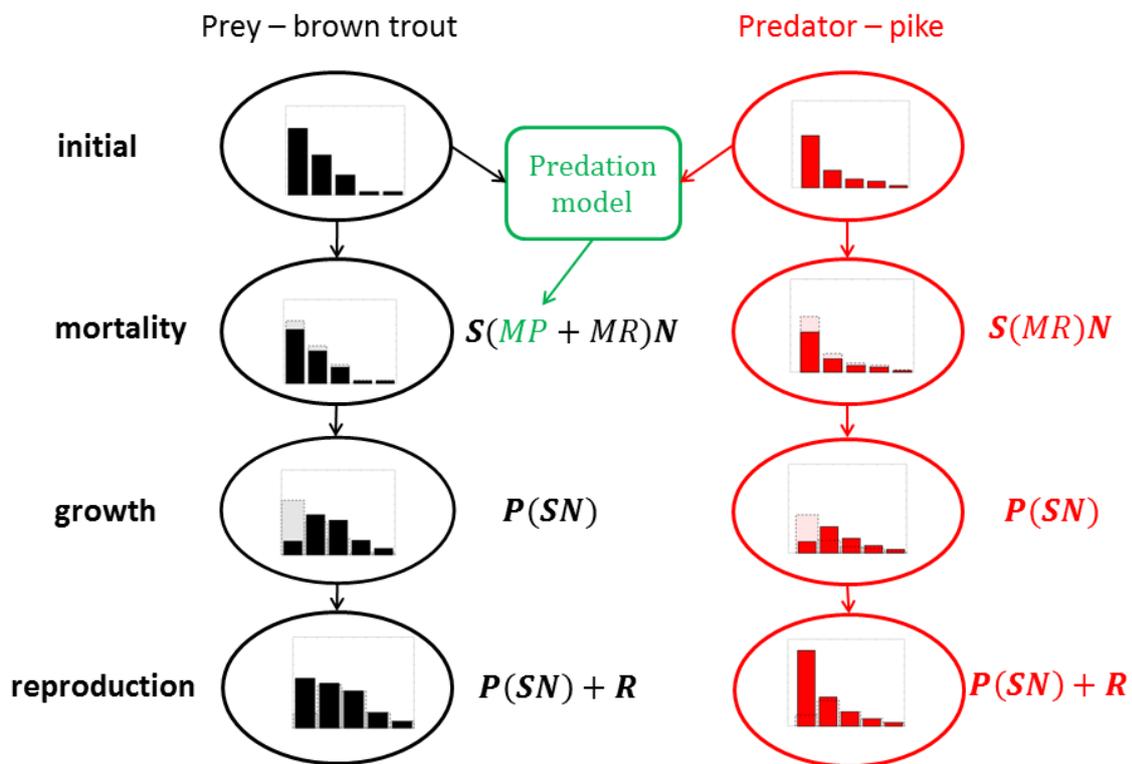


Figure 5.3. Schematic of the two-species length-structured model with one-way predator-prey coupling.

The prey species predation mortality rate was determined using a length-based modification of the species interaction theory incorporated in the age-structured multispecies Virtual Population Analysis (MSVPA) model derived by Gislason and Helgason (1985). Multiple age-structured predator and prey species are incorporated in MSVPA species interaction theory; however, we require a species interaction theory for a single, length-structured predator and prey species. In order to describe the dynamics of a predator-prey species interaction within a broader fish assemblage an alternative prey biomass term was also introduced. This prey resource represents all other potential



food (other fish and other organisms) that the predator may consume from the ambient environment in addition to the target prey species. Henceforth, the length-structured predator and prey species are referred to as *target* species because the dynamics of these species are explicitly tracked in the model. The ambient biomass resource is assumed to be known *a priori* and is prescribed as constant in time. Thus, the species interaction theory provides a simple description of a stable ecosystem within which the predator and prey species interact.

Predation mortality suffered by the target prey is determined from the rate at which target prey species biomass is removed by predation. For prey species in length class m , the annual rate of biomass loss to predation is the product of the instantaneous annual predation mortality MP_m and the biomass of prey class m in that year, that is

$$MP_m \times w_m^B \bar{N}_m^B, \quad (15)$$

where w denotes the weight of fish, \bar{N} is the average abundance in a given year, subscript m refers to prey length class and superscript B denotes prey species. Estimation of MP_m is achieved by balancing this biomass loss term with the target prey biomass consumed by all predator classes.

The average annual food requirement for predators in length class l is the product of the annual predator food ration and the abundance of the predator \bar{N}_l^P , i.e.

$$c_l w_l^P \times \bar{N}_l^P, \quad (16)$$

where c_l and w_l^P are the annual specific food ration and the weight of predators in length class l , respectively. The annual specific food ration is the amount of food required per unit weight of predator flesh in a year and herein it is assumed to vary by length class. This dietary requirement must be met by the target prey species and other potential food in the ecosystem.

Prey mortality caused by this predation pressure is estimated by apportioning the required annual biomass of food for the predator population based on the *availability* of target prey biomass relative to the total biomass *available* to predators in each length class. The concept of ‘available food’ was introduced by (Gislason and Helgason, 1985) to take account of the suitability of prey items. In brief, only a fraction of the total biomass of potential prey is suitable to any given predator because of, for example, physical restrictions (e.g. size refuge) and habitat separation, and this fraction is defined to be the available biomass. Therefore, potential prey is weighted according to its suitability as food for the predator. The relative composition of prey items in the predator diet is assumed to be in direct proportion to the *available* prey biomass.



The total biomass of food available to a predator in length class l comprises two components:

1. the sum over all prey length classes of available prey biomass $\Phi^l = \sum_m \Phi_m^l$;
2. the fraction of the total ambient biomass resource available to the predator Φ_X^l .

The latter term incorporates all species and taxa present in the surrounding environment not explicitly included in the length-structured model.

Therefore, the annual rate of consumption of prey in length class m by predators in length class l is

$$(c_l w_l^P \times \bar{N}_l^P) \frac{\Phi_m^l}{\sum_m \Phi_m^l + \Phi_X^l}, \quad (17)$$

where Φ_m^l is the biomass of prey class m available to predator l and Φ_X^l is the portion of alternative biomass in the ecosystem suitable for predator class l . The distribution of predation pressure across length classes of prey is more straightforward to explain with an example. Consider two prey length classes with biomasses of $p_1 = 100$ kg and $p_2 = 200$ kg and $p_X = 1700$ kg of other food (fish, invertebrates etc.) suitable for consumption by a predator. The available or suitable biomasses incorporate predator selectivity and are less than the corresponding potential prey biomasses in the environment. In this case, prey class 1 will meet the proportion $p_1/(p_1 + p_2 + p_X) = 0.05$ or 5% of the annual predator maintenance requirement and prey class 2 will contribute 10% and the other prey biomass will contribute the remaining 85%.

The total annual rate of consumption of prey class m by the entire predator population is obtained by summing prey consumption rate (17) over each predator length class l . This annual rate of consumption must equal the annual removals of the prey and so

$$MP_m w_m^B \bar{N}_m^B = \sum_l c_l w_l^P \bar{N}_l^P \frac{\Phi_m^l}{\sum_m \Phi_m^l + \Phi_X^l}. \quad (18)$$

Therefore, the predation mortality for prey class m is

$$MP_m = \frac{1}{w_m^B \bar{N}_m^B} \sum_l c_l w_l^P \bar{N}_l^P \frac{\Phi_m^l}{\sum_m \Phi_m^l + \Phi_X^l}. \quad (19)$$

Some population interaction mechanisms are evident from Equation (19). Annual prey mortality increases as length-specific annual specific predator rations c_l increase irrespective of prey selection. Furthermore, if the biomass of alternative prey in the environment available to a predator is substantially greater than the biomass of available target prey ($\Phi_X^l \gg \sum_m \Phi_m^l$) then target prey



mortality will be relatively small. Later versions of MSVPA (e.g., Garrison and Link, 2005) have explicitly included different prey selectivity behaviours in addition to proportion-by-availability.

Available fraction of potential prey biomass

The suitability of prey for a particular predator will be determined by a number of factors (Gislason and Helgason, 1985) that may include:

- the size or length of the prey relative to the predator;
- the habitat overlap between predator and prey; and
- the vulnerability of the prey owing to behavioural or physiological traits.

Herein, emphasis is placed on the size-preference component of the availability weighting for potential food because it is the most easily quantified factor from pike stomach data. Furthermore, pike predation has been noted to be highly size-selective (Nilsson and Brönmark, 2000; Hyvärinen and Vehanen, 2004) leading to prey above a certain size enjoying size refuges from predation (Hyvärinen and Vehanen, 2004). Prey size refuges can lead to large differentials in mortality rates for prey of different sizes and the concept of prey availability was developed to represent such differences.

For length-structured predator and prey populations the fraction of potential prey suitable as food for the predator will differ for predators in each length class across all prey length classes. This fraction denoted G_{jm}^{il} is a suitability measure or weighting which must lie between 0 and 1. Thus, the biomass of prey in length class m available to a predator in length class l is

$$\Phi_m^l = G_m^l w_m^B \bar{N}_m^B. \quad (20)$$

This weighting is assumed to depend on the respective lengths of predator and prey in each length class. Size preference of the predator for the prey species is assumed to have the following lognormal form, adopted by (Garrison and Link, 2005; Gislason and Helgason, 1985) among others,

$$g(s_p, s; \beta_s, \sigma_s) = \exp\left(-\left(\ln\left(\frac{s_p}{s}\right) - \ln \beta_s\right)^2 / 2\sigma_s^2\right), \quad (21)$$

where s_p is the predator size, s is the prey size, β_s is the optimal size ratio for the predator and σ_s is a measure of how particular the predator is about the size of its prey. The fish size metric can be either length or weight. This flexibility is important because the target prey species in the



population model is length-distributed whereas the ambient biomass resource is mass or weight-distributed. Both weight-dependent and length-dependent forms of the size preference curve will be used in the model following parameterisation based on predator-prey length and weight data.

Each size preference suitability weighting is calculated by assuming predators and prey take the mid-length value of their respective length classes, e.g. l_l^P for class l of the predator species and l_m^B for class m of the prey species m . Thus, size preference in the length-structured model is defined by a matrix of size preference weights with elements

$$G_m^l = \exp\left(-\left(\ln\left(\frac{l_l^P}{l_m^B}\right) - \ln\beta_L\right)^2 / 2\sigma_L^2\right) \quad (22)$$

where β_L is the optimal length ratio and σ_L measures predator tolerance for variations about optimal prey length. Size preferences are normalised to lie on the range [0,1] and $g_m^l = 1$ if the ratio of predator length to prey length equals the optimal ratio β_L .

Alternative prey resource from ambient environment

The two-species predator-prey population model presented herein seeks to describe the length-based interactions between one predator species and one prey within a larger fish assemblage. Predatory fish species in large waterbodies with complex food webs may feed upon a variety of prey – fish or other organisms – and are unlikely to feed upon one prey species alone. It is a trivial task to generalise the predation model for multiple target prey (and predator) species; however, each fish species explicitly modelled in the length-structured framework requires detailed data on mortality, growth, fecundity, and the relationship between spawning stock and juvenile recruitment in order to accurately describe its population dynamics. Such onerous data requirements restrict the scope of age- or length-structured models to fish that are monitored carefully, e.g. fish of significant economic value. For example, data on stock-recruitment for perch and roach in Irish lakes is quite limited. Furthermore, in an ecosystem-based fisheries model the influence of other prey at lower trophic levels, such as plankton or macroinvertebrates, on the interaction of species within the fish assemblage should be incorporated if possible. Therefore, a parsimonious representation of the alternative prey resource available to the target predator species is required.

Size spectrum representations of complex food webs summarise myriad biological and ecological information in a relatively simple form (cf. e.g. Andersen and Beyer, 2006; Andersen *et al.*, 2016; Guet *et al.*, 2016). Underlying this representation is the assumption that organism size is the key



determinant governing biological processes and organism interactions. For example, many fish predators are themselves prey as juveniles – the trophic level of an individual and hence the community structure depends primarily on size and not on species. In the present model, a time-invariant biomass size-spectrum is used to represent the prey resource potentially available to the predator in addition to the target prey species. This alternative prey resource spectrum represents smaller organisms and all fish in the assemblage whose length-structured population dynamics are not explicitly tracked. This may include individuals from the target species that are too small to be represented within the length-structured model. By adopting an ambient prey biomass resource that remains constant in time, we implicitly assume that the productivity of the system is sufficient to annually replenish biomass lost to predation, and that the ecosystem is in equilibrium. The potential prey biomass size spectra B_X dependence on organism mass m is given by

$$B_X(m) = \kappa_c m^{1-\lambda}, \quad (23)$$

where κ_c corresponds to absolute biomass abundance or density and λ is the spectrum exponent. Power-law relationship (23) characterises the entire ambient prey biomass with just two parameters and is ideal for incorporating the effects of data-limited species in the model.

The fraction of the potential resource available to the predator is calculated using the mass- or weight-based size preference function shown in Equation (21). The available ambient biomass resource is then obtained by integrating over the size spectrum

$$\Phi_X^l = \int_{m_0}^{\infty} B_X(m) g(m_l^P, m) dm \quad (24)$$

where m_l^P is the predator weight, m_0 is a minimum organism weight consumed by the predator (see Andersen and Beyer (2006) for further details on the integral). In physical terms, the food available to the predator is calculated from a combination of the ambient abundance of the prey of a given size and the preference of the predator for prey of that size.

5.2.3 Model parameterisation for case study

The two-species predator-prey population model described above was applied to the specific case of population-level interactions between pike and trout in designated wild trout lake fisheries in Ireland. The aim was to explore and understand the ecological interactions between the two target species and to quantify the effect of candidate management actions on these interactions. Accurate



model representation of the pike-trout interactions in a specific lake requires careful parameterisation of the model based on the ecological and biological data available for that lake. The minimum parameter set necessary to fully parameterise the model is listed in Table 5.1. In this section, the sources of data upon which parameter estimates are based, the methods used to determine estimates and the level of uncertainty in estimates are presented.

Pike stomach data from the dietary study reported in Section 2 were collected from pike in Lough Conn and Derravaragh. Historical catch data was also available from Lough Conn (O’Grady and Delanty, 2001a). The model was thus parameterised for the simulation of pike-trout interactions on Lough Conn.

