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The Ecological Role of *Loligo forbesii* in the Moray Firth Ecosystem, Northeast Scotland

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Abstract**—**The squid *Loligo forbesii* is suspected to be an important species in marine food webs, as it can strongly impact its prey and be impacted upon by predation, competition, fishing and/or climate variability. To quantify these impacts in the food web, the measurement of its trophic position and ecological role within well-studied ecosystems is essential. An Ecopath model was balanced and run for the Moray Firth ecosystem and was used to investigate the significance of this squid's trophic roles. The network analysis routine included in Ecopath with Ecosim (EwE) was used to estimate trophic interaction, system indicators (health condition and developmental stage) and food web features. Results indicated that within the Moray Firth squid occupy a top trophic position in the food web and also a major prey item for many other species. Results from Omnivory Index (OI) showed that squid is a generalized feeder transferring energy across wide trophic levels and is more important as a predator than that as a prey in the Moray Firth ecosystem. The results highlight the importance of taking squid into account in the management of Europe's living marine resources**.**

Keywords—Ecopath, *Loligo forbesii*, moray firth, squid, trophic-level.

I. Introduction

CECAPHALOPODS play an important ecological role in marine ecosystems as they function both as prey and predators [1]. They transfer energy from primary consumers especially zooplanktons and small neritic fishes to tertiary consumers [2], [3]. Their role can be significant in energy pathways as they can be heavily preyed upon [4]. As predator, they have high consumption rates and a generalist feeding strategy that could cause reasonable predation mortality on early life stages of fishes [5]. Cephalopods are large group of organisms comprising of both demersal (cuttle fish, octopus and squids) and pelagic species mainly squids [6], [7]. They are important members of marine food chain [8] occupying central to top positions in marine food webs [7].

Within cephalopods, squids in general play a very important ecological role due to their high abundance and range of distribution [5]. Squids are an important species in the food web of most pelagic ecosystems. This is most likely because of its abundance (compared to other cephalopods), feeding behaviour, importance as fishery resource, and food resources for a range of predators [4], [9], [10]. Any changes in squid's abundance could influence population size of its predators and prey [11].

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Squid have been reported as principal prey for numerous marine species [12], [13]. These predators of squid include fish among which are bluefin tuna (Thunnus thynnus), bib (*Trisopterus luscus*), monk fish (*Lophius piscatorius*), cod (*Gadus morhua*), blue fish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*) and summer flounder (*Platichthys flesus*) [4], [14]-[19] pinnipids, and small toothed/sperm whales (*Physeter macrocephalus*) [20], [21]. Other squid predators in the marine food web considered as top predators include; marine birds [22], seals [23], [24], cetaceans [13], minke and sperm whales [21], [23], [25], and bottlenose dolphins (*Tursiops truncatus*).

When considering squid as predators, their direct impact can significantly affect fish communities [26], [27] and indirect impact on fish species via the low trophic level species and zooplankton communities they consume. Reference [28] described them as active carnivores which feed primarily on crustaceans, other cephalopods and small fish. The juveniles feed on crustaceans and small fishes, the adults on fish and other cephalopods [27]. Reference [29] reported that *L. forbesii* diets consisted of poor cod (*Trisopterus minutus*), Norway pout (*Trisopterus esmarkii*), transparent goby, and small clupeids like sprat (*Sprattus sprattus*). Squid eat large amount of food making them voracious and opportunistic predators which enable them fuel their growth. The primary effect of this impact could be a change in composition and recruitment success of other functional groups in the ecosystem.

The Moray Firth, North east Scotland, has a record of some level of occurrence of *L. forbesii* particularly making it an important fishery in this area for decades [10]. A large proportion of squid is exploited in continental shelf of Moray Firth and the North Sea [27] making *L. forbesii* the third important shellfish species after Norway lobster and scallop [11], [30]. In the Moray Firth, its distribution and fishery stretch from Fraserburgh to Nairn where fishing on traditional stock occurs where exploitation rate has risen substantially over time (1980-1990) [27], resulting in modification of bottom trawls gears [31] thereby impacting on the trophic level.

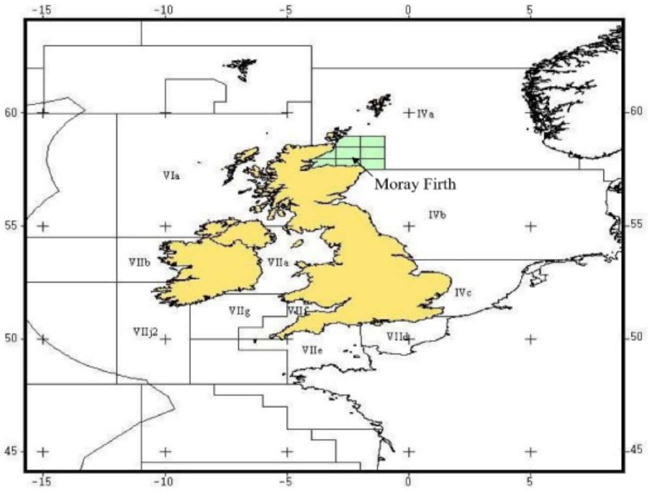

Fig. 1 Location of study area: The axis labels show latitude (degrees North) and longitude (degrees East). Green rectangles were used to calculate the habitat area in the Ecopath model

The fishing activity would affect Moray Firth ecosystem trophic structure and functioning in some ways, thereby modifying their features and affecting the interactions established between their biological and physical components. The likely impact could include; induced alterations of the trophic structure of the marine food web [7], increase or decrease in biomass [32], and alteration of physical and chemical conditions of the environment such as benthic production and suspended sediments [33], [34]. Climate variability is also likely to impact as squid could be sensitive to environmental conditions. Changes in parameters such as sea surface temperature (SST) and CO_2 concentration [31], and salinity/sea surface salinity (SSS) [24], [35], [36] have reported in the Moray Firth ecosystem.

