Movements of female lumpfish (*Cyclopterus lumpus*) around Iceland

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Lumpfish (*Cyclopterus lumpus*) migrate from their offshore feeding areas to the coastal areas of Iceland during March and April where they remain for several months before spawning. Their movements during this time are poorly documented. Using the results of an extensive tag-recapture study (the largest documented for lumpfish) which took place between 2008 and 2014, the movement of female lumpfish around Iceland was investigated and the implications for fisheries management were considered. Of 9710 female fish tagged, 880 were recaptured and 82 of these were recaptured after more than 250 days at liberty (DAL). There was a negative relationship between length at tagging and recapture rate indicating that between 2008 and 2014, the fishery was selecting for smaller fish. Lumpfish showed extensive movements with fish tagged in coastal areas being recaptured up to 587 km from their tagging location and were capable of swimming up to 49 km day^{-1}. Fish were most frequently caught in the area in which they were tagged; however, movement between areas was common. There were indications of homing behaviour with 75% of the fish, which were recaptured after 250 DAL, caught within 80 km of their tagging location. Fish which were tagged offshore before the fishing season showed no clear pattern of where they would be recaptured. These extensive movements and homing behaviour are discussed in the context of the management of the lumpfish fishery.

Keywords: lumpsucker, maturity, migration, spawning, TAC.

Introduction

Lumpfish (*Cyclopterus lumpus*) are found in the north Atlantic and exhibit a semi-pelagic lifestyle, inhabiting both the pelagic and demersal zone (Blacker, 1983; Holst, 1993; ICES, 2012). Outside the breeding season, lumpfish are in open water far from land (Holst, 1993) and from approximately March to August, mature fish are present in coastal waters where they come to breed. Lumpfish lay their eggs in a nest site which is guarded by the male. Before the eggs are laid, lumpfish will perform complex mating rituals with nest cleaning, fin brushing, and body quivering (Goulet *et al.*, 1986). After the eggs are laid, the female leaves and plays no further part in the guardianship of the eggs. The males may also guard multiple batches of eggs from different females at the same time. The events following hatching remain unclear: it has been claimed that the larvae will attach themselves to the male (Davenport, 1985); however, Fulton (1907) and Mochek (1973)

stated that the larvae rapidly dispersed after hatching. A third hypothesis is that they attach themselves "immediately" to some substratum in the intertidal zone (Pampoulie *et al.*, 2014) which possibly could include the male. A portion, at least, of larvae and juveniles are known to spend the first few months in tidal pools before migrating out into open water (Mochek, 1973; Moring, 2011) but yolk sac larvae and juveniles <30 mm are also found associated with floating seaweed clumps between 10 and 30 km from land (Ingólfsson, 2000).

There have been several tagging studies of lumpfish, including one from Iceland (Schopka, 1974), but most of these are published in "grey" literature. From these studies, it is apparent that lumpfish are capable of travelling large distances from their offshore feeding areas to the coastal breeding areas (Schopka, 1974). Movement of lumpfish along coastal areas of more than 100 km has been noted in Iceland, Denmark, and Canada (Bagge, 1967; Schopka, 1974;

Blackwood, 1983: Grant, 2001; Fréchet *et al.*, 2011). The mentioned studies have also all noted that lumpfish which are recaptured after 1 year at liberty are frequently recaptured close to their original tagging location indicating homing behaviour. The number of times lumpfish will spawn in its lifetime is still unclear but there are several studies which demonstrate that a proportion will spawn at least twice (Bagge, 1967; Schopka, 1974; Blackwood, 1983; Fréchet *et al.*, 2011; Kasper *et al.*, 2014). However, tag loss is suspected to be an issue during tagging studies of lumpfish, which complicates the estimation of post-spawning mortality (Thorsteinsson, 1981; Fréchet *et al.*, 2011, Kasper *et al.*, 2014).

The fishing for lumpfish in Iceland is carried out using gillnets during the breeding season. To participate in the fishery, a boat must have both a permit to fish for lumpfish and a licence for the current year. Permits are limited to 458 and no new permits are issued. A new boat can only enter the fishery by transferring an existing permit to the new boat. The coastline of Iceland is divided into seven regions (A–G). A licence allows a boat to fish within one preselected region. Fishing takes place between 20 March and 2 June for regions D–G, and 1 April to 14 June for regions A and C (Figure 1). Area B (Breiðafjörður) is divided into two sub-regions; fishing can take place in the outer region from 1 April to 14 June. Due to the breeding of eider ducks (*Somateria mollissima*) fishing in inner Breiðafjörður can only take place between 20 May and 2 August.