Table 5.1. List of model parameters grouped according to biological process and including a description, notation, and the associated species.

Life-history or ecological process	Parameter description	Species	Notation
Reproduction	Density-independent SR term	Trout, pike	α_B, α_P
	Density-dependent SR term		β_B, β_P
	Spawning and nursery habitat area		A_B, A_P
	Age at juvenile recruitment		a_r^B, a_r^P
	Proportion of recruits entering each length class (vector)		r_B, r_P
Growth	LVB Brody growth constant	Trout, pike	κ_B, κ_P
	LVB length-at-infinity		L_∞^B, L_∞^P
	Length-specific instantaneous (residual) natural mortality		MR_l^B, MR_l^P
Mortality	Instantaneous (management or angling) removals mortality	Trout, pike	F^B, F^P
	Size or length-selectivity of removals		s_l^B, s_l^P
Species interaction (predation)	Length-dependent annual specific predator ration	Pike	c_l
	Length-based and mass-based predator size preference parameters		(β_L, σ_L) (β_W, σ_W)
	Alternative prey resource spectrum – absolute abundance parameter	Alternative, ecosystem prey	κ_c
	Alternative prey spectrum exponent or slope		λ

Stock-recruitment relationships for trout and pike

Empirical stock-recruitment (SR) data are relatively rare for fish species that are not commercially valuable because resources for monitoring programmes are limited and because of the slow, incremental nature of data collection (one data point per population per year). Thus, SR data for



freshwater species in recreational fisheries are far less widespread than for exploited marine species in commercial fisheries. For example, it appears that no long-term studies of stock-recruitment dynamics for adfluvial trout have been undertaken in Irish lakes. Redd count and electrofishing surveys in natal streams have sporadically been undertaken under the auspices of IFI (and its institutional predecessors). However, redd count and electrofishing surveys provide an index of spawning stock production only, and unless combined with absolute estimates of juvenile recruitment and adult spawning stock, they are not sufficient for the development of a robust SR relationship. Similarly, no long-term programmes (such as annual mark-recapture schemes) have been undertaken to estimate pike SR in Irish lakes. Therefore, empirical SR curves for the target species were extrapolated from other ecosystems in order to conduct a pike-trout population modelling case study for an Irish wild trout lake fishery.

The extrapolation of SR relationships from monitored (“donor”) systems with SR data to unmonitored (“recipient”) systems where SR data are absent is widely used in salmon stock assessments (Ó Maoiléidigh *et al.*, 2004; Prévost *et al.*, 2003; White *et al.*, 2016). Prévost *et al.* (2003) noted that direct extrapolation from a donor system to a recipient system may significantly underestimate SR uncertainty in the donor system, and described the implementation of a Bayesian hierarchical modelling method for a more accurate representation of uncertainty. However, for simplicity we adopted the direct extrapolation procedure for the pike-trout model and attempted to provide a reasonable estimate of extrapolation uncertainty by representing juvenile area in the stock-recruitment relationship as a probability distribution.

Trout can adopt a range of life-history strategies, including river resident (fluvial), river-lake migratory (adfluvial) and river-sea migratory (sea trout, *Salmo trutta*), depending on spawning and nursery environments, environmental pressures, and genetics. Stock-recruitment data have been recorded for trout in a small, sub-alpine lake (Borgstrøm *et al.*, 2010) and for resident trout in a large stream (Grossman *et al.*, 2017). Elliott (1989) describes a stock-recruitment study for sea trout in a small stream section in the Lake District, UK. Sea trout are sea-migratory trout that spawn in freshwater streams and may coexist with river-resident or lake-migratory populations. Poole *et al.* (2006) described a SR analysis of data from long-term monitoring of a sea trout population in the Burrishoole system in county Mayo, in the west of Ireland. The Burrishoole system comprises a large network of shallow streams and three lakes, two freshwater and one brackish, with approximately 12.5 ha of accessible fluvial area (calculated using the ArcGIS tool based on a predictive model (McGinnity *et al.*, 2012) modified to include first order stream contributions). Poole *et al.*, (2006)



concluded that a Beverton-Holt model best described the population-wide reproductive dynamics of the sea trout stock (Figure 5.4). This observation is consistent with the conclusions of Milner *et al.*, (2003) regarding the nature of compensatory SR density dependence for salmonids on large river systems.

The Burrishoole sea-migratory trout population represents the closest analogue to lake-migratory populations of trout in designated Irish lake fisheries of all the published case-studies described previously in terms of geographical coverage and life-history strategy. A collapse in sea trout angler catch observed in the mid-western region of Ireland encompassing Burrishoole during the late 1980s has been attributed to an increase in marine mortality caused by changes in the marine environment (Poole *et al.*, 2006). The freshwater reproduction phase of the sea trout life-cycle and hence the relationship between spawning stock and juvenile recruitment is thought to have remained unchanged over the period spanning the SR data (1971–1999). Thus, extrapolation of the SR relationship to other systems is not invalidated by the very specific set of environmental circumstances that have influenced Burrishoole sea trout population dynamics. Therefore, we estimated the SR relationship from this dataset and applied it to an Irish wild trout lake fishery – Lough Conn. Extrapolation of the SR relationship from sea trout to lake-migratory trout inevitably introduces some added model uncertainty owing to phenotypical differences but it was assumed that the uncertainty in spawning habitat area estimates is the dominant factor in overall SR. In the Burrishoole data, both sea trout smolts and un-silvered autumn trout are treated as juvenile recruits. In order to incorporate the SR relationship in the length-structured model, all recruits were assumed to be of age 2 — a typical assumption for many length-structured stock assessment models (Punt *et al.*, 2013).

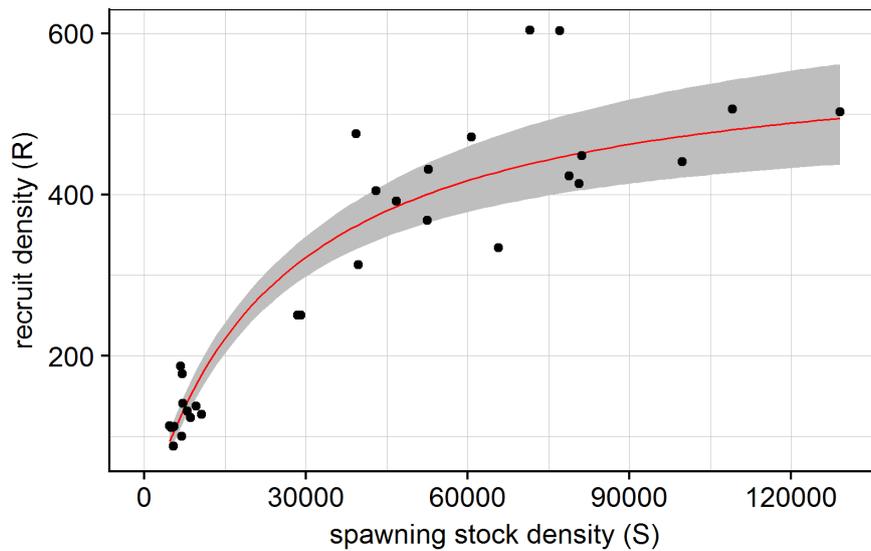


Figure 5.4. Burrishoole sea trout stock-recruitment data and empirical Beverton-Holt curve fit with 95% confidence bands. Spawning stock density is measured in terms of egg deposition.

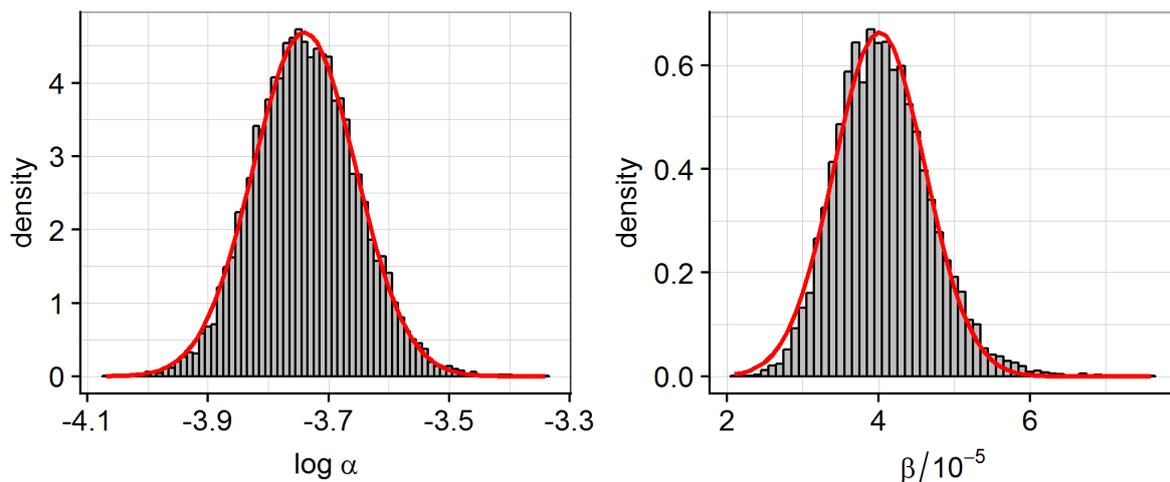


Figure 5.5. Probability distributions of stock-recruitment parameters $\log \alpha$ and β and normal distribution fits (red).

An application of Bayesian statistical inference to Burrishoole sea trout data yielded posterior probability distributions for the donor system SR parameters α^B and β^B (or $\beta^{B'}$). The underlying statistical model for the sea trout data assumed a lognormal process error so that juvenile output R is related to egg deposition S through a log transformation of Equation (11). Thus, Figure 5.5 illustrates the distributions of parameters $\log \alpha^B$ and β^B . Both distributions were found to be approximately normal (as shown by fitted theoretical normal curves) and so α^B has a lognormal distribution through back transformation. These distributions provide the range of possible values for α^B and β^B with associated probabilities so we can understand how likely each parameter is to



take a particular value. Notice that the most likely $\log \alpha^B$ value was found to be approximately -3.7 corresponding to an egg-to-recruit survival rate of about 2.5%. Details of the nonlinear regression within Bayesian framework are omitted for brevity.

The Freshwater Biological Association (<https://www.fba.org.uk>) at Windermere has conducted one of the few long-term population monitoring programmes (annual mark-recapture and gillnetting) for pike reported in scientific literature. Langangen *et al.*, (2011) generated synthetic age-structured abundance estimates based on the empirical dataset. We utilised this synthetic age-structured data to derive empirical SR parameters based on a Ricker model. Langangen *et al.*, (2011) classified recruits as age 3 pike and the adult stock as age 3–9 pike. Thus, the age at recruitment parameter for pike in the length-structured model was fixed at $a_r = 3$. A Ricker model was adopted to describe over-compensatory density dependence in the pike stock-recruitment relationship, which is likely to arise because of the cannibalistic tendencies of pike (Raat, 1988), whereby recruitment is negatively affected by an over-abundance of adults.

Stock and recruitment *density* data was obtained by dividing the synthetic pike abundance data calculated by Langangen *et al.*, (2011) by spawning and juvenile habitat area. Suitable spawning and nursery habitat for pike is most easily defined by depth ranges (Minns *et al.*, 1996) and so we define pike spawning and nursery habitat area to correspond to areas of lakes with depths of less than two metres. Weed or vegetation coverage is widely known to be important for pike spawning (see Section 3.5 of this report, Casselman and Lewis (1996) and Grimm (1981) but much more difficult to quantify. On Windermere, potential spawning habitat has been estimated to comprise 202 hectares from a total lake area of 1482 hectares (Mortimer and Worthington, 1942). The SR density data and the most likely SR curve (along with 95% confidence bands) obtained from nonlinear regression are shown in Figure 5.6.

Probability distributions of Ricker model SR parameters α^P (or more precisely $\log \alpha^P$) and β^P , shown in Figure 5.7, were determined by fitting a log-transformed Ricker relationship to the empirical Windermere data within a Bayesian statistical framework.

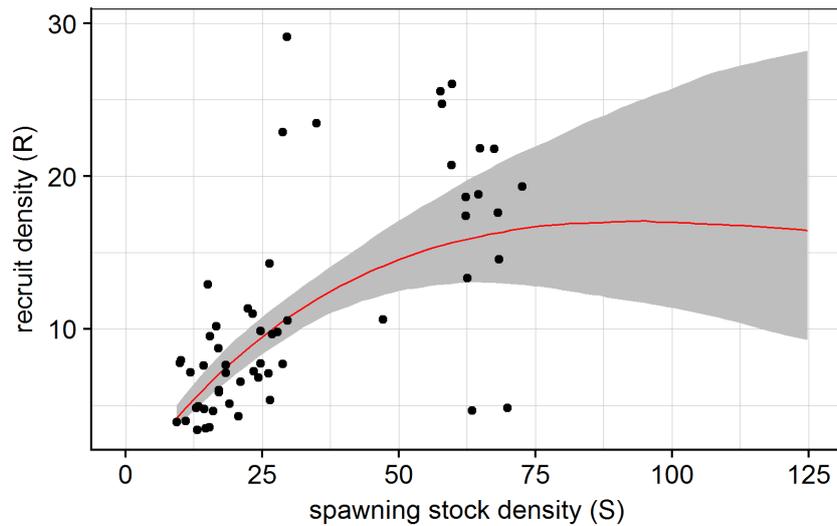


Figure 5.6. Spawner and recruit data (Langangen *et al.*, 2011) and empirical Ricker curve fit with 95% confidence bands for pike in Windermere.