In an attempt to gain understanding into the ecological role of organisms, and to assess the effects of fishing on the ecosystems, several ecological models have been developed. Among these models is the Ecopath with Ecosim (EwE) software, developed in the early 1980s [37] which is increasingly gaining acceptance in modelling marine ecosystems [7]. Some of the EwE models built included squids as either a single species or as a functional group [38], [39] and used to determine their ecological role in most marine ecosystems. The models have also been used to assess the specific role of squid [11], [40]-[42]. Reference [43] applied “depletion” stock assessment models to estimate squid population size in Scottish waters. Reference [17] developed EwE model for North Sea ecosystem and this model was adapted by [11] to investigate the role of *L. forbesii* in the Moray Firth.

This study aims to expand on the [11] study and to use the range of software options within Ecopath to identify the trophic position and ecological role of the squid *L. forbesii,* in the Moray Firth marine ecosystem. Specifically, the trophic level, Omnivory Index, Electivity, Mortality and Niche overlap Indexes were calculated as well as investigation of trophic flow (using flow analysis), and mixed trophic impacts using network analysis plug-in. The study aims to improve the understanding of the interactions between the squid and other functional groups in the Moray Firth in order to better predict the possible effects that changes in squid biomass could have on the energy flow patterns and function of the Moray Firth ecosystem.

II. Materials and Methods

A. Study Area

The study area is around the coast of the Moray Firth located in the North East coast of Scotland, between 57º 49' 00" north latitude and 03º 43' 36" west longitude. The Moray Firth has approximately 800 km of coastline. The inner area of the Moray Firth of 1,513.47 km^2 has been designated as a Special Area of Conservation (SAC) since March 2005 to conserve the habitat area for the bottlenose dolphin *Tursiops truncatus* [44], [45]. The River Spey and River Ness are the two main rivers which flow into sea in this region. Water depth ranges from 20-100 m. Sediment type of the sea floor from the coastline to 100 m offshore comprises sand, mud and gravel, most of which is sand, while the mud and gravel are found in the south of the Moray Firth [46], [47]. In this study, the habitat area in the model covers the surface area of 26,181.49 km^2, which is in area IVa of the International Council for the Exploration of the Sea (ICES) (Fig. 1).

III. Ecosystem Modelling

A. Figures Defining Moray Firth Ecosystem

In this study, species included in the model were selected based on the following criteria: (1) the distribution and abundance in the Moray Firth, and (2) relationship with squids as prey or predators. Species were grouped together if there was a similarity in size, feeding pattern, and predators. Most of the initial basic parameters were taken from the existing North Sea model, which was based on data sources from 1991 [17]. Data on some species such as marine mammals, seabirds and fish species related to *L. forbesii* as prey or predators were gathered from published papers and other relevant documents. Finally, the structure of the Moray Firth model consisted of 47 functional groups within 7 main groups: marine mammals and seabirds (5 functional groups), fishes (30 functional groups), invertebrates (8 functional groups), zooplankton (1 functional group), phytoplankton (1 functional group), detritus (1 functional group) and discards (1 functional group).

B. Basic Parameters and Diet Composition

Data for this study for functional groups; basic input parameters, diet composition, and fisheries was compiled from survey data, existing literatures and stock assessment sources from the Moray Firth ecosystem and the North Sea [17]. Additional data was gathered from nearby existing marine ecosystems such as the English Channel [17], the Western Channel [17], and the Irish Sea [48]. The bulk of the data for this work was collected from the data base of [11]. Improvement was made on input parameters and increased precision on diet proportion by adjusting only data from unreliable sources in balancing the model.

C. Mass Balanced Ecosystem Model with Ecopath

The Moray Firth ecosystem model was developed using Ecopath with Ecosim (EwE) version 6 [37], [49], [50]. The EwE software tool is a common and flexible framework for quantifying food webs as well as analyzing ecosystem dynamics [51]. The core routine of Ecopath is derived from the Ecopath programme of [52]. EwE consists basically of three components which includes Ecopath, (a static, mass balanced snap shot of the ecosystem); Ecosim (a time dynamic simulation module for policy exploration); and Ecospace (a spatial and temporal dynamic module for exploring impact and placement of protected area). Using input parameters, diet composition, and fisheries data (gathered from different sources), Ecopath model has been used to evaluate the trophic position and ecological importance of *L. forbesii*. The Ecopath model [37] is built on the master linear equation (1) and requires that for each functional group (i) in a typical ecosystem, mass balance should occur over a given time period, usually one year (except for seasonal modelling). The functional group represents organisms (either as a mixed group of species, individual species or an ontogenic fraction of a species) inhabiting an ecosystem at a particular period of time such that:

$$Bi \,.\, (P/B)_i = \sum Bj.\,(Q/B)_{ji}.\, DC_{ji} + Y_i + Ei + BAi + Bi.\,(P/B)i.(1\text{-}EE_i) \quad (1)$$

where Bi is the biomass of prey i, P/B_i the production/biomass ratio, Y_i the total fishery catch rate, E_i the net migration rate, BAi the biomass accumulation rate, EE_i the ecotrophic efficiency, proportion of the production that is utilized in the system, B_j the biomass of consumers or predators j, Q/B_j the consumption per unit of biomass of j and DC_{ji} the fraction of prey i in the diet of predator j (diet composition).