The lumpfish fishery is an effort controlled fishery with restrictions on the number of nets and the number of consecutive days a boat can fish within a season. A recommendation for a total allowable catch (TAC) for lumpfish has been given each year by the Marine Research Institute (Iceland) since 2011 (first applied to the 2012 fishing season), which is then taken into consideration by the Ministry of Fisheries when setting the number of fishing days for the season. Limitations on the number of days, beyond the time frame for the fishery fixed by regulation, were first implemented in 2005, but pre-2012, this was following recommendations from National Association of Small Boat Owners based on the market price for roe.

The recommendation of a TAC is based on the assumption that lumpfish in Iceland form a single population and is not composed of several non-interbreeding populations in different areas. For fisheries management, it is important to recognize whether the management unit in question consists of a single population, several isolated populations, or a metapopulation. If several fish populations are indeed separate, but managed as a single unit, less productive populations of the unit can become depleted (Hutchinson, 2008). Due to the aggregation of fisheries data, the extinction of these units could be well under way before aggregate data analyses would question the health of the complex (Frank and Brickman, 2000). A recent genetic study by Pampoulie *et al.* (2014) showed a lack of genetic divergence among lumpfish in Iceland. While this indicates that there may be exchange of adults or juveniles between areas, the rate of exchange could still be at such a low level that more localized management would be appropriate to prevent localized depletion of lumpfish. To investigate the degree of mixing of lumpfish between areas, data from tagging studies carried out between 2008 and 2014 were analysed; this is the largest tagging study of lumpfish documented at the time of writing and was partially reported in Kasper *et al.* (2014). This dataset covers the main distribution area of lumpfish in Iceland. It also provided an ideal dataset to confirm/challenge the possibility of homing behaviour in lumpfish and investigate the current selectivity of the lumpfish fishery.

Material and methods

A total of 9710 female lumpfish, total length 25–56 cm (Figure 2), were tagged around Iceland (Figure 1) from 2008 to 2014 between weeks 7 and 34 (Figure 3; Table 1); 1192 of these fish were tagged after the fishing season had finished in all areas. Most of these ($n = 9568$) were caught by commercial fishermen using lumpfish gillnets with 267 mm mesh size. Fish were removed from the nets and placed in a tank with flow-through sea water. Only fish which did not show any signs of damage such as floating or bleeding were tagged. Fish total length was measured, maturity assessed using criteria from Table 2, and the fish were tagged with Peterson disk tags (Floy) attached with a nickel pin through the rear of the dorsal fin. An additional 143 female lumpfish were tagged aboard R/V Bjarni Sæmundsson during the Icelandic annual groundfish survey in March 2012–2014 (Figure 4). These fish were caught by bottom trawl with tow duration of 1 h. The Peterson tag was labelled with a unique tag number, and contact name, address and phone number.

In regard to management of the lumpfish fishery, Iceland is divided into seven regions (A–G). For the purpose of this study, release sites were grouped into 11 areas (Figure 1). "Regions" refers to the fishery regions for lumpfish around Iceland as laid out by the Ministry of Fisheries of Iceland, "areas" will refer to the areas defined for the purpose of this study (A–D, E1–E5, and F) (Figure 1). Areas A–C and F are the same as the respective lumpfish regions. Area D denotes the western half of region D and covers the coastline from the border between region C and D to the tip of the Vatnsnes peninsula. Area E1 denotes the eastern side of Region D and covers Skagi peninsula. Area E2 is solely in region E, and covers Tröllaskagi peninsula. Area E3 is solely in region E and covers Flateyjarskagi peninsula. Area E4 is solely in region E and covers Tjörnes peninsula. Area E4 is solely in region E and covers Melrakkaslétta peninsula and the northern coast of Langanes peninsula. There is very little directed fishing for lumpfish in region G and no fish were tagged or recaptured in this area. Area E was split due to its large area and higher tagging effort in comparison with other areas. In area E, the fishing tends to occur along the sides of the fjords and the coastline facing the open sea. There is very little fishing effort within the inner parts of the fjords, probably due to lack of fish, thus these present logical boundaries for each area, i.e. each area in region E consists of a single peninsula.