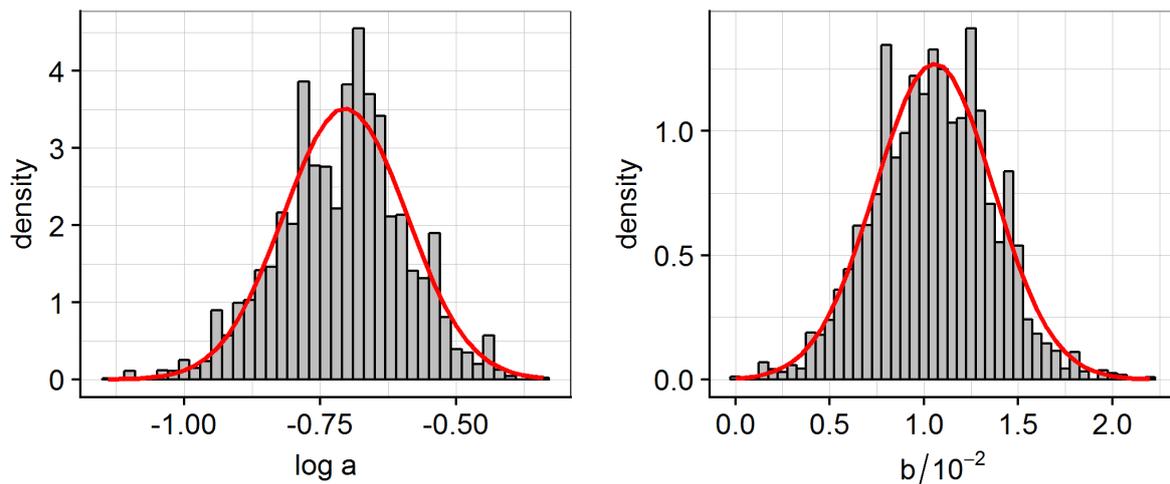


Figure 5.7. Probability distributions of stock-recruitment (Ricker curve) parameters $\log a$ and b and normal distribution fits (red).

In order to extrapolate a SR relationship from a system with SR data to a system without data, it is preferable to express the SR relationships in terms of densities (abundances per unit area) rather than absolute abundances. This is achieved by dividing through the SR relationship by the spawning or nursery area A_{don} , e.g. for the Beverton-Holt curve (11)

$$r = \frac{\alpha S / A_{don}}{1 + \beta A_{don} (S / A_{don})} = \frac{\alpha s}{1 + \beta' s} \quad (25)$$

where $r = R / A_{don}$ and $s = S / A_{don}$ are recruits and spawning stock measure per unit area, respectively, and $\beta' = \beta A_{don}$. Direct extrapolation to a recipient system is achieved by assuming



that the SR dynamics are identical in both systems apart from differences in spawning habitat area. Therefore, recruitment R in the recipient system is given by:

$$R \equiv rA_{rec} = \frac{\alpha A_{rec}}{1 + \beta' S} = \frac{\alpha S}{1 + \beta \frac{A_{don}}{A_{rec}} S}, \quad (26)$$

where A_{rec} is the spawning area for the recipient system. Density dependent control $\beta A_{don}/A_{rec}$ is stronger in the recipient system if $A_{don} > A_{rec}$ and vice versa. Statistical estimates of α and β (or β') were derived from the donor system data (see Figure 5.4 and Figure 5.6). Direct extrapolation from the donor to the recipient systems was possible provided spawning or nursery area estimates A_{don} and A_{rec} , respectively, were available for both systems.

Uncertainty in the extrapolation from donor to recipient systems was included through the recipient-to-donor system spawning habitat area ratio $a_{ratio} = A_{rec}/A_{don}$ term. The uncertainty incorporated in the habitat area estimate was intended to approximate all uncertainty arising from the assumption that the SR relationships are identical for both juvenile nursery systems and that accessible fluvial habitat area estimates capture all between-system variation.

The ratio of spawning and nursery habitat areas for Lough Conn trout and Burrishoole sea trout was represented using the probability distribution shown in histogram form in Figure 5.8(a). Based on fluvial habitat area estimates for nursery streams to Lough Conn, the area ratio term a_{ratio} was represented by a probability distribution with a most likely value around the point estimate $a_{ratio,0} \simeq 1.7$ and reasonable credibility for values between 1 and 3. For convenience, we assumed that the area ratio distribution was lognormal, so that the probability of the ratio values decreases quickly below the point estimate and more slowly above the point estimate.

Based on a combination of shallow area estimates for Lough Conn, historical records of pike removals from Lough Conn and Langangen *et al.*'s (2011) estimate for adult pike population, we proposed a habitat ratio probability distribution of the form shown in Figure 5.8(b). Langangen *et al.*, (2011) estimated an associated total adult pike population of 10,000–15,000 from 1980 to 2000. Annual reports from the Inland Fisheries Trust from the 1960s provide annual gillnetting return data for all designated wild trout fisheries. The maximum gillnetting return on Lough Conn during the period from 1963 to 1969 when removal effort was high was 1073 adults. Therefore, it was estimated that pike recruitment – and hence the habitat ratio term a_{ratio} – has a high probability of lying somewhere between 0.5 and 2 times that of Windermere.

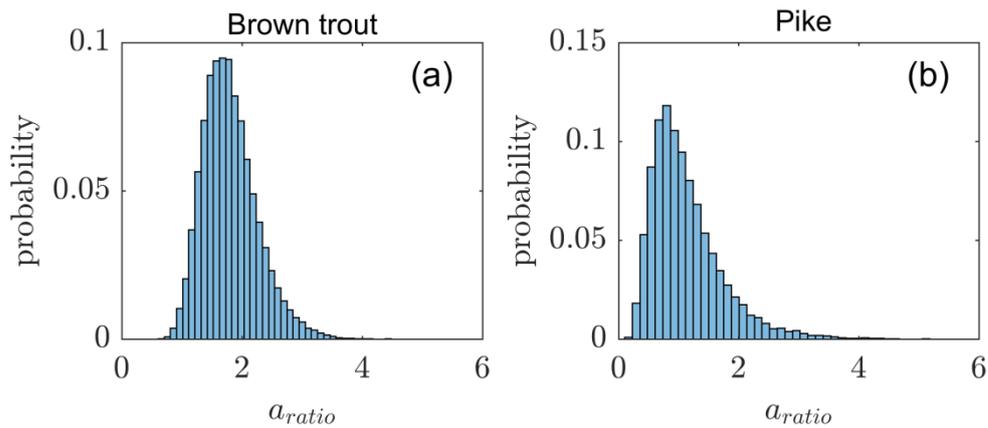


Figure 5.8. Probability distribution for the ratio of recipient-to-donor system spawning habitat area for (a) trout in Lough Conn and Burrishoole nursery streams and (b) pike in Lough Conn and Windermere.

Growth and mortality data

Model representation of growth processes requires only standard LVB growth parameters L_{∞} and κ which were determined from back-calculated length-at-age data. Such data is routinely derived from scale samples collected as part of IFI fish stock surveys. Furthermore, estimates of pike growth in both Lough Conn and Derravaragh were obtained by analysing a sub-sample of the scales collected from each pike caught during the dietary study. Back-calculated length-at-age estimates for trout sampled during a whole lake fish stock survey conducted on Lough Conn in 2016 are shown in Figure 5.9. Regression of the LVB growth curve (7) against mean length-at-age data yielded estimates of asymptotic length of $L_{\infty} = 50.5\text{cm}$ and growth constant $\kappa = 0.25 \text{ yr}^{-1}$ for trout. Similarly, Figure 5.9 also shows the pike length-at-age data for a selection of pike sampled during the dietary study and the corresponding LVB growth parameter estimates obtained from the fitting process are $L_{\infty} = 105\text{cm}$ and $\kappa = 0.22 \text{ yr}^{-1}$. Growth parameters for both species were assumed to be constant in time (no density dependent changes are allowed) and uncertainty in the parameter estimates were not considered in the uncertainty analysis of the model case study.

Residual natural mortality was estimated to be 0.3 yr^{-1} for all intermediate length-classes of trout and 0.31 yr^{-1} for all intermediate length classes of pike. The latter value is an average of male and female natural mortality parameter estimates determined from the stock assessment conducted by Langangen *et al.*, (2011) for the pike population on Windermere. Patterson *et al.*, (2001) note that uncertainty for natural mortality rates is difficult to estimate given a lack of appropriate data and that it is common to assume that natural mortality has a uniform distribution over a range of plausible values, i.e. is equally likely to take any value in that plausible range. However, Quinn and



Collie (2005) note that natural mortality is a U-shaped function of age, with highest mortality during early life history and at older ages. For this reason, auxiliary residual mortality of 0.2 yr^{-1} was added to the largest pike and trout length classes. Pike recruit to the model at age 3 corresponding to lengths above 35cm and were considered of intermediate age so no auxiliary mortality was applied to the smallest length class. Trout recruit to the model age 2 (lengths greater than 16cm) and so an added mortality of 0.2 yr^{-1} was applied to the smallest length class.

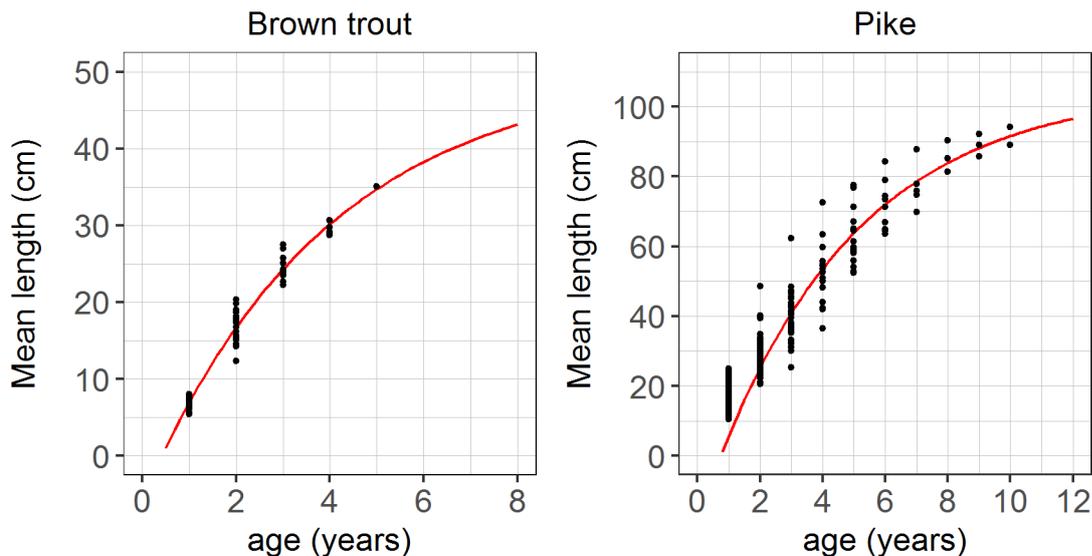


Figure 5.9. Back-calculated length-at-age data (black) and LVB growth curve (red) regressed on mean length-at-age for trout sampled in the Lough Conn fish stock survey in 2016 and pike sampled during the 2016-2017 dietary study.

Length classes

Length class definitions for the length-structured population model of pike-trout interactions in Lough Conn are shown in Table 5.2. These length classes were chosen based on the length-at-age data for the respective species shown in Figure 5.9, e.g. expected back-calculated pike lengths at age 3 lie between 30cm and less than 50cm. Furthermore, the asymptotic length L_{∞} is 105cm and so the total span of all length classes was chosen to be from 30cm to 105cm. Length class intervals of 15cm were chosen so that the sample sizes of each pike length class from the dietary study were not too small. Similar reasoning based on growth data was used to define the trout length classes.



Table 5.2. Pike and trout length classes for the length-structured population model.

Species	Pike		Trout	
	Range (cm)	Mid-length (cm)	Range (cm)	Mid-length (cm)
1	30–45	37.5	16–24	20
2	45–60	52.5	24–32	28
3	60–75	67.5	32–40	36
4	75–90	82.5	40–48	44
5	90–105+	97.5	48–56+	52

Predation mortality – pike dietary data

Length-specific predation mortalities are calculated from Equation (19) and depend on estimates of:

- annual specific food consumption c_l for pike;
- available fraction of potential trout biomass across all trout and pike length classes Φ_m^l ;
- available fraction of alternative prey biomass available to pike in each length class; and
- weights of pike and trout at the mid-point lengths for each length class.

Expected weights for fish in each length class were estimated based on mid-point lengths of the respective classes and the species length-weight regressions. Connor *et al.*, (2017) derived length-weight relationship estimates from ten years of annual fish stock surveys on Irish lakes for ten of the most commonly encountered species and categorised relationships by alkalinity for the three most abundant species including trout. The high alkalinity length-weight regression coefficients were used to derive trout weights from lengths in the Lough Conn case study because of Lough Conn's classification as a typology 12 lake (Kelly *et al.*, 2017). Lengths and weights were recorded for all pike samples collected as part of the dietary study from which length-weight relationship specific to Lough Conn was obtained.

Heikinheimo and Korhonen (1996) used a bioenergetics model to estimate the annual specific food requirements of pike populations in two lakes in north-eastern Finland. The populations were separated into two different age groups: the first comprising pike aged 1–2 years old and the second comprising pike aged 3–6 year old. Annual specific food consumption of the younger age group of pike was estimated to be 7–5 grams per one gram (g g^{-1}) of pike, whereas for pike aged 3–6 years old it was 4–3g g^{-1} . This means that on average 1–2 year old pike and 3–6 year old pike require respectively between 5 and 7 times and between 3 and 4 times their own body weight to survive, grow and reproduce. These annual rations are similar to the food conversion factors used by O'Grady *et al.*, (1996) for estimating trout and roach consumption by pike on Lough Corrib. These values were translated to pike length classes in an *ad hoc* manner:



- pike in length class 1 (30cm, 45cm) were considered to be approximately two years old and were assigned an annual specific food ration of 6g g^{-1} ;
- pike in length class 2 (45cm, 60cm) were estimated to be 3–4 years old with an annual specific food ration of 4g g^{-1} ;
- pike in length class 3 and 4 were considered to be 4–6 years old with an annual specific food ration of 3g g^{-1} ; and
- the largest pike (in length class 5) were assumed to have an annual specific food ration of 2g g^{-1} .

The biomasses of target prey and alternative prey from the ambient environment available to predators are important determinants of prey mortality as discussed in Section 5.2.2. In order to calculate the fraction of potential prey biomass (Equation (22) for target prey and Equation (24) for alternative prey) available to a predator it was necessary to parameterise the size preference curve (21) for both length and weight. We attempted to estimate the size preference parameters – starting with length – from empirical data collected during the pike dietary study reported in Section 2.