D. Parameterization

The Ecopath model was balanced with a combination of input parameters. If three of the basic parameters (B_i, P/B, Q/B_i, or EE_i) are entered Y_i, BA_i, and DC_{ji} must be entered for all groups to achieve balancing as in (1). Trophic interactions among groups are presented by a diet matrix that quantitatively describes the fractions that every group has in each other group's diet.

In order to achieve balancing the model, these input data for individual functional groups was adjusted within the range of values reported in the literature to obtain outputs within a given range. The expected range of values varies among functional groups [53]. EE and P/Q values are expected to fall within 0 and 1, and 0.1 and 0.3/0.35 respectively. After the missing parameters (output) have been estimated using (1) and mass balance achieved within each group, energy balance is also ensured within individual group using the second master (2):

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (2)$$

Among the ecological parameters and indicators calculated by Ecopath routine of EwE software included.

E. Trophic Level

The trophic level (TL) was used to estimate the trophic position of individual species or functional group in the food web according to [54]. Within EwE trophic level (TL) of functional groups was calculated in the model using (7). Following [55] as incorporated into a routine, trophic level for each functional group was estimated using (3);

$$TLj = 1 + \textstyle\sum_{i=1}^{n} DCji\,.\,TLi \quad (3)$$

where TLj is the trophic level of *L. forbesii*, TL_i is the trophic level of its prey i.

F. Omnivory Index (OI)

Omnivory Index (OI) is a measure of the distribution of feeding interactions among trophic levels by functional group. OI was calculated according to [53] using the equation below:

$$OI_j = \textstyle\sum_{i=1}^{n} [TLi - (TLj - 1)]2.\,DCji \quad (4)$$

where OI_j is the OI of a predator j, TL_i is the trophic level of prey i, TL_j is trophic level of predator j and DC_{ji} is the fraction of prey i in the diet of predator j. Zero (0) value indicates consumer specialize on a single trophic level, large values indicate consumer feeds on many trophic levels.

G. Electivity Index

Electivity index is a selection index which describes predator's preference for prey. The index is used to standardize forage ration (S_i) as suggested by [56]. This index is independent of prey availability and is given by:

$$S_i = \frac{(\frac{ri}{Pi})}{\sum_{n=1}^{n} rn/Pn} \quad (5)$$

where r_i and P_i are the relative abundance of a prey in a diet of predator and the prey's relative abundance in the ecosystem, and n is the number of groups in the system. Standardized forage ratio takes values from between 0 and 1, with $S_i = 0$ partial feeding and S_i = exclusive feeding. The vale is implemented in Ecopath by transforming the forage ratio to vary -1 and 1.

H. Mortality Index

Predation mortality coefficient suggests the rate of squid consumption by it predators while the fishing mortality would suggest its contribution to fishery.

$$P/B_i = Z = F_i + M2_i + BA_i + E_i + M0 \quad (6)$$

where Fi is the Fishing mortality coefficient, $M2_i$ is the Predation mortality coefficient, BA_i is Biomass accumulation coefficient, E_i is the Net migration coefficient, $M0_i$ is other mortality coefficient. The mortality coefficients are estimated from the following equations:

$$M2_i = (\textstyle\sum Bi.\,Q/Bi\,.\,DCji)/Bi \quad (7)$$

$$F_i = Y_i/B_i \quad (8)$$

$$MO_i = (1 - EE_i).\ P/B_i \quad (9)$$

where Q/B_i is the consumption biomass ratio of predator j, DC_{ji} is the proportion of prey constitutes to the diet of predator j, B_i is the average biomass of i, and Ci is the catch of i.

I. Flow Analysis

Trophic flow diagram of the ecosystem was built using Ecopath routine. Trophic flow diagram shows the movement of energy from one trophic level to the next or via the food web. The diagram shows the position of squid and other functional groups revealing their relative role, impact, and relative biomass in the ecosystem.

J. Mixed Trophic Impacts (MTI)

After the model was balanced, network analysis routines [57] incorporated in EwE, were used to estimate system properties and flow indicators. Mixed trophic impacts (MTI) which are routines in Network Analysis are used as indicators of relative impact of a change in the biomass of one group on other groups within the ecosystem. Given the mass balance model of a trophic network, the MTI was estimated for each pair of functional groups (i,j) of the trophic web by constructing an n, diet (positive direct impact) x n, consumption (negative direct impact) matrix, based on the concept of [58] using (10) below. MTI are the sum of direct and indirect impacts. The indirect impact normally results from intergroup competition and trophic cascade.

$$MTI_{i,j} = DC_{i,j} - FC_{j.i} \quad (10)$$

where i,jth element represents the interaction between the impacting group i and the impacted group j, DC_{ji} is the fraction of prey i in the diet of predator j, and $FC_{j,i}$ is a host composition term given the proportion of the predation on j that is due to i as a predator. During calculation of host composition, fishing fleets are considered as 'predators'.