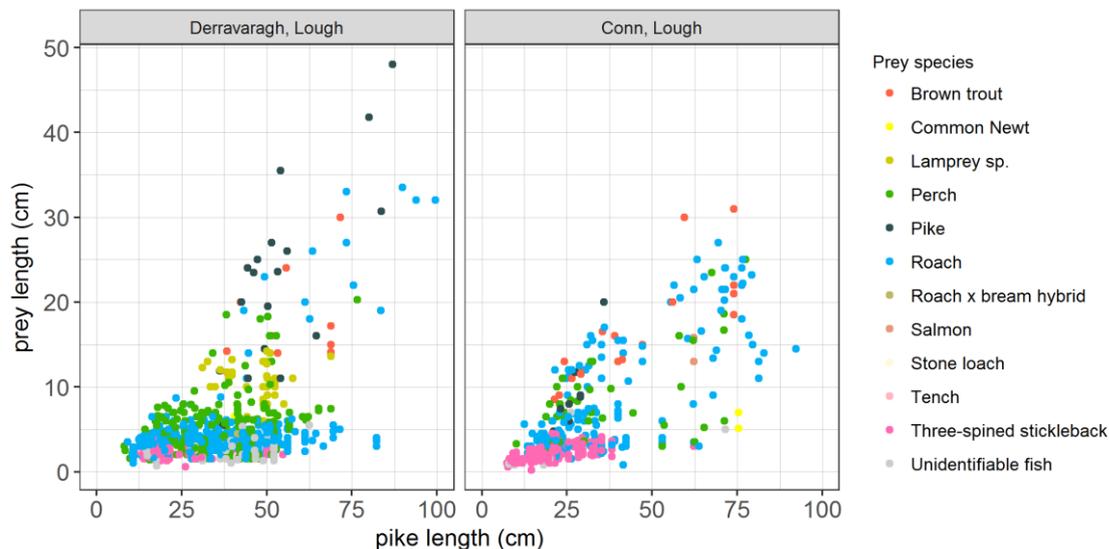


Figure 5.10. Overview of pike and prey length data from dietary study on Lough Derravaragh and Lough Conn.

An overview of prey length data obtained from pike stomach samples on both lakes is presented in Figure 5.10, where the estimated lengths of all fish prey items obtained in stomach samples are compared to the measured pike lengths from which the stomach samples were obtained. Prey lengths were estimated based on the prey remains found in the stomach. Morphometrics were used to estimate length where only partial skeletal remains were found. It is evident from Figure 5.10 that sample sizes for pike-prey length data are relatively limited for the larger pike length classes and



so it was not possible to estimate size preference parameters for pike in each length class separately. Instead, prey length data for all pike across all lakes were pooled and a single optimal length ratio β_L parameter and length ratio tolerance parameter σ_L for pike estimated. This is consistent with the approach adopted by Gislason and Helgason (1985), who estimated one pair of size preference coefficients per predator species in their application of the MSVPA to the North Sea fish community.

A histogram of pike-prey length ratios is shown in Figure 5.11. Each prey item was treated as an independent sample and although prey species are highlighted in the figure, prey species preference was ignored when fitting Equation (21) to the data. A nonlinear regression applied to the length-ratio data yielded an estimate of $\beta_L = 5.7$ for the optimal length ratio and $\sigma_L = 0.56$ for the length ratio tolerance σ_L . These preliminary estimates require further examination because, as noted by Floeter and Temming (2003), the data presented in Figure 5.11 show the length preference of pike in an environment with a particular prey abundance. Both prey abundance and size preference influence diet composition; the extraction of size preference from the pike diet composition data requires further examination of the prey fish abundances in the ambient environment of pike.

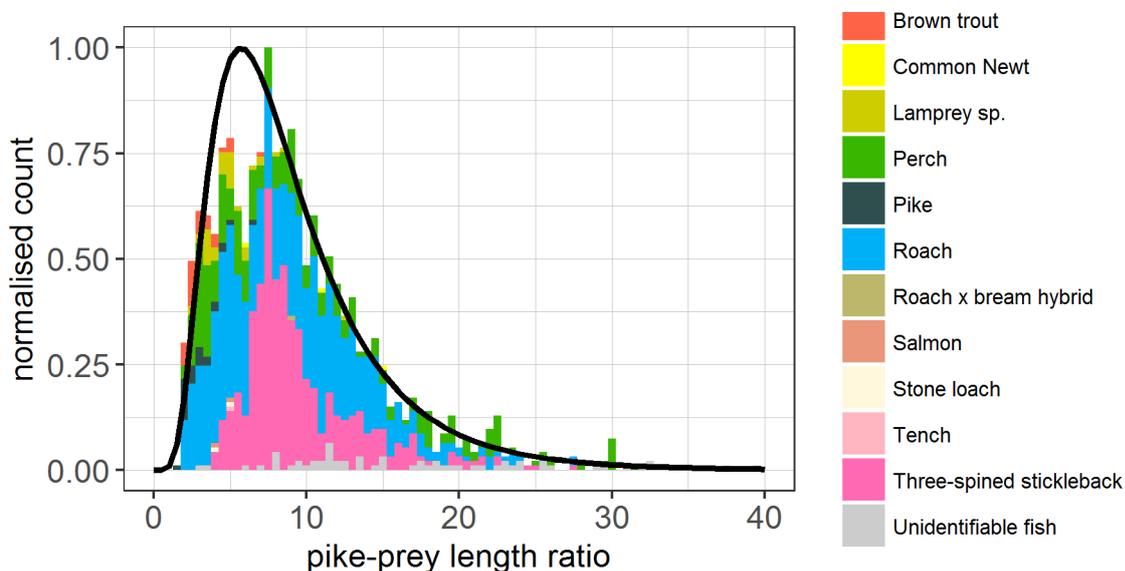


Figure 5.11. Empirical predator-prey length ratio distribution and fitted lognormal curve (black) for prey items recorded in pike stomachs from Loughs Conn and Derravaragh.

A biomass size-spectrum, expressed in the form of a two-parameter power-law relationship in Equation (23), was used to represent the distribution of prey biomass in the ambient lake environment. The size-spectrum exponent or slope determines how the biomass is distributed in the ecosystem: larger exponents indicate a greater abundance of small fish and fewer large fish.



Andersen and Beyer (2006) predicted a theoretical size spectrum slope of approximately 2 based on metabolic and growth requirements at the individual level. For the purposes of this case study, an estimate of the biomass size spectrum slope was obtained from empirical fish stock survey data from Lough Conn by adopting an approach similar to that used by Sweeting *et al.*, (2009) and Emmrich *et al.*, (2011), among others. This approach involved discretising the continuous biomass size spectrum by dividing the range of fish masses sampled into logarithmic size classes ($m, 2m$) and aggregating or “binning” individual fish masses in each discrete size class. The biomass of all individuals in each size class was summed and finally normalised by the span of the size class to obtain an empirical biomass distribution.

Empirical aggregate and normalised biomass distributions are presented in Figure 5.12. The normalised biomass distribution does not show monotonically increasing biomass with decreasing fish size as predicted by size spectrum theory. This suggests that the CEN standard multi-mesh monofilament gillnets, which are the dominant gear in the WFD multi-method sampling approach to the whole lake fish stock survey on Lough Conn (Kelly *et al.*, 2017), are not fully selective for fish below size class 6 ($2^6 = 64\text{g}$). In fact, it is known that young-of-the-year and juvenile fish abundance is underestimated in multi-mesh gillnet surveys (Prchalová *et al.*, 2009). Nevertheless, the size spectrum slope can be estimated from the subset of fully selected fish sizes (greater than or equal to size class 6). The community size spectrum at small sizes, including the smallest prey fish and other organisms such as macroinvertebrates, was determined by extrapolation from the empirical size spectrum fit. Figure 5.13 shows a linear regression of log-transformed normalised fish community biomass against size class index, which corresponds to \log_2 of the lower size class limit. A size spectrum slope of $\lambda = 2.29$ was estimated from this linear regression with an associated standard error of $SE(\lambda) = 0.16$. Large confidence intervals occurred because the fish community was sampled effectively over a relatively small range of size classes (6–10).

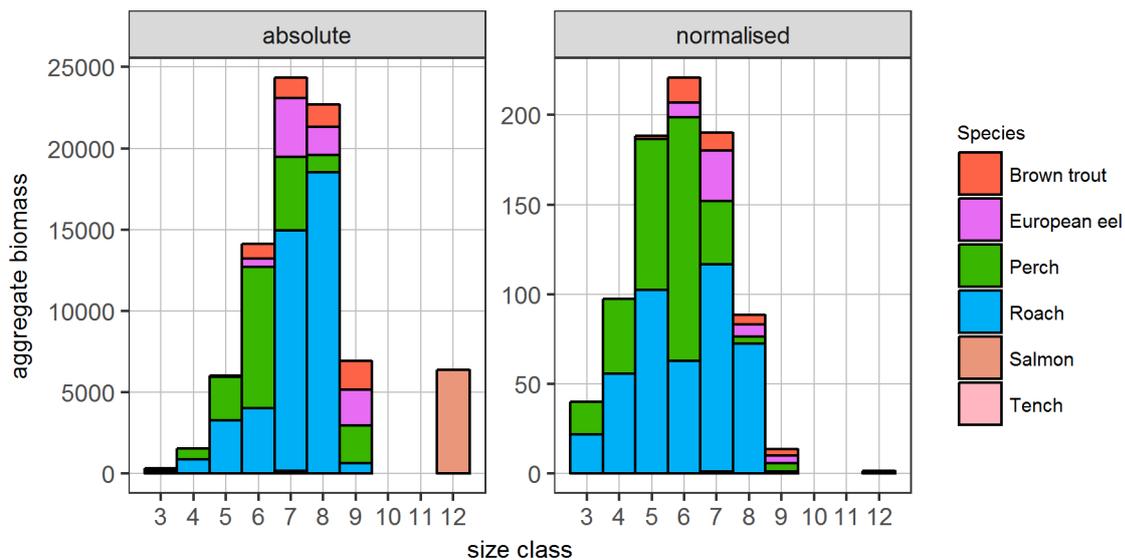


Figure 5.12. Absolute and normalised (by size class width) aggregate biomasses for fish community data from a whole lake fish stock survey (WFD multi-method sampling approach) of Lough Conn in 2016.

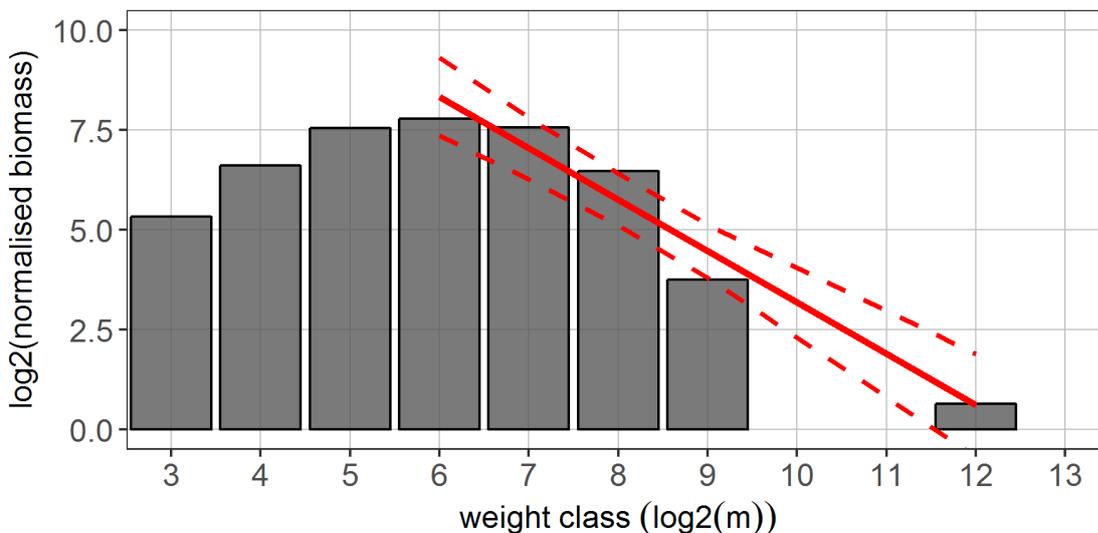


Figure 5.13. Linear regression with confidence intervals of log-log transformed normalised fish biomass data from WFD multi-method whole lake fish stock survey of Lough Conn (2016).

Estimates of the absolute level of prey biomass (represented by parameter κ_c in Equation (23)) in the ambient environment were very difficult to determine. Empirical biomass size spectrum analysis of CEN net lake survey data provided an estimate for the shape of the biomass distribution but not the absolute biomass. An informal scaling method was developed based on a comparison between a surplus production estimate of total exploitable trout biomass from Fitzgerald *et al.*, (2018), time-averaged over the period 1975–2001, and the biomass of exploitable trout sampled in the whole



lake fish stock survey (CEN standard multi-mesh monofilament gillnets augmented by a limited number of Dutch fyke nets and eight-panel benthic braided nets) for Lough Conn conducted in 2016. From this comparison, we concluded that the exploitable trout survey sample biomass represents approximately one thousandth of the estimated absolute exploitable trout stock biomass. This information combined with empirical fish stock biomass data yielded an estimate of $\kappa_c = 1.12 \times 10^5$ kg. The uncertainty in this estimate is very large. Therefore, we used this 'best' estimate of κ_c to represent a 'medium' level of alternative prey abundance, $\kappa_c/3$ to represent low levels of alternative prey abundance, and $3\kappa_c$ to represent high levels of alternative prey abundance. The behaviour of the model was then analysed across three levels of alternative prey biomass in the ambient environment where the range of prey biomasses covers almost one order of magnitude. The three levels of alternative prey biomass are expressed relative to aggregate trout biomass in Section 5.3 for both model output and whole lake fish stock survey data to illustrate in real terms what the above definitions of a 'scarce', 'moderate' or 'plentiful' biomass of alternative prey represent.