IV. Results

A. Features of the Pelagic Moray Firth Ecosystem

After balancing the model by making changes in input data, the basic values estimated by the Ecopath routine are given in Table I. Ecotrophic Efficiency (EE) values for all functional groups were below 1 and seem to inversely relate to trophic levels. EE value for squid was estimated at 0.92 with Epibenthic invertebrates having the highest value of 0.99. Cetaceans, seals and marine birds have the lowest value of 0.00 as they are top predators occupying top most trophic positions. The calculated values for Production/Consumption (P/Q) ratio ranged between 0.001 (for most top predators) to 0.39 (for mixed pelagic) with squid having a value of 0.225. Omnivory Index (OI) calculated showed that squid have a value of 0.24. The highest value of 1.070 belonged to crabs and the lowest value of 0.001 belonged to herring. Zero (0) value was estimated for lesser argentine, phytoplankton and detritus groups suggesting them as specialized consumers i.e. they feed on a single trophic level as the species occupy the bottom trophic position.

Moray Firth ecosystem had a low ratio for the total primary production/total respiration (Pp/R) and low connectance index of 1.42 and 0.24 respectively (Table II). The total systems throughput was 5837 ton/km2/year with mean trophic level of the catch at 3.42. Primary production/biomass required to sustain fishery landing was estimated at 558 t km^2/year i.e. 26% of the total primary production calculated. Total primary production/total respiration ratio is an index used to suggest the developmental stage of an ecosystem (Christensen and Pauly, 1993) whether the system is healthy or polluted.

B. Trophic Level of *L. forbesii*

Functional groups in the Moray Firth ecosystem had trophic level (TL) in a range of 1.00-4.48 with phytoplankton, detritus and discards groups having a definitional value of 1. The lower values generally belonged to functional groups of small organisms with a gradual increase that cumulated at top predators. TL for squid was estimated at 4.15. Predators in the food web with trophic level (TL) $\geq$3.0 are represented in Fig. 2. The groups with TL $\geq$ 3.75 are described as apical predators of which *L. forbesii* belong with a TL value of 4.15. Other apical predators with TL values in descending order included; harbour porpoise (4.48), monk fish (TL = 4.42), seals (TL = 4.40), toothed whales (TL = 4.32), spurdog (TL = 4.25), adult Atlantic cod (TL = 4.24), large demersal fish (TL = 4.06), grey gurnard (3.96), baleen whales (3.93), skates and rays (3.93), and saithe (3.85).

C. Food Web Analysis

The synthesis of energy links by trophic level involving *L. forbesii* in the ecosystem model is shown in Fig. 3. A total of 5 trophic levels in the ecosystem existed. Trophic Level 5 (the highest trophic position) was occupied by Harbour porpoise, monk fish, seals, toothed whales, squid, spurdog, adult Atlantic cod and large demersal fish. Squid also was at TL 5 and linked several trophic levels cutting across both pelagic and demersal pathways. Level 4 had the highest range of predators among which included; baleen whales, adult haddock, Atlantic cod and whiting, mackerel, and seabirds. TL 1 was occupied traditionally by phytoplankton, detritus and discards.

D. *L. forbesii* Role as Predator

A comparison of prey consumption by squid and two other apical predators (adult Atlantic cod and top predators) in Moray Firth ecosystem is shown in Fig. 4. Top predators were the main predator of most functional groups with sandeel being the most dominant prey. Squid is also a major predator in the ecosystem. While top predators dominated most groups, squid dominated small demersal fish, and the second dominant predator of sandeel, squid, mixed pelagic and juvenile Atlantic cod. Squid and Adult cod are cannibals feeding on themselves.
The fraction of predation mortality caused by squid, adult.

Atlantic cod and top predators on their prey in the marine web is shown in Fig. 5. Squid was the main cause of M2 on mixed pelagic, and small demersal. M2 by squid was also high in sandeel and juveniles of Atlantic cod, haddock, and whiting and followed to a lesser degree by top predators. Squid also exhibited high cannibalism. In the case of adults of haddock and whiting, the impact was due to adult Atlantic cod and to a minor extent by top predators. The main M2 exhibited by adult Atlantic cod was on adult haddock and adult whiting. Like squid, there was also cannibalism in Atlantic cod.

TABLE I
INPUT PARAMETERS & RESULTS (BOLD) FOR FINAL RUN OF THE ECOSYSTEM MODEL REPRESENTING MORAY FIRTH ECOSYSTEM: VALUES IN BRACKET REPRESENT CLOSEST ESTIMATE FROM WANGVORALAK (2012)

No	Group Name	TL	B (t/km2)	P/B(/year)	Q/B(/year)	EE	P/Q	OI
1	Baleen Whales	3.939	0.03	0.02	9.9	**0**	**0**	**0.212**
2	Toothed Whales	4.325	0.01	0.02	17.6	**0**	**0**	**0.139**
3	Harbour Porpoise	4.484	0.002	0.02	17.6	**0**	**0**	**0.109**
4	Seals	4.409	0.009	0.09	26.8	**0**	**0**	**0.137**
5	Seabirds	3.228	0.011	0.28	(216.6)217	**0**	**0**	**0.832**
6	A. Haddock	3.758	0.104	1.14	4.4	**0.961**	**0.26**	**0.306**
7	J. Haddock	3.268	0.216	2.54	11(10.98	**0.607**	**0.23**	**0.346**
8	Saithe	3.85	0.22	0.95	3.6	**0.117**	**0.26**	**0.241**
9	Monk fish	4.421	0.044(0.042)	0.7	1.9	**0.992**	**0.37**	**0.126**
10	Common Dab	3.232	3	0.67	3.36	**0.327**	**0.2**	**0.018**
11	Lemon sole	3.155	0.31	0.86	4.32	**0.169**	**0.2**	**0.02**
12	Long Rough Dab	3.361	0.35	0.7	3.4	**0.485**	**0.21**	**0.198**
13	Grey Gurnard	3.967	0.077(0.097)	0.821(1.58)	3.2	**0.718**	**0.49**	**0.213**
14	Skates and Rays	3.936	0.066	0.78	2.3	**0.069**	**0.34**	**0.172**
15	Four-bearded Rockling	3.102	0.021	0.57	5	**0.807**	**0.11**	**0.004**
16	Sandeel	3.021	3.122	2.28	10.1	**0.965**	**0.23**	**0.082**
17	Sole	3.116	0.15(1.05)	0.8	3.1	**0.155**	**0.026**	**0.024**
18	Plaice	3.2	0.70	0.85	3.42	**0.127**	**0.25**	**0.033**
19	Flounder	3.496	0.25	1.1	3.2	**0.034**	**0.34**	**0.189**
20	Dragonet	3.231	0.294	1.5	6	**0.751**	**0.25**	**0.013**
21	Large demersal fish	4.06	0.112	0.55	2.54	**0.427**	**0.22**	**0.359**
22	Small demersal	3.47	2.555	1.42	3.7	**0.817**	**0.38**	**0.355**
23	Mackerel	3.478	1.72	0.6	1.73	**0.405**	**0.35**	**0.263**
24	Horse Mackerel	3.474	0.579	1.2	3.51	**0.264**	**0.34**	**0.499**
25	Sprat	2.88	0.579	2.28	6	**0.625**	**0.38**	**0.191**
26	Lesser-Argentine	3.098	0.244	0.44	10.27(1)	**0.937**	**0.04**	**0**
27	Herring	3.105	1.966	0.8	4.34	**0.398**	**0.18**	**0.001**
28	A. Whiting	3.597	0.352	0.89	5.46	**0.496**	**0.16**	**0.687**
29	J. Whiting	3.669	0.24	2.36	13.7	**0.911**	**0.17**	**0.275**
30	Norway Pout	3.104	3.285	0.78(0.98)	5.05	**0.895**	**0.19**	**0.002**
31	Spurdog	4.252	0.016	0.6	2	**0.33**	**0.3**	**0.176**
32	A. Atlantic Cod	4.242	0.161	1.19	3.5	**0.217**	**0.34**	**0.103**
33	J J. Atlantic Cod	3.549	0.07	1.79(2.79)	8.54(8.55)	**0.936**	**0.33**	**0.311**
34	Shrimp & Prawns	2.121	**1.468**	3	10	**0.99**	**0.3**	**0.118**
35	S Squids	4.15	0.251	4.5	20	**0.922**	**0.23**	**0.243**
36	Poor- Cod	3.288	0.094	0.77	6.7	**0.936**	**0.11**	**0.154**
37	Mixed Pelagic	3.167	0.11	4	10.19(10.2)	**0.935**	**0.39**	**0.058**
38	Octopus	3.731	0.071	4.5	20	**0.903**	**0.23**	**0.527**
39	Epibenthic Invertebrate	2.306	270.79	0.26	1.73	**0.996**	**0.15**	**0.26**
40		3.086	1.354	0.5	2.51	**0.908**	**0.2**	**1.07**
41	Benthic infauna invert	2.095	231.64(235.8)	0.91	6.05	**0.993**	**0.15**	**0.1**
42	Lobsters	3.34	0.064	0.94	4.7	**0.829**	**0.2**	**0.381**
43	Norway Lobster	2.956	1.1	0.37	1.85	**0.876**	**0.2**	**0.429**
44	Zooplankton	2.098	17.726	4.83	16.1	**0.99**	**0.3**	**0.098**
45	Phytoplankton	1	7.5	286	-	**0.575**		**0**
47	Discards	1	0.132	25	83.3	**0.558**	0.3	**0**
48	Detritus	1	50	-	-	**0.514**	-	**0.364**

E. L. forbesii Role as Prey

Selectivity index which shows how predators prefer squid consumption is presented in Fig. 6. The main predators of squid are shown with their degree of preference. Crab, cephalopods, marine mammals, spurdog, mackerel, haddock, Atlantic cod, whiting, and demersal fish positively selected squids. Others in this category included monk fish, grey gurnard and long rough dab. Seals, adult whiting and adult Atlantic cod negatively preferred squid in their diet i.e. they can only prey on squid as an alternative to their main food source. Other groups in the model completely avoided squid. Among the economically important fish stocks, squid is most preferred by mackerel followed by haddock. Adult Atlantic cod rarely feeds on squid. Among marine mammals squid is mostly preferred by baleen whales.

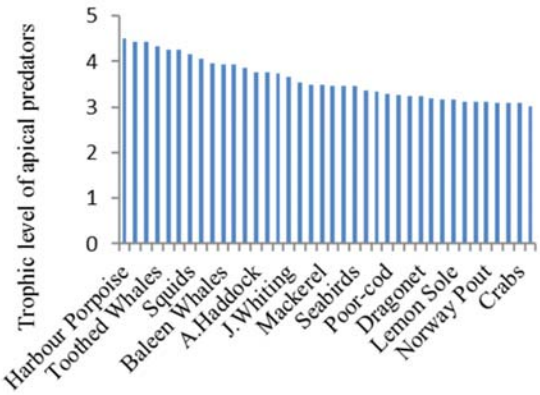

Fig. 2 Trophic level (TL) estimates of predators with TL ≥3.0 in Moray Firth ecosystem food web (in descending order)

F. Balanced Role in the Ecosystem

A comparative analysis of the Mixed Trophic Impacts (MTI) between squid, adult Atlantic cod and top predators on functional groups in Moray Firth ecosystem are presented in Fig. 7. All functional groups were both negatively and positively impacted, with the exception of adult haddock. The main trophic impact on squid and adult Atlantic cod was caused by cannibalism with high negative impact. The highest negative impact on juveniles of whiting and haddock was caused by squid. Squid had a positive impact on sandeel, adult Atlantic cod, juvenile Atlantic cod and mixed pelagic, which is being interpreted as indirect trophic impact because squid preyed on adult Atlantic cod, their main predator.