5.2.4 Sensitivity analysis

Before evaluating the performance of various management strategies subject to parameter uncertainty it is prudent to first assess the sensitivity of model outputs to changes in *estimated* biological input parameters through a sensitivity analysis. Such analyses seek to quantify how small perturbations or changes in input parameters affect model outputs. These biological and ecological population model parameters are estimated either from data if present or expert judgement if data are absent, and are inherently uncertain because of variability and incompleteness of data as is evident from Section 5.2.3. On the other hand, in management strategy evaluations (MSEs), fisheries management parameters such as removals (fishing mortality) or size limits may be *prescribed exactly* according to particular management scenarios. The primary goal for the sensitivity analysis was to identify the estimated biological input parameters to which the model outputs are most sensitive. Such information is valuable both from the perspective of deciding on future sampling programmes and also for designing/realising efficient methods for measuring uncertainty.

Perturbations in the model outputs caused by changes in the inputs can be measured using rates of change referred to as sensitivities and elasticities, c.f. e.g. Caswell (2001). Elasticities and sensitivities measure the rates of change of the model response and summarise model response information in a form suitable for tabulation for comparison (c.f. e.g. Fredenberg *et al.*, 2017). For



example, an exhaustive sensitivity analysis of the model response to all biological and ecological parameters in Table 5.1 would require tabulation of sensitivity or elasticity measures. For brevity, we restricted our analysis of model sensitivity to the availability of the alternative prey resource and to the stock-recruitment parameters for both target species for which a graphical analysis of model response is more intuitive.

Pike management operations and trout angling regulations on designated trout lake fisheries have been implemented with the aim of enhancing trout abundance on these fisheries. Therefore, some measure of trout abundance or biomass must be used to quantify the success of any proposed management strategy. The corresponding sensitivity analysis must also examine the response of these particular model outputs. We selected the exploitable trout biomass (aggregate trout biomass for all length classes above a minimum length limit of 30cm) and the mean weight of exploitable trout at steady state as the model output metrics. The two-species system reaches steady state once losses from population length classes owing to mortality and growth are exactly balanced by additions owing to recruitment and growth and further advances in time yield negligible changes in the populations.

5.2.5 Uncertainty analysis and management strategy evaluation

Langsdale (2008) discussed the challenges posed by uncertainty arising in natural resource model forecasts for natural resource managers and emphasised the importance of acknowledging and conveying this uncertainty to stakeholders. In a fisheries context, Patterson *et al.*, (2001) present a comprehensive technical review of uncertainty estimation in fish stock assessment and forecasting. Given the importance of the SR relationship to fish population dynamics, any uncertainty analysis of model projections must include uncertainty in the stock-recruitment parameters and the habitat area extrapolation parameter. Therefore, we incorporated uncertainty in the SR parameters for both species and in the ambient prey biomass parameter κ_c (estimates for which are very uncertain and which was revealed to strongly influence model outcomes by the sensitivity analysis) in the management strategy evaluation.

Propagation of input model uncertainty through to model outcomes or responses was achieved by simulating an ensemble of model outcomes from random realisations of input parameters. This random realisation and simulation process involved the following:

- randomly draw a $\log \alpha$ (SR parameter) value for each species from the fitted normal distributions shown in Figure 5.5 and Figure 5.7;



- derive a corresponding β value using the SR parameter correlation relationships mentioned in Section 5.2.3;
- generate a random a_{ratio} based on the lognormal distribution displayed in discretised form in Figure 5.8 and 5.9;
- simulate the population interactions based on this particular realisation of the SR relationship and save the model outcomes; and

repeat the above steps 20,000 times to construct a distribution of model outcomes.

The management strategy evaluation involved calculating exploitable biomass and mean weight for trout at steady state for different combinations of trout and pike removals and across each alternative prey resource scenario. Ensembles of model outcomes were computed for three trout fishing pressures and three pike removals pressures across three alternative prey biomass scenarios, giving a total of 27 different model configurations.

5.3 Results and analysis

5.3.1 Sensitivity analysis

The presence of other prey species is understood to be an important factor in determining the coexistence or otherwise of pike and trout (Hein *et al.*, 2013). In order to understand how and by how much the ambient prey resource affects the prey population abundance we conducted a sensitivity analysis of prey abundance to perturbations in the prey resource spectrum abundance.

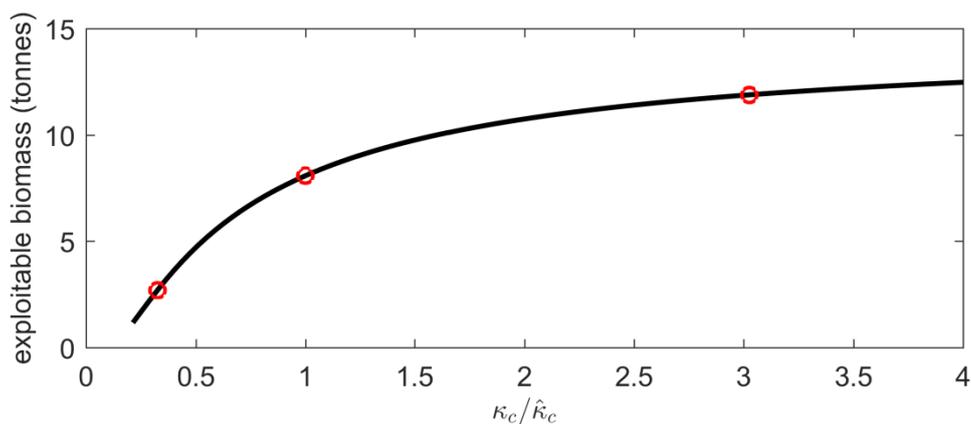


Figure 5.14. Exploitable biomass response to changes in the normalised ecosystem (alternative) prey biomass $\kappa_c/\hat{\kappa}_c$. Three κ_c values ($\hat{\kappa}_c/3$, $\hat{\kappa}_c$ and $3\hat{\kappa}_c$) corresponding to different alternative prey biomass scenarios are highlighted with red circles.



Model responses to changes in the alternative prey biomass spectrum parameter κ_c are shown in Figure 5.14. The particular responses considered were aggregate abundance (sum of abundances across all length classes) and exploitable biomass of trout at steady state. In practical terms, steady state corresponds to the system state after projecting the population 50 years from the initial state. The initial state was prescribed as a pike population of 2,000 and a trout population of 10,000 individuals. Figure 5.14 shows how the model projections of steady-state trout abundance and exploitable biomass become increasingly sensitive to absolute ecosystem prey abundance as this resource decreases. Three values of the alternative prey biomass abundance parameter κ_c are highlighted: $\hat{\kappa}_c/3$, $\hat{\kappa}_c$ and $3\hat{\kappa}_c$ where $\hat{\kappa}_c$ is the best estimate for the biomass of alternative prey in the ecosystem. As the alternative ecosystem prey abundance parameter decreases, the rate of change of the model response increases, and so the system is said to be more sensitive for smaller values of κ_c .

This behaviour is a consequence of the predation model mechanism for representing the (target) predator-prey species interaction within the wider ecosystem, i.e. predation mortality suffered by the target prey species depends on the ratio of target prey species to total prey species available biomass. A careful examination of how different levels of ambient prey abundance affect the species interactions was necessary because of the influential nature of the total ambient prey abundance parameter and the significant uncertainty in that parameter. This was achieved by examining model sensitivity to variations in other likely influential parameters for three different κ_c values ($\hat{\kappa}_c/3$, $\hat{\kappa}_c$ and $3\hat{\kappa}_c$) corresponding to three scenarios where the alternative prey biomass resource is plentiful, moderate and scarce, respectively.

The importance of target predator and prey species stock-recruitment parameters to overall population interactions was discussed in Section 5.2.1. Therefore, a sensitivity analysis of prey species and predator species SR parameters across three levels of alternative prey biomass was considered in order to understand how the projected population dynamics change along a gradient of ecosystem prey abundances. The exploitable trout biomass response to changes in the density-independent SR parameters for each species, i.e. trout egg-to-recruit survival at low densities α_B and pike recruits-per-adult at low densities, are shown in Figure 5.15. In each case, the SR parameter was varied over the 99% confidence intervals obtained from the model fitting process based on empirical data (see probability distributions in Figures 5.5 and 5.7). Exploitable trout abundance increases with increasing egg-to-recruit survival and the rate of increase is greater when the biomass of alternative prey in the ecosystem is more plentiful (and interactions between small trout and pike



are weakest). On the other hand, the exploitable trout biomass decreases with increasing pike recruits-per-adult. This decrease appears most severe when the biomass of alternative prey in the ecosystem is scarce. When the alternative prey resource is more plentiful, then the influence of pike recruitment is reduced as might be intuitively expected. However, competition between prey species is not captured in the model and so any potential benefit to trout of increased cropping of competitor prey species by pike cannot be evaluated using this tool.

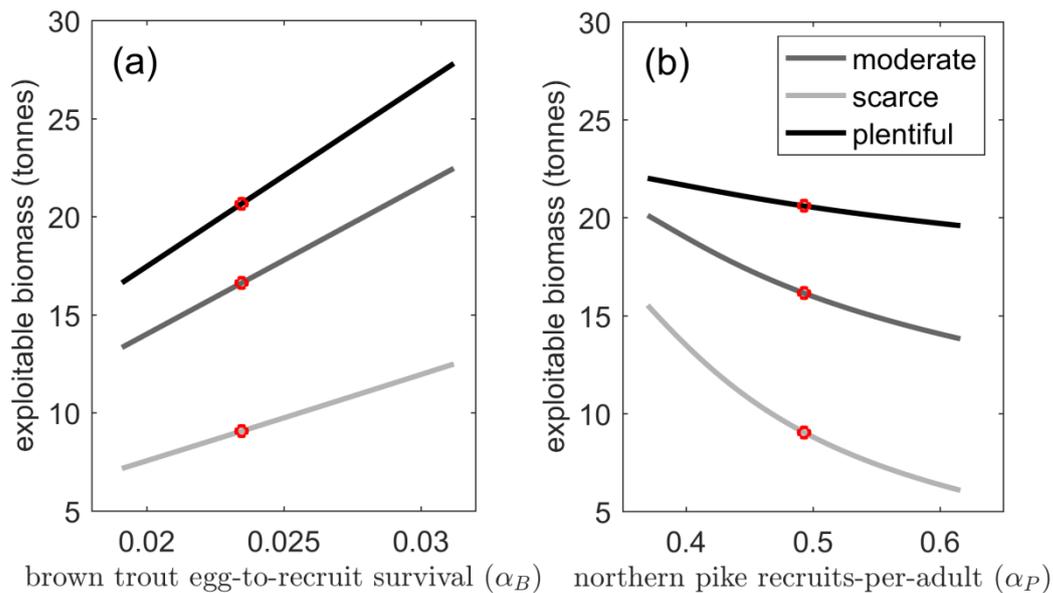


Figure 5.15. Variation in exploitable trout biomass with (a) trout egg-to-recruit survival α_B and (b) pike recruits-per-adult α_P for three different levels of alternative prey biomass in the ecosystem.

5.3.2 Uncertainty analysis and management strategy evaluation

A preliminary uncertainty analysis of model outcomes in the absence of fishing removals is presented in Figure 5.16. The particular model responses examined were biomass and mean weight of exploitable trout at steady state. Uncertainty in model outcomes was assessed for the three different alternative prey abundance scenarios described above. Including uncertainty in the SR parameters caused considerable uncertainty in the exploitable biomass estimates as indicated by the spread of the exploitable biomass probability distributions across all alternative prey abundance scenarios. However, the mean weight of exploitable trout was much less uncertain for the moderate to plentiful alternative prey resource scenarios. This observation can most likely be explained by the fact that uncertainty in growth, which affects the proportions of individuals in each length class, is not incorporated. Furthermore, juvenile recruits enter the smaller length classes in fixed proportions under the assumptions of the model.

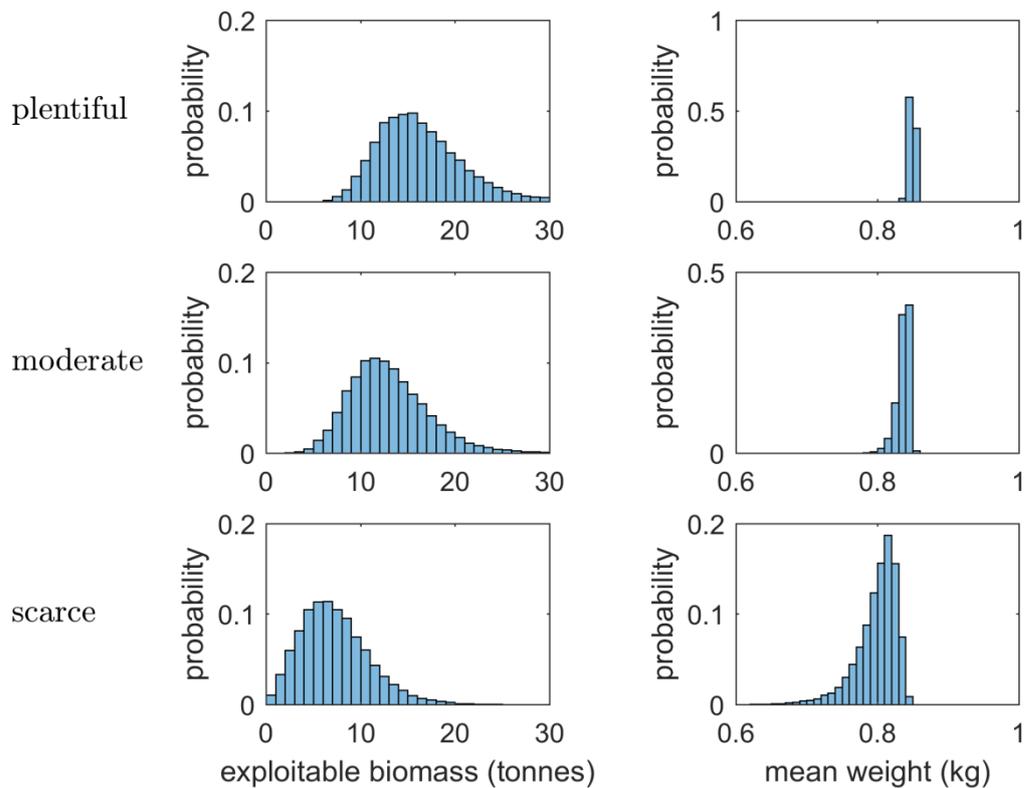


Figure 5.16. Distribution of model outcomes when incorporating uncertainty in trout stock-recruitment parameters for three different alternative prey biomass scenarios.

Figure 5.17 illustrates a preliminary management strategy evaluation of the effect of different pike and trout exploitation pressures across three alternative prey scenarios ranging from a scarce to a plentiful resource. Fishing mortalities of 0.15 yr^{-1} and 0.3 yr^{-1} were designated as 'low' and 'medium' removal or fishing pressures and correspond to annual removal fractions of 14% and 26%, respectively. Fishing mortality producing maximum sustainable yield F_{MSY} is assumed to approximately equal 0.3 yr^{-1} for many species (cf. e.g. Deriso, 1982). All combinations of fishing mortalities for pike and trout were examined. For example, the low trout fishing pressure and medium pike removal case corresponds to fully selective fishing mortalities (see Equation (6)) of 0.15 yr^{-1} for trout and 0.3 yr^{-1} for pike. Length-specific gear selectivity (see Equation (6)) for trout angling and pike management were specified to reproduce size regulations, e.g. gear selectivity for length classes of trout below 30cm and those of pike above 85cm was zero. Several different trends are observable from Figure 5.17; however, it is important to first note that the confidence intervals indicated by the error bars were very wide in all cases. These wide error bars reflect the uncertainty in transporting stock-recruitment relationships from donor to recipient systems. The level of uncertainty observed in the current model outputs suggests that general trends can be accepted,



i.e., the relative effects of different management strategies, but absolute levels of predicted trout biomass are less reliable.

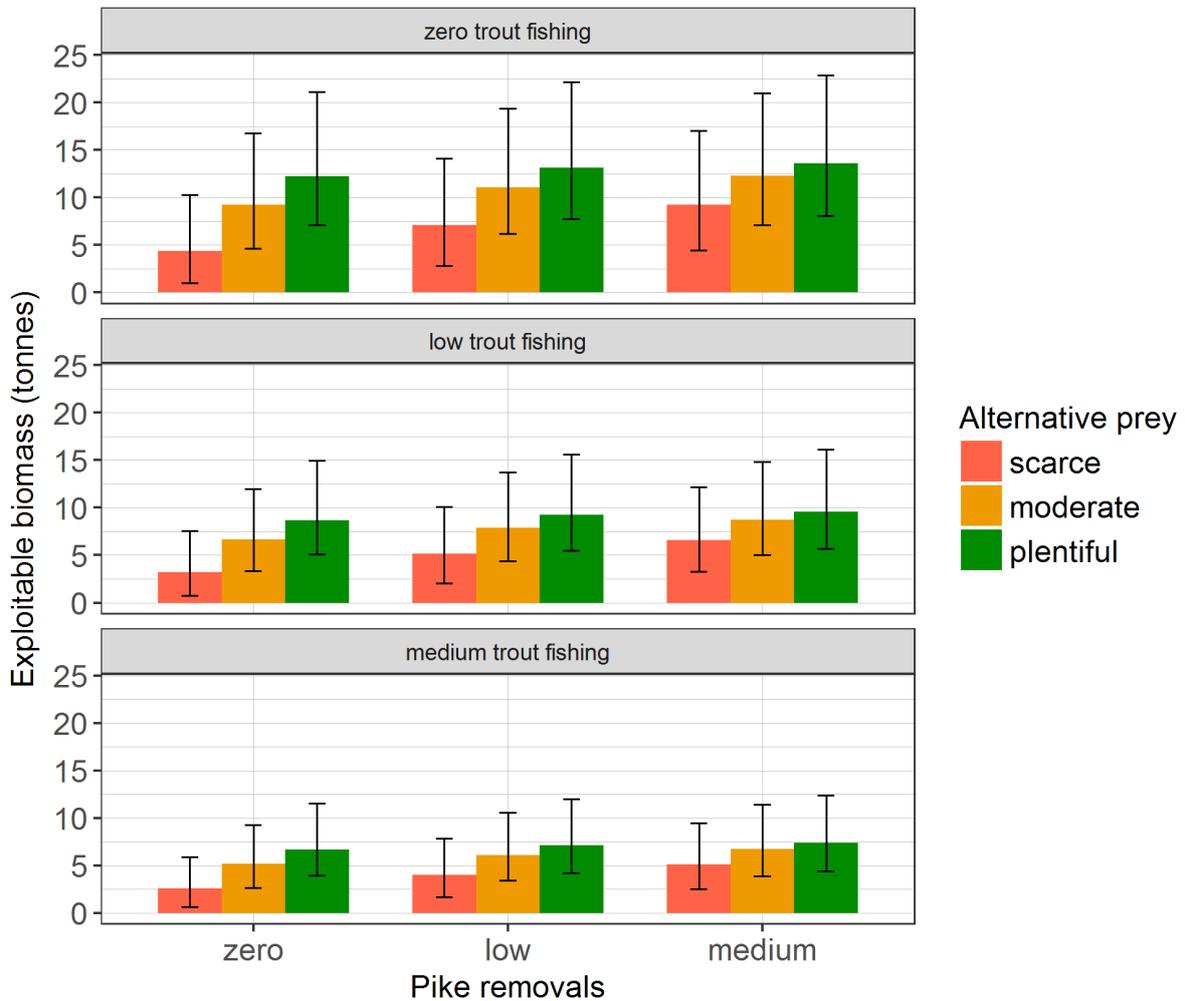


Figure 5.17. Biomass of exploitable trout (> 30cm) at different levels of pike and trout removals for three different alternative prey abundance scenarios.

Several important elements in the MSE results emerge from Figure 5.17. Pike removals had the greatest positive effect on trout biomass when alternative prey was 'scarce' across all levels of trout fishing pressure. Median exploitable trout biomass (i.e. biomass of trout greater than 30cm in length) increased by a factor of 1.6 and 2.1 by imposing low and medium levels of pike removals, respectively, in the scarce alternative prey scenario in the absence of trout fishing (see the top row of Figure 5.17). On the other hand, median exploitable trout biomass increased by a factor of only 1.07 and 1.11 with plentiful alternative prey and no trout fishing. This MSE result implies that pike



removals may be an effective management tool in systems with little alternative prey, but may have almost no effect on trout biomass in systems with abundant alternative prey, e.g. roach. A similar outcome was observed for empirical fish survey and pike removal data for Lough Sheelin (see Chapter 4).

The relative effects of pike and trout removals were also compared in the moderate alternative prey resource scenario. A greater than 15% increase in median trout biomass was observed when pike removals were increased from 'zero' to 'low' in the context of low trout fishing; however, a greater than 20% increase in the median trout biomass was observed when the trout fishing level was reduced from 'medium' to 'low' in the context of low pike removals. This suggests that, in the moderate alternative prey resource scenario, some reduction in trout fishing mortality may be slightly more beneficial to trout populations than an increase in pike removals.

Potential alternative prey biomasses in the 'scarce', 'moderate' and 'plentiful' scenarios are defined in terms of the theoretical biomass quantity κ_c . A more intuitive measure of potential alternative prey biomass may be obtained by expressing the biomass of alternative prey over the size range defined by the maximum and minimum modelled trout lengths (16cm and 56cm corresponding to approximately 47g and 1956g, respectively) relative to the aggregate biomass of trout. For example, the potential alternative prey biomasses in the 'scarce', 'moderate' and 'plentiful' scenarios are 2.5, 7.4 and 22.2 times greater than the median aggregated trout biomass calculated in the 'moderate' alternative prey scenario assuming no angling or management removals. As a reference, fish stock survey data from Lough Conn in 2016 shows that the biomass of other fish prey species is approximately 14 times greater than that of trout over the length range (16cm, 56cm). Similarly, the biomass of alternative prey species recorded in the whole lake fish stock survey of Lough Derravaragh in 2017 is almost 45 times that of trout over this length range (excluding large, deep-bodied hybrids and tench which have attained a size refuge from pike).

Other length-based management regulations such as harvest slot limits or protected slot limits for either pike or trout may also be explored using the length-structured model. This provides scope for evaluating candidate sets of management tools, depending on specified policy objectives.

5.4 Discussion

A size-structured population projection model was developed to evaluate potential management actions in wild trout lake fisheries. The model behaviour was explored through a sensitivity analysis



which highlighted how variations in several influential model parameters can cause relatively large changes in the model projections. The biomass of alternative prey in the ecosystem was observed to significantly influence the strength of the interaction between pike and trout. In particular, the impact of pike predation was mitigated by increases in the available alternative prey biomass. Other influential (and uncertain) model inputs included pike and trout stock-recruitment parameters.

A scenario-based evaluation of the effects of different pike and trout removal pressures was also presented. A reduction in trout fishing pressure from a medium to a low level was observed to have a more beneficial effect on the exploitable trout biomass than the introduction of a low level of pike removals. Some caution must be exercised when interpreting the model results because the uncertainty in the MSE results is large compared to MSEs for commercial marine fisheries; however, commercial marine fisheries are typically underpinned by detailed catch-at-length or catch-at-age data. Furthermore, model assumptions may restrict possible model behaviour. For example, competition between the target prey species and other prey species in the assemblage is not represented in the model. In ecological terms, predation on one prey species could benefit another prey species occupying the same trophic niche. Model limitations and uncertainty in model outputs must be recognised when considering the implications of the MSE.



6. References

- Adams, C. E. (1991) Shift in pike, *Esox lucius* L., predation pressure following the introduction of ruffe, *Gymnocephalus cernuus* (L.) to Loch Lomond. *Journal of Fish Biology*, **38 (5)**, 663-667.
- Allott, N., G. Free, K. Irvine, P. Mills, T. E. Mullins, J. J. Bowman, W.S.T. Champ, K. J. Clabby, and M. L. McGarrigle (1998) Land use and aquatic systems in the Republic of Ireland. In: *Studies in Irish Limnology*. Giller, P.S. (Ed). Essays on the occasion of the XXVII Congress of Societas Internationalis Limnologiae (SIL). Brunswick Press Ltd.
- Amundsen, P. A., Gabler, H. M., and Staldvik, F. J. (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. *Journal of fish biology*, **48 (4)**, 607-614.
- Andrews, S. N., Zelman, K., Ellis, T., Linnansaari, T., and Curry, R. A. (2018) Diet of striped bass and muskellunge downstream of a large hydroelectric dam: A preliminary investigation into suspected Atlantic salmon smolt predation. *North American Journal of Fisheries Management*, **38 (3)**, 734-746.
- Andersen, K. H. and Beyer, J. E. (2006) Asymptotic Size Determines Species Abundance in the Marine Size Spectrum. *The American Naturalist*, **168 (1)**, 54–61.
- Andersen, K. H., Jacobsen, N. S. and Farnsworth, K. D. (2016) The theoretical foundations for size spectrum models of fish communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **73 (4)**, 575–588.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. (2014) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67(1)**, 1-48.
- Beard, T.D., Arlinghaus, R., Cooke, S. J., McIntyre, P.B., De Silva, S., Bartley, D. and Cowx, I.G. (2011) Ecosystem approach to inland fisheries: research needs and implementation strategies. *Biological Letters*, **7 (4)**, 481-483.
- Beaudoin, C. P., Tonn, W. M., Prepas, E. E. and Wassenaar, L. I. (1999) Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia*, **120**, 386-396.



- Beverton, R. J. H., and Holt, S. J. (1957) *On the Dynamics of Exploited Fish Populations* (Facsimile). Dordrecht, Springer, Netherlands.
- Beyer, J. E. (1989) Recruitment stability and survival — simple size-specific theory with examples from the early life dynamic of marine fish. *Dana*, **7**, 45–147.
- Borgstrøm, R., Museth, J., & Brittain, J. E. (2010) The brown trout (*Salmo trutta*) in the lake, Øvre Heimdalsvatn: long-term changes in population dynamics due to exploitation and the invasive species, European minnow (*Phoxinus phoxinus*). *Hydrobiologia*, **642(1)**, 81–91.
- Bracken, J.J. (1973) The age and growth of pike *Esox Lucius* from four Irish trout rivers. *Irish Fisheries Investigations. Series A (Freshwater)*, **No. 12**.
- Bracken, J. J. and Champ, W. S. T. (1971) Age and growth of pike in five Irish limestone lakes. *Scientific Proceedings of the Royal Dublin Society, Series B*, **3**, 1-33.
- Brander, K., Neuheimer, A., Andersen, K. H., & Hartvig, M. (2013) Overconfidence in model projections. *ICES Journal of Marine Science*, **70 (6)**, 1065–1068.
- Bunnefeld, N., Hoshino, E., and Milner-Gulland, E. J. (2011) Management strategy evaluation: a powerful tool for conservation? *Trends in Ecology & Evolution*, **26 (9)**, 441–447.
- Byström, P., Karlsson, J. A. N., Nilsson, P. E. R., Van Kooten, T., Ask, J., and Olofsson, F. (2007) Substitution of top predators: effects of pike invasion in a subarctic lake. *Freshwater Biology*, **52**, 1271-1280.
- Caffrey, J. (2010) *IFI Biosecurity Protocol for field survey work*. Inland Fisheries Ireland
- Caffrey, J.M., Baars, J.-R., Barbour, J.H., Boets P, Boon, P., Davenport, K., and Lucy, F.E. (2014) Tackling invasive alien species in Europe: the top 20 issues. *Management of Biological Invasions*, **5**, 1-20.
- Campbell, D. and Hutchinson, G. (2007) *Lough Melvin Nutrient Reduction Programme. Strand 3: Technical Report . Economic value of fish species*. The Queens University of Belfast.
<https://www.fisheriesireland.ie/extranet/fisheries-research-1/52-lough-melvin-nutrient-reduction-programme-strand-3-technical-report-1/file.html>



- Carlsson, N. O., Sarnelle, O. and Strayer, D. L. (2009) Native predators and exotic prey—an acquired taste? *Frontiers in Ecology and the Environment*, **7 (10)**, 525-532.
- Casselman, J. M. and Lewis, C. A. (1996). Habitat requirements of northern pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, **53 (S1)**, 161–174.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis and Interpretation*.(Second edition) Sinauer Associates, Sunderland, M.A., USA.
- Champ, W. S. T. (1977) Trophic status of fishery lakes. In: *Lake pollution prevention by eutrophication control*: 65-78. Downey, W.K., Ní Uid, G. (Eds). Proceedings of a seminar, Killarney 10-11 May. National Science Council, Dublin, Stationary Office.
- Champ, W. S. T. (1998) Phosphorous/chlorophyll relationships in selected Irish lakes: ecological consequences and suggested criteria for ecosystem management. In: *Eutrophication in Irish Waters*: 91-105. Wilson, J.G. (Ed). Royal Irish Academy.
- Chapman, L. J. and Mackay, W. C. (1990) Ecological correlates of feeding flexibility in northern pike (*Esox lucius*). *Journal of Freshwater Ecology*, **5**, 313-322.
- Chapman, L. J., Mackay, W.C. and Wilkinson, C.W. (1989) Feeding flexibility in northern pike (*Esox lucius*): fish versus invertebrate prey. *Canadian Journal of Fisheries and Aquatic Sciences*, **46 (4)**, 666-669.
- Chen, Y., Kanaiwa, M., & Wilson, C. (2005) Developing and evaluating a size-structured stock assessment model for the American lobster, *Homarus americanus*, fishery. *New Zealand Journal of Marine and Freshwater Research*, **39 (3)**, 645–660.
- Connor, L., Matson, R. and Kelly, F. L. (2017) Length-weight relationships for common freshwater fish species in Irish lakes and rivers. *Biology and Environment: Proceedings of the Royal Irish Academy*, **117B (2)**, 65–75.
- Connor, L., Coyne, J., Corcoran, W., Cierpal., D., Ni Dhonnaibhain, L., Delanty, K., McLoone, P., Morrissey, E., Gordon, P., O’ Briain, R., Matson, R., Rocks, K., O’ Reilly, S., Brett, A., Garland, D. and Kelly, F.L. (2018) *Fish Stock Survey of Lough Derravaragh, July 2017*. National Research Survey Programme, Inland Fisheries Ireland, 30144 Lake Drive, Citywest Business Campus, Dublin 24.