V. Discussions

This work aimed to describe the trophic position and ecological roles of squid, *L. forbesii* in the Moray Firth ecosystem. The model showed that *L. forbesii* occupies a high trophic level and exploits a wide diversity of trophic resources. In this system, the impacts of squid predation on the food web and fish stock are enormous [7], [11], [59], [60]. This is in agreement with [61] who reported that availability of predators/prey of organism, fishing pressure and environmental conditions have intense impacts on the structure and function of the ecosystem [62]-[64] . The main prey consisted of zooplanktons, small demersal fish, sandeel and cephalopods as well as fish juveniles. The major identified predators include; cephalopods, cetaceans, mackerel, haddock, whiting, demersal fish and crab. The squid's EE value of 0.922 showed that the species is heavily predated on but moderately exploited. Omnivory Index (OI) of 0.243 indicates that squid feeds on many trophic levels identifying its role in the ecosystem which agree with the isotope signature [65]; hence the transfer of energy across a varied array of groups. Reference [7] reported that OI could be used to infer on trophic width of squid.

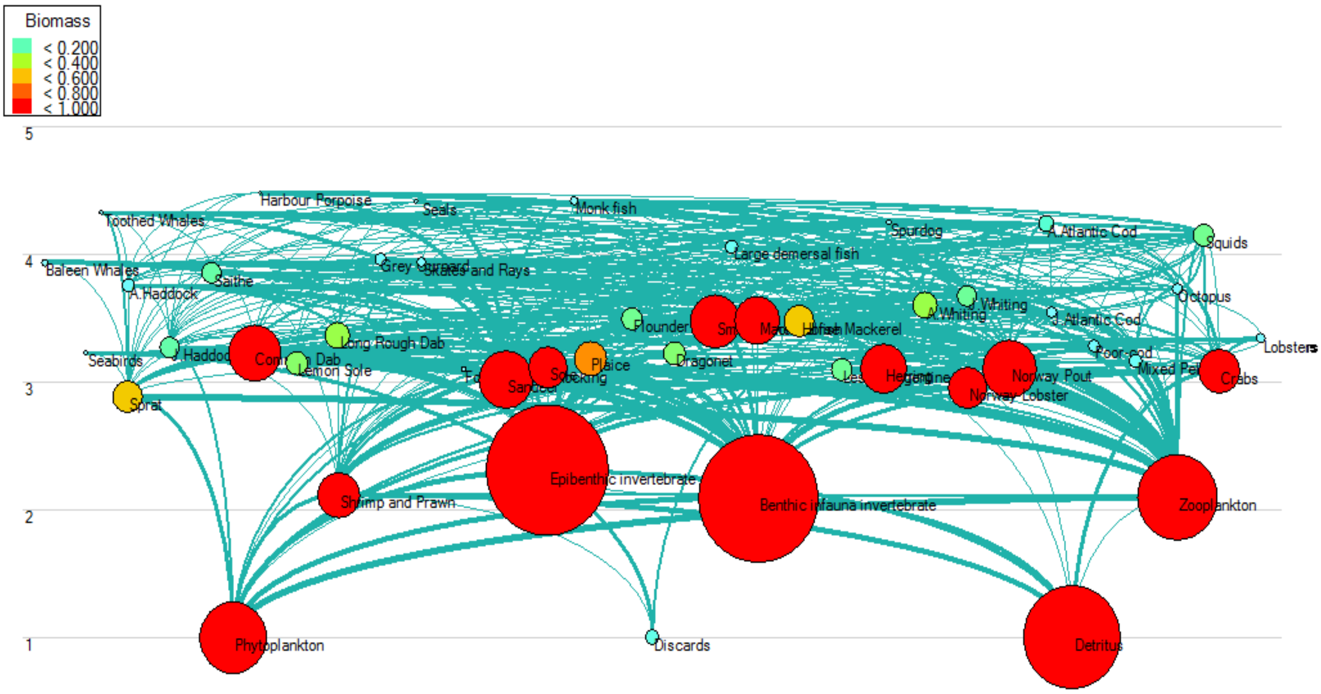

Fig. 3 A food web diagram of the Ecopath model for Moray Firth showing trophic interaction among groups. 1-5 represents trophic levels

The model identified *L. forbesii* as an important predator occupying a wide range of trophic position, with a trophic level of 4.15 (Table I), only 7.4% less than harbour porpoise being the highest top predator in the ecosystem. With the high trophic level, squid exploits a high diversity of trophic resources, reflecting the plasticity of its feeding behaviours and dietary habits [11], [27], [29], [60]. Comparing the trophic position with jumbo squid (*Dosidicus gigas*) of central Chile and central Gulf of California (with 1% and 15% less than the highest predators respectively) could suggest that squid occupy a high position in the global marine ecosystem [66], [67]. Isotope findings also confirm the position of squid in the ecosystem [65]. With this trophic position, squid could assume the position of a top predator with its implications. Fishing on squid could lead to changes in species composition with small, fast growing and earlier maturing species predominating (as is the case with top predators) [68]. Top predators encourage biodiversity in ecosystems [69]. Increase in the preferred prey of squid and other predators as competition would reduce the number of prey organisms. However, the trophic position of squid range from 2 to 4 with some squid occupying medium to top position [13], [40], [60], [69], [70]. This variation could be a consequence of squid's different trophic behaviour and ecology features of individual ecosystem [40]. Squid further serves as a link between prey and consumers up to top predator, transferring most of the primary production across a wide range of trophic levels (Fig. 3).

The role of *L. forbesii* could be seen as a major consumer of zooplankton, small demersal fish and most fish stocks juveniles [27]. High levels of cannibalism took place [5], [65], [69] which could be as a result of the grouping together of juveniles and adult squid, as well as their recruitment taking place in the same ecosystem [18]. This finding agrees with [5] who reported jumbo squid to prey on organisms less than 5-15% of its size. The model identified sandeel (probably for the first time) as a major prey of squid. The role of squid as prey suggests it relevance in the energy pathway of a food web. Squid's consumption by its predators in the ecosystem surpassed fishing mortality during exploitation plus other sources of mortality (M2 and M0). Up to half of the functional groups feed on squid with about 82% having a positive preference (Fig. 4) [4], [60].

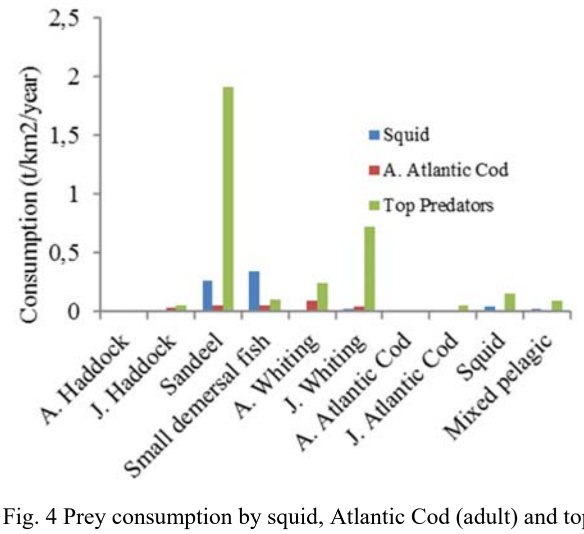

Fig. 4 Prey consumption by squid, Atlantic Cod (adult) and top predators (cetaceans, seals, and sea birds) as estimated by EwE for Moray Firth ecosystem (A = adult, J = juvenile)

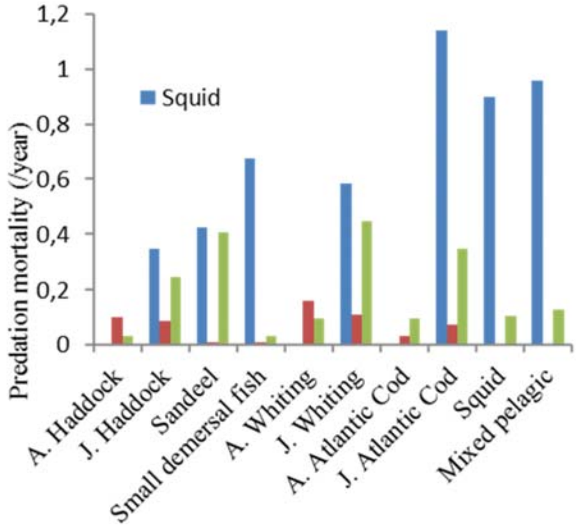

Fig. 5 Predation mortality by squid, adult Atlantic cod and and top predators (cetaceans and marine birds) on their principal prey, as estimated by EwE for Moray Firth ecosystem (A = adult, J = juvenile)

Predation mortality from the model (Fig. 5) provided an estimate of the impacts that predators have on *L. forbesii* population in the Moray Firth further showing the importance of squid as prey organism [4], [5], [12], [13], [16], [20], [21], [71]. The model identified the top predators (harbour porpoise, baleen whales, toothed whales and seals), cephalopods, and fish (most of which are commercial stocks) as squid's main predators. This is in line with most studies which identified the importance of squid as prey for marine mammals and large fish [13], [21], [23]-[25]. The absence of sea birds from the model output agrees with [22] observation that birds do not feed on *L. forbesii* in the Moray Firth.

Mixed trophic impact results showed that *L. forbesii* have an overall impact on groups in the food web [11], [17]. The model results also highlight that *L. forbesii* have both top - down and bottom-up impact on the food web which identify squid as significant organisms in the marine food webs and the important functional relationships they have with their prey and predators.

The ratio of 1.4 between total primary production (P) and total respiration (R) (Table II) characterized. Moray Firth as immature ecosystem undergoing early development in terms of structure and flows which agrees with the value (1.5) of down and bottom-up impact on the food web which identify squid as significant organisms in the marine food webs and the important functional relationships they have with their prey and predators.