- Cooke, S. J., Arlinghaus, R., Bartley, D. M., Beard, T. D., Cowx, I. G., Essington, T. E. and Watson, R. (2014) Where the waters meet: sharing ideas and experiences between inland and marine realms to promote sustainable fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, **71 (10)**, 1593–1601.
- Cortés, E. (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **54 (3)**, 726-738.
- Craig, J.F. (2008) A short review of pike ecology. *Hydrobiologia*, **601 (1)**, 5-16.
- Curtis, J. A. (2017) *Pike (Esox lucius) stock management in designated brown trout (Salmo trutta) fisheries: Anglers' preferences* (No. 563). ESRI Working Paper.
- DeBates, T. J., Paukert, C. P. and Willis, D. W. (2003) Fish community responses to the establishment of a piscivore, northern pike (*Esox lucius*), in a Nebraska sandhill lake. *Journal of Freshwater Ecology*, **18**, 353-359.
- Deriso, R. B. (1982) Relationship of fishing mortality to natural mortality and growth at the level of maximum sustainable yield. *Canadian Journal of Fisheries and Aquatic Sciences*, **39(7)**, 1054–1058.
- Drouineau, H., Mahévas, S., Bertignac, M. and Fertin, A. (2008) Assessing the impact of discretisation assumptions in a length- structured population growth model. *Fisheries Research*, **91** (June), 160–167.
- Elliott, J. M. (1989) The natural regulation of numbers and growth in contrasting populations of brown trout, *Salmo trutta*, in two Lake District streams. *Freshwater Biology*, **21(1)**, 7–19.
- Emmrich, M., Brucet, S., Ritterbusch, D. and Mehner, T. (2011) Size spectra of lake fish assemblages: responses along gradients of general environmental factors and intensity of lake-use. *Freshwater Biology*, **56 (11)**, 2316–2333.
- Ensing, D. (2015) Pike (*Esox lucius*) could have been an exclusive human introduction to Ireland after all: a comment on Pedreschi *et al.* (2014). *Journal of Biogeography*, **42**, 604-607.



- Eklöv, P. and Hamrin, S. F. (1989) Predatory efficiency and prey selection: interactions between pike *Esox lucius*, perch *Perca fluviatilis* and rudd *Scardinius erythrophthalmus*. *Oikos*, **56 (2)**, 149-156.
- Fitzgerald, C. J., Delanty, K. and Shephard, S. (2018) Inland fish stock assessment: Applying data-poor methods from marine systems. *Fisheries Management and Ecology*. <https://doi.org/10.1111/fme.12284>
- Fitzmaurice, P. (1981) The spread of roach *Rutilus rutilus* (L.) in Irish waters. *Proceedings of the 2nd British Freshwater Conference, Liverpool*. Liverpool, UK: University of Liverpool, 154-161.
- Fitzmaurice, P. (1983) Some aspects of the biology and management of pike (*Esox-lucius*) stocks in Irish fisheries. *Journal of Life Sciences. Royal Dublin Society*, **4**, 161-173.
- Floeter, J. and Temming, A. (2005) Analysis of prey size preference of North Sea whiting, saithe, and grey gurnard. *ICES Journal of Marine Science*, **62 (5)**, 897–907.
- Fredenberg, C. R., Muhlfeld, C. C., Guy, C. S., D'Angelo, V. S., Downs, C. C., and Syslo, J. M. (2017) Suppression of invasive lake trout in an isolated backcountry lake in Glacier National Park. *Fisheries Management and Ecology*, **24**, 33–48.
- Gargan, P.G (1986) The Biology of the Fish and Faunal Communities of Lough Sheelin, Co. Cavan, A Eutrophic Lake in the Irish Midlands. PhD Thesis. University College Dublin.
- Gargan, P. G. and O'Grady, M.F. (1992) Feeding relationships of trout *Salmo trutta*, perch *Perca fluviatilis* L and roach *Rutilus rutilus* L. in Lough Sheelin Ireland. *Irish Fisheries Investigations: Series A (Freshwater)*, **35**.
- Garrison, L. and Link, J. (2005) An Expanded Multispecies Virtual Population Analysis Approach (MSVPA- X) to Evaluate Predator-Prey Interactions in Exploited Fish Ecosystems. *Fisheries Science*, (January), 1–92.
- Gislason, H. and Helgason, T. (1985) Species interaction in assessment of fish stocks with special application to the North Sea. *Dana*, **5 (1957)**, 1–44.



- Grimm, M. P. (1981) The composition of northern pike (*Esox lucius* L.) populations in four shallow waters in the Netherlands, with special reference to factors influencing 0+ pike biomass. *Aquaculture Research*, **12**, 61-76.
- Grossman, G. D., Carline, R. F., and Wagner, T. (2017) Population dynamics of brown trout (*Salmo trutta*) in Spruce Creek Pennsylvania: A quarter-century perspective. *Freshwater Biology*, **62(7)**, 1143–1154.
- Guiet, J., Poggiale, J.-C., and Maury, O. (2016) Modelling the community size-spectrum: recent developments and new directions. *Ecological Modelling*, **337**, 4–14.
- Haight, S. and von Hippel, F. A. (2011) Invasive pike establishment in Cook Inlet Basin lakes, Alaska: diet, native fish abundance and lake environment. *Biological Invasions*, **13**, 2103-2114.
- Hayden, B., McLoone, P., Coyne, J. and Caffrey, J. M. (2014) Extensive hybridisation between roach, *Rutilus rutilus* L., and common bream, *Abramis brama* L., in Irish lakes and rivers. *Biology and Environment: Proceedings of the Royal Irish Academy*, **114 (1)**, 35-39.
- Hansson, S. (1998) Methods of studying fish feeding: a comment. *Canadian Journal of Fisheries and Aquatic Sciences*, **55 (12)**, 2706-2707.
- Harwood, J. and Stokes, K. (2003) Coping with uncertainty in ecological advice: lessons from fisheries. *Trends in Ecology & Evolution*, **18 (12)**, 617–622.
- Healy, A. (1956) Pike (*Esox lucius* L.) in three Irish lakes. *Royal Dublin Society*, **27 (4)**, 51-63.
- Hein, C. L., Öhlund, G., and Englund, G. (2011) Dispersal through stream networks: modelling climate-driven range expansions of fishes. *Diversity and Distributions*, **17**, 641-651.
- Hein, C. L., Öhlund, G., and Englund, G. (2014) Fish introductions reveal the temperature dependence of species interactions. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20132641. <http://dx.doi.org/10.1098/rspb.2013.2641>
- Heikinheimo, O. and Korhonen, A. P. (1996) Food consumption of northern pike (*Esox lucius* L.), estimated with a bioenergetics model. *Ecology of Freshwater Fish*, **5 (1)**, 37–47.



- Hesthagen, T., Sandlund, O. T., Finstad, A. G., and Johnsen, B. O. (2015) The impact of introduced pike (*Esox lucius* L.) on allopatric brown trout (*Salmo trutta* L.) in a small stream. *Hydrobiologia*, **744**, 223-233.
- Higgins, T. M., Grennan, J. M. and McCarthy, T. K. (2008) Effects of recent zebra mussel invasion on water chemistry and phytoplankton production in a small Irish lake. *Aquatic Invasions*, **3**, 14-20.
- Hyslop, E. J. (1980) Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology*, **17 (4)**, 411-429.
- Hyvärinen, P., and Vehanen, T. (2004) Effect of brown trout body size on post-stocking survival and pike predation. *Ecology of Freshwater Fish*, **13 (2)**, 77–84.
- IFI (2015a) Economic Contribution of Brown trout Angling in Ireland, National Strategy for Angling Development, Inland Fisheries Ireland, Dublin, Ireland.
<https://www.fisheriesireland.ie/national-strategy-for-angling-development/socio-economics/530-the-economic-contribution-of-brown-trout-angling-in-ireland/file.html>
- IFI (2015b) Economic Contribution of Pike Angling in Ireland, National Strategy for Angling Development, Inland Fisheries Ireland, Dublin, Ireland.
<https://www.fisheriesireland.ie/national-strategy-for-angling-development/socio-economics/528-the-economic-contribution-of-pike-angling-in-ireland/file.html>
- IFI (2018) *Fish Stock Survey of Selected Lakes and River Sites in the Owenriff Catchment 2017*. National Research Survey programme, Inland Fisheries Ireland, 3044 Lake Drive, Citywest Business Campus, Dublin 24.
- Ivlev, V. S. (1961) *Experimental Ecology of the Feeding of Fishes*. Yale University Press, New Haven, Connecticut, USA.
- Jacobsen, L. and Engström-Öst, J. (2018) Coping with Environments; Vegetation, Turbidity and Abiotics. In: C. Skov and Anders Nilsson, P. (Eds.) *Biology and Ecology of Pike* (pp. 40-69). CRC Press.



- Jacobsen, B. H., Hansen, M. M., and Loeschcke, V. (2004) Microsatellite DNA analysis of northern pike (*Esox lucius* L.) populations: insights into the genetic structure and demographic history of a genetically depauperate species. *Biological Journal of the Linnean Society*, **84**, 91-101.
- Javahery, S., Nekoubin, H. and Moradlu, A. H. (2012) Effect of anaesthesia with clove oil in fish. *Fish Physiology and Biochemistry*, **38 (6)**, 1545-1552.
- Jepsen, N., Aarestrup, K., Økland, F. and Rasmussen, G. (1998) Survival of radiotagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia*, **371**, 347.
- Kamler, J. F., and Pope, K. L. (2001) Nonlethal methods of examining fish stomach contents. *Reviews in Fisheries Science*, **9 (1)**, 1-11.
- Karagiannakos, A., (1996) Total Allowable Catch (TAC) and quota management system in the European Union. *Marine Policy*, **20 (3)**, 235-248.
- Kennedy, M. (1969) Irish pike investigations; 1. Spawning and early life history. *Irish Fisheries Investigations, Series A (Freshwater)*, **5**, 4-33.
- Kennedy, M., and Fitzmaurice, P. (1968) The biology of the bream *Abramis Brama* (L) in Irish waters. In: *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, **67**, 95-157.
- Kennedy, M., and Fitzmaurice, P. (1974) Biology of the rudd *Scardinius erythrophthalmus* (L) in Irish waters. In: *Proceedings of the Royal Irish Academy. Section B: Biological, geological, and chemical science*, **74**, 245-303.
- Kennedy, R. J., Rosell, R., Millane, M., Doherty, D. and Allen, M. (2018) Migration and survival of Atlantic salmon *Salmo salar* smolts in a large natural lake. *Journal of fish biology*. <https://doi.org/10.1111/jfb.13676>
- Kelly, F.L., Connor, L., Delanty, K., McLoone, P., Coyne, J., Morrissey, E., Corcoran, W., Cierpal, D., Matson, R., Gordon, P., O' Briain, R., Rocks, K., O' Reilly, S., Puttharee, D., McWeeney, D., Robson, S. and Buckley, S. (2017) *Fish Stock Survey of Lough Conn, August 2016*. National Research Survey Programme, Inland Fisheries Ireland, 30144 Lake Drive, Citywest Business Campus, Dublin 24.



- Kennedy, M. (1969) Irish pike investigations; 1. Spawning and early life history. *Irish Fisheries Investigations, Series A (Freshwater)*, **5**, 4-33.
- Kerins, C., Monahan, K. and Champ, W. S. T. (2007) *Lough Sheelin and its Catchment Water Quality Status and Nutrient Loadings, 1998-2005*. Shannon Regional Fisheries Board Report.
- Langangen, Ø., Edeline, E., Ohlberger, J., Winfield, I. J., Fletcher, J. M., James, J. Ben and Vøllestad, L. A. (2011). Six decades of pike and perch population dynamics in Windermere. *Fisheries Research*, **109 (1)**, 131–139
- Lapointe, N.W., Cooke, S.J., Imhof, J.G., Boisclair, D., Casselman, J.M., Curry, R.A., Langer, O.E., McLaughlin, R.L., Minns, C.K., Post, J.R. and Power, M. (2013) Principles for ensuring healthy and productive freshwater ecosystems that support sustainable fisheries. *Environmental Reviews*, **22 (2)**, pp.110-134.
- Langsdale, S. (2008) Communication of climate change uncertainty to stakeholders using the scenario approach. *Journal of Contemporary Water Research and Education*, **140 (1)**, 24–29.
- Link, J. S., Ihde, T. F., Harvey, C. J., Gaichas, S. K., Field, J. C., Brodziak, J. K. T. and Peterman, R. M. (2012) Dealing with uncertainty in ecosystem models: The paradox of use for living marine resource management. *Progress in Oceanography*, **102**, 102–114.
- Lynch, A. J., Cooke, S. J., Deines, A. M., Bower, S. D., Bunnell, D. B., Cowx, I. G. and Jr., B. T. D. (2016) The social, economic, and environmental importance of inland fish and fisheries. *Environmental Reviews*, **24 (2)**, 115–121.
- Mauck, W. L., and Coble, D. W. (1971) Vulnerability of some fishes to northern pike (*Esox lucius*) predation. *Journal of the Fisheries Board of Canada*, **28 (7)**, 957-969.
- McCombie, A. M. (1959) Some relations between air temperatures and the surface water temperatures of lakes. *Limnology and Oceanography*, **4**, 252-258.
- McGinnity, P., De Eyto, E., Gilbey, J., Gargan, P., Roche, W., Stafford, T. and MILLS, P. (2012) A predictive model for estimating river habitat area using GIS-derived catchment and river variables. *Fisheries Management and Ecology*, **19 (1)**, 69–77.
- Met Éireann (2017) <https://www.met.ie/cms/assets/uploads/2017/08/YP-Fun-Facts-Seasons.pdf>



- Millane, M., Kelly-Quinn, M. and Champ, W. S. T. (2008) Impact of the zebra mussel invasion on the ecological integrity of Lough Sheelin, Ireland: distribution, population characteristics and water quality changes in the lake. *Aquatic Invasions*, **3**, 271-281.
- Millane M. (2008) Impact of the zebra mussel *Dreissena polymorpha* (Pallas 1771) invasion on the ecological integrity of L. Sheelin, Ireland. A thesis presented to the school of Biology and Environmental Science, University College Dublin, in fulfilment of the requirements for the Ph.D. Zoology degree.
- Milner, N. J., Elliott, J. M., Armstrong, J. D., Gardiner, R., Welton, J. S., and Ladle, M. (2003) The natural control of salmon and trout populations in streams. *Fisheries Research*, **62 (2)**, 111–125.
- Minns, C. K., Randall, R. G., Moore, J. E. and Cairns, V. W. (1996) A model simulating the impact of habitat supply limits on northern pike, *Esox lucius*, in Hamilton Harbour, Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, **53 (S1)**, 20–34.
- Mittelbach, G. G. and Persson, L. (1998) The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, **55 (6)**, 1454-1465.
- Mortimer, C. H. and Worthington, E. B. (1942) Morphometric data for Windermere. *Journal of Animal Ecology*, **11 (2)**, 245–247.
- Nicholson, M. E., Rennie, M. D., and Mills, K. H. (2015) Apparent extirpation of prey fish communities following the introduction of Northern pike (*Esox lucius*). *The Canadian Field-Naturalist*, **129**, 165-173.
- Nilsson, P. A. and Brönmark, C. (2000) Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, **88 (3)**, 539-546.
- Nilsson, P. A., Brönmark, C. and Pettersson, L. B. (1995) Benefits of a predator-induced morphology in crucian carp. *Oecologia*, **104 (3)**, 291-296.
- NRC. (2006) *Dynamic Changes in Marine Ecosystems: Fishing, Food Webs, and Future Options*. Washington, DC: The National Academies Press. <https://doi.org/10.17226/11608>



- Öhlund, G., Hedström, P., Norman, S., Hein, C. L. and Englund, G. (2015) Temperature dependence of predation depends on the relative performance of predators and prey. *Proceedings of the Royal Society of London B: Biological Sciences*, **282 (1799)**, DOI;10.1098/rspb.2014.2254.
- O' Grady, M.F. (1981) Some direct gill net selectivity tests for brown trout populations. *Irish Fisheries Investigations. Series A (Freshwater)*, **No. 22**, 9pp.
- O' Grady, M.F. (1986) *The Lough Derravaragh Catchment – A Review of the Fish Stock Situation and Future Management Options*. Central Fisheries Board, Dublin. 8 pp.
- O'Grady, M.F., Gargan, P., Byrne, C., Igoe, F. and O'Neill, J. (1996) A fish stock survey report for Loughs Corrib, Mask and Carra and future management options for this fishery resource. Central Fisheries Board, Dublin.
- O' Grady, M.F. and Delanty, K. (2001a) *A Review of Changes in the Fish Stocks of Loughs Conn and Cullin over time (1978–2001) and Recommendations in Relation to the Long-term Management of these Lakes and the River Moy as Salmonid Fisheries* Available at <https://www.fisheriesireland.ie/documents/646-a-review-of-changes-in-the-fish-stocks-of-loughs-conn-and-cullin-over-time-1978-2001/file.html>
- O' Grady, M. F., and Delanty, K. (2001b) *Current status of Fish stocks in Lough Sheelin, a Review of Fluctuations of Fish populations in this Water and Management Recommendations for its Management as a Trout Fishery*. Irish Central Fisheries Board report 26pp. Available at <http://www.fisheriesireland.ie/documents/647-the-current-status-of-fish-stocks-in-lough-sheelin/file.html>
- Ó Maoiléidigh, N., McGinnity, P., Prévost, E., Potter, E. C. E., Gargan, P., Crozier, W. W. and Roche, W. (2004) Application of pre-fishery abundance modelling and Bayesian hierarchical stock and recruitment analysis to the provision of precautionary catch advice for Irish salmon (*Salmo salar* L.) fisheries. *ICES Journal of Marine Science*, **61 (8)**, 1370–1378.
- Patankar, R., Von Hippel, F. A., and Bell, M. A. (2006) Extinction of a weakly armoured threespine stickleback (*Gasterosteus aculeatus*) population in Prator Lake, Alaska. *Ecology of Freshwater Fish*, **15**, 482-487.
- Patterson, K., Cook, R., Darby, C., Gavaris, S., Kell, L., Lewy, P. and Stefánsson, G. (2001) Estimating uncertainty in fish stock assessment and forecasting. *Fish and Fisheries*, **2 (2)**, 125–157.



- Pearre, S. Jr. (1982) Estimating prey preference by predators: uses of various indices, and a proposal of another based on χ^2 . *Canadian journal of fisheries and aquatic sciences*, **39 (6)**, 914-923.
- Pedreschi, D., Kelly-Quinn, M., Caffrey, J., O'Grady, M. and Mariani, S. (2014) Genetic structure of pike (*Esox lucius*) reveals a complex and previously unrecognized colonization history of Ireland. *Journal of Biogeography*, **41 (3)**, 548-560.
- Pedreschi, D., Mariani, S., Coughlan, J., Voigt, C.C., O'Grady, M., Caffrey, J. and Kelly-Quinn, M. (2015) Trophic flexibility and opportunism in pike *Esox lucius*. *Journal of Fish Biology*, **87 (4)**, 876-894.
- Pierce, R. B., and Tomcko, C. M. (2005) Density and biomass of native northern pike populations in relation to basin-scale characteristics of north-central Minnesota lakes. *Transactions of the American Fisheries Society*, **134**, 231-241.
- Pine III, W. E., Martell, S. J. D., Walters, C. J. and Kitchell, J. F. (2009) Counterintuitive Responses of Fish Populations to Management Actions. *Fisheries*, **34 (4)**, 165–180.
- Pinkas, L. and Iverson, I. L. K. (1971) Food habits of albacore, bluefin tuna and bonito in Californian waters. California Department of Fish and Game, *Fish Bulletin*, **152**, 1-105.
- Pintor, L. M., & Byers, J. E. (2015) Individual variation in predator behavior and demographics affects consumption of non-native prey. *Behavioral Ecology*, **26 (3)**, 797-804.
- Plagányi, É. E. (2007) *Models for an ecosystem approach to fisheries* (Fisheries). Rome: Food and agriculture and organization of the United Nations.
- Plagányi, É. E., Punt, A. E., Hillary, R., Morello, E. B., Thébaud, O., Hutton, T. and Rothlisberg, P. C. (2014). Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish and Fisheries*, **15 (1)**, 1–22.
- Poole, W.R., Dillane, M., DeEyto, E., Rogan, G., McGinnity, P. and Whelan, K. (2006) Characteristics of the Burrishoole Sea Trout Population: Census, Marine Survival, Enhancement and Stock-Recruitment Relationship 1971–2003 in *Sea Trout: Biology, Conservation and Management* (eds: Harris, G. and Milner, N.). Blackwell Publishing, Oxford.



- Prchalová, M., Kubečka, J., Říha, M., Mrkvička, T., Vašek, M., Jůza, T., .and Křížek, J. (2009) Size selectivity of standardized multimesh gillnets in sampling coarse European species. *Fisheries Research*, **96 (1)**, 51-57.
- Prévost, E., Parent, E., Crozier, W., Davidson, I., Dumas, J., Gudbergsson, G. and Sættem, L. M. (2003) Setting biological reference points for Atlantic salmon stocks: transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling. *ICES Journal of Marine Science*, **60 (6)**, 1177–1193.
- Punt, A. E., Huang, T. and Maunder, M. N. (2013) Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusc species. *ICES Journal of Marine Science*, **70 (1)**, 16–33.
- Punt, A.E. and Kennedy, R. (1997) Population modelling of Tasmanian rock lobster, *Jasus edwardsii*, resources. *Marine and Freshwater Research*, **48 (8)**,967–980.
- Quinn II, T. J. and Collie, J. S. (2005) *Sustainability in single-species population models*. Philosophical Transactions of the Royal Society of London B: Biological Sciences, The Royal Society, **360**, 147–162.
- Quinn II, T. J. and Deriso, R. B. (1999) *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Raat, A. J. P. (1988) *Synopsis of biological data on the northern pike *Esox lucius* Linnaeus, 1758*. Rome.
- Ricker, W. E. (1954). Stock and Recruitment. *Journal of the Fisheries Research Board of Canada*, **11 (5)**, 559–623.
- Rue., H., A. Riebler, S. H. Sorbye, J. B. Illian, D. P. Simpson, and F. K. Lindgren. (2017) Bayesian computing with INLA: A review. *Annual Review of Statistics and Its Application*, **4**, 395-421.
- Sainsbury, K. J., Punt, A. E. and Smith, A. D. M. (2000) Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science*, **57 (3)**, 731–741.
- Sepulveda, A.J., Rutz, D.S., Ivey, S.S., Dunker, K.J. and Gross, J.A. (2013) Introduced northern pike predation on salmonids in south-central Alaska. *Ecology of Freshwater Fish*, **22 (2)**, 268-279.



- Skov, C., Lousdal, O., Johansen, P. H. and Berg, S. (2003) Piscivory of 0+ pike (*Esox lucius* L.) in a small eutrophic lake and its implication for biomanipulation. *Hydrobiologia*, **506 (1-3)**, 481-487.
- Spens, J., and Ball, J. P. (2008) Salmonid or non salmonid lakes: predicting the fate of northern boreal fish communities with hierarchical filters relating to a keystone piscivore. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1945-1955.
- Spens, J., Englund, G., and Lundqvist, H. (2007) Network connectivity and dispersal barriers: using geographical information system (GIS) tools to predict landscape scale distribution of a key predator (*Esox lucius*) among lakes. *Journal of Applied Ecology*, **44**, 1127-1137.
- Strauss, R.E. (1979) Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society*, **108**, 344-352.
- Sullivan, P. J., Lai, H.-L. and Gallucci, V. F. (1990). A Catch-at-Length Analysis that Incorporates a Stochastic Model of Growth. *Canadian Journal of Fisheries and Aquatic Sciences*, **47 (1)**, 184-198.
- Sutton, T. M., Cyterski, M. J., Ney, J. J., and Duval, M. C. (2004) Determination of factors influencing stomach content retention by striped bass captured using gillnets. *Journal of Fish Biology*, **64 (4)**, 903-910.
- Sweeting, C. J., Badalamenti, F., D'Anna, G., Pipitone, C. and Polunin, N. V. C. (2009) Steeper biomass spectra of demersal fish communities after trawler exclusion in Sicily. *ICES Journal of Marine Science*, **66 (1)**, 195-202.
- Toner, E.D. (1959) Pike in trout waters. *Salmon and Trout Magazine*, **5**, 104-110.
- Vinson, M. R. and Angradi, T. R. (2011) Stomach emptiness in fishes: sources of variation and study design implications. *Reviews in Fisheries Science*, **19 (2)**, 63-73.
- von Bertalanffy, L. (1938) A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology*, **10 (2)**, 181-213.
- Wahl, D. H. and Stein, R. A. (1993) Comparative population characteristics of muskellunge (*Esox masquinongy*), northern pike (*E. lucius*), and their hybrid (*E. masquinongy* × *E. lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, **50 (9)**, 1961-1968.



- Walsh, S. (2012) *A Summary of Climate Averages for Ireland*. Met Éireann, Dublin.
- Went, A. E. J. (1978) The zoogeography of some fishes in Irish waters. Fishery Leaflet, Department of Fisheries (Trade and Information Section).
- Winfield, I. J., Fletcher, J. M. and James, J. B. (2012) Long-term changes in the diet of pike (*Esox lucius*), the top aquatic predator in a changing Windermere. *Freshwater Biology*, **57**,373-383.
- Wheeler, A. and Jones, A. K. (1989). Fishes. *Cambridge manuals in archaeology*. Cambridge: University Press.
- White, J., Ó Maoiléidigh, N., Gargan, P., de Eyto, E., Chaput, G., Roche, W. and Marnell, F. (2016) Incorporating natural variability in biological reference points and population dynamics into management of Atlantic salmon (*Salmo salar* L.) stocks returning to home waters. *ICES Journal of Marine Science*, **73** (6), 1513–1524.
- Whitehead, H., and Walde, S. J. (1992) Habitat dimensionality and mean search distances of top predators: implications for ecosystem structure. *Theoretical Population Biology*, **42**, 1-9.



Iascach Intíre Éireann
Inland Fisheries Ireland

**Inland Fisheries Ireland
3044 Lake Drive,
Citywest Business Campus,
Dublin 24,
Ireland.
D24 Y265**

**www.fisheriesireland.ie
info@fisheriesireland.ie**

+353 1 8842 600