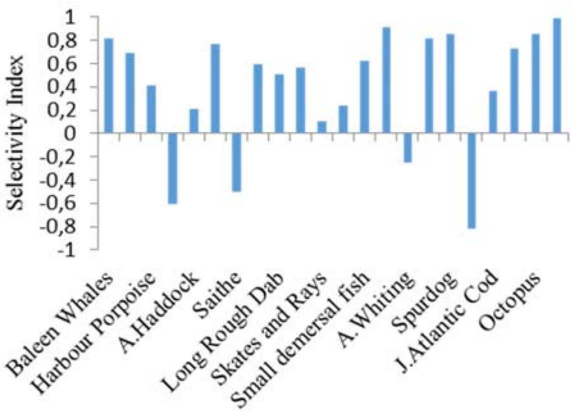

Fig. 6 showing the selectivity index (i.e. the degree of squid preference by its predators in the Moray Firth ecosystem) (A = adult, J = juvenile)

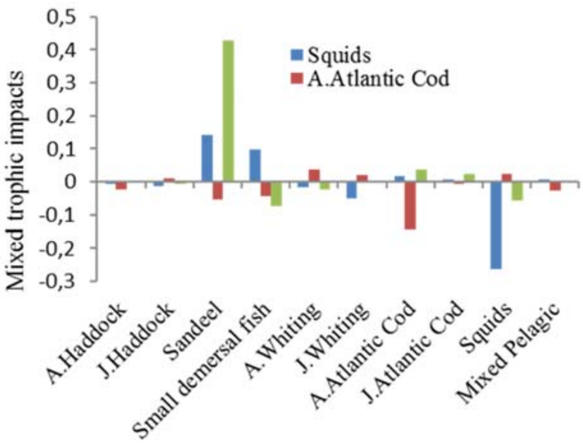

Fig. 7 Mixed trophic impacts for squid, Atlantic Cod (adult) and top predators (cetaceans and seals) as estimated by EwE for Moray Firth ecosystem (A = adult, J = juvenile)

TABLE II
SUMMARY STATISTICS OF THE PRESENT STUDY AND OTHER UK MARINE ECOSYSTEMS

Parameter	Moray Firth1	Moray Firth2	North Seas3	Irish Seas4	English Channels3	Western Chanels 5
Sum of consumption (t/km2/year)	2333	2289	6157	3905	1361	1590
Sum of all export (t/km2/year)	655	712	4692	6945	7815	2153
Sum of respiratory flows (t/km2/year)	1501	1435	2658	1330	716	796
Sum of all flows into detritus (t/km2/year)	1348	1393	36867	12837	7435	2683
Total system throughout (t/km/year)	5837	5828	12786	25017	16359	7223
Sum of all production (t/km/year)	2551	2540	4692	9371	7815	3424
Mean trophic level of the catch	3.418	3.38	3.6	3.61	2.57	2.44
Gross efficiency (catch/net p.p.)	0.0004	0.0004	0.0022	0.0022	0.0004	0.0011
Calculated total net primary production (t/km2/year)	2145	2145	2607	8275	7547	2949
Total primary production/total respiration (t/km2/year)	1.4	1.5	0.98	6.22	10.54	3.7
Net system production	644	710		6945		2153
Total primary production/total biomass	3.84	3.88	4.71	33.71	33.29	14.9
Total biomass/total throughout	0.095	0.095	0.04	0.01	0.01	0.027
Total biomass (exceeding detritus) (t/km2)	558	552	554	245	227	1978
Total catch (t/km2/year)	0.81	0.85	5.88	2	3.12	3.378
Connectance Index	0.24	0.25	0.22	0.22	0.13	0.17
System Omnivory Index	0.22	0.23	0.23	0.33	0.17	0.135

The ratio of 1.4 between total primary production (P) and total respiration (R) (Table II) characterized Moray Firth as immature ecosystem undergoing early development in terms of structure and flows which agrees with the value (1.5) of [11]. According to [72] total primary production and total respiration ratio less than 1(<1) or greater than 1 (>1) signifies a mature and immature ecosystem respectively. In addition, ecosystems with values less than 1 indicate the ecosystem is experiencing organic pollution. This implies Moray Firth ecosystem is yet free from a prevailing organic pollution experienced in the North Sea. Other ecosystems have different range of values showing that they are at different stages of development. The entire North Sea ecosystem with the value of 0.98 indicates a mature ecosystem, while other ecosystems are at various immature stages of development; Western Channel (3.7), Irish Sea (6.22) and English Channel (10.54). The ecosystem have short food chains and low connection index [72], [73]. Energy in the ecosystem is transferred predominantly by the classic food web. The short food chain has phytoplankton cells that are grazed upon by zooplankton which, in turn are taken up by fish and which are then eaten by marine mammals and birds.

One is aware that the use of large number of groups in the model could cause increase in errors as many of the input data might not be precise. However, the use of large number of groups in this model was necessary as it forms a part of preliminary ideal model [11] for Moray Firth ecosystem thereby forfeiting precision for details. Generally, getting precision in Ecopath, requires the use of small number of groups. We recommend, therefore, that to achieve precision, small number of groups should be explored in subsequent models. Also, the models should include bottlenose dolphin (BND) as an important functional group and squid group be split into juvenile and adult groups while other insignificant functional groups with unreliable data be omitted. Moray Firth is renowned as a home of BND which has been designated as a candidate Special Area of Conservation (cSAC) [10], [11] housing a reasonable population of BND [74], [75].

VI. CONCLUSIONS

The squid *L. forbesii* play a significant role in Moray Firth ecosystem. Squid's position of 4.15 (at the 5th) trophic level and contributions to the ecosystem in abundance, production, consumption, predation rates, and potential fishery makes it an important species. Because of this, it does appear the assertion that squid is gradually assuming the role of top predators in most ecosystems [65], [76] could hold for Moray Firth ecosystem. Consequently, squid should be taken into account in future modelling and government policies on conservation and fishery regulations for Moray Firth.

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