Displacement distance, the distance between release and recapture, was calculated using Google Earth (http://www.google.com/earth/) and was defined as the shortest distance between the two points without crossing land. The number of days between release and recapture is referred to as days at liberty (DAL). Dispersal rates (km day^{-1}) were calculated using displacement distance and DAL. Fish which were at liberty for <3 days were excluded from analysis on movements to allow the fish time to re-orientate itself and disperse. Sixty fish were captured and re-released, in these cases the second location was used in the analysis of movement between areas, displacement distance was the shortest distance between the tagging location and final recapture position via the point where it was captured and re-released, and DAL was the number of days from the initial release until the second capture. Recapture rate for different maturity stages was examined for fish tagged on or before week 19 using χ^2 test. Week 20 was chosen as it allowed 3 weeks before the fishing season ended in regions D–G and gave a significant number of Stages 3 and 4 for this to be examined; fish at Stages 3 and 4 were not caught until Week 15. The return
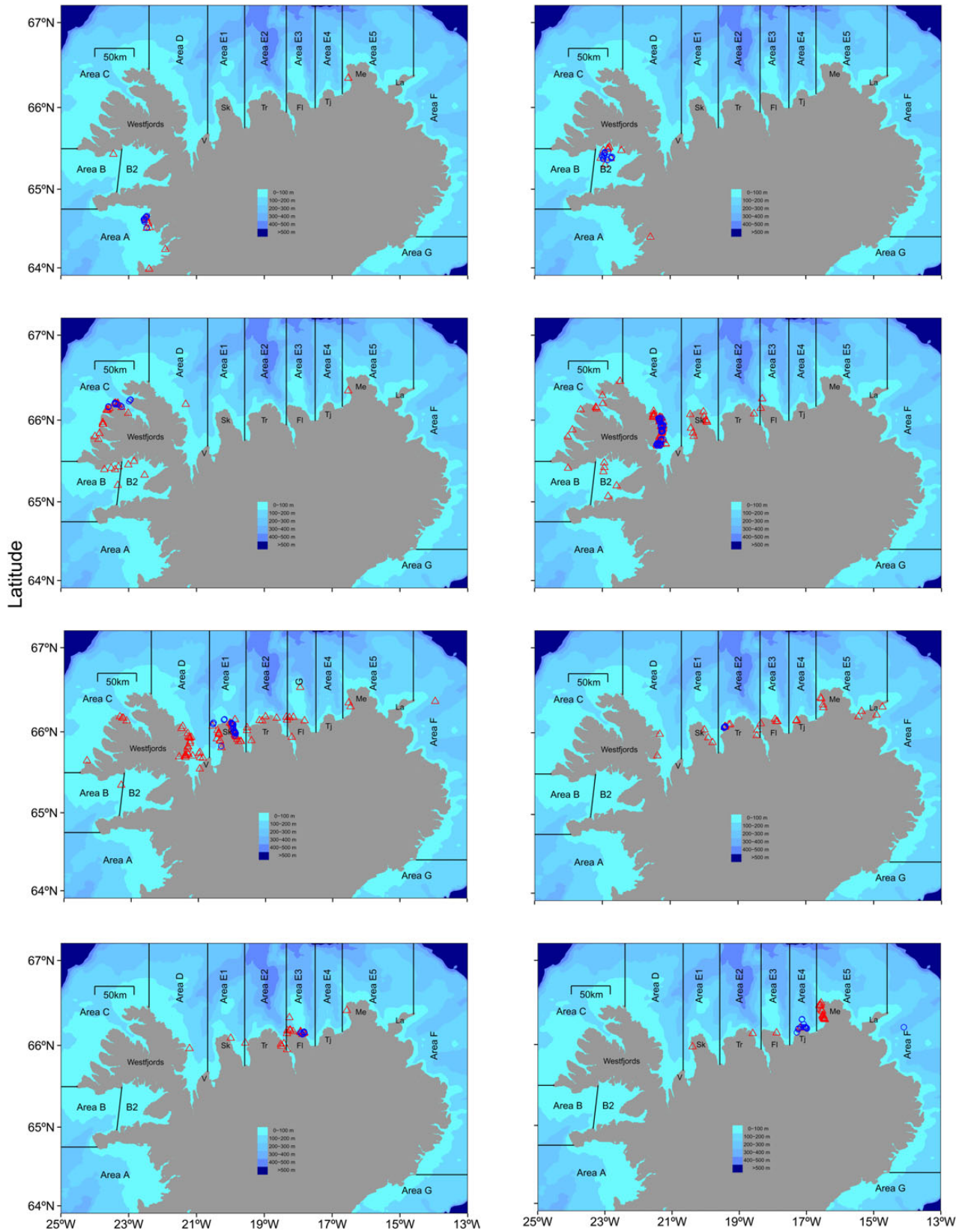
Figure 1. Location of release (blue circles) and recapture locations (red triangles) of tagged female lumpfish in the different areas around Iceland. The peninsulas mentioned in the text are marked V, Vatnses; Sk, Skagi; Tr, Tröllaskagi; Fl, Flateyjarskagi; Tj, Tjörnes; Me, Melrakkaslétta; La, Langanes. G marks the island of Grímsey.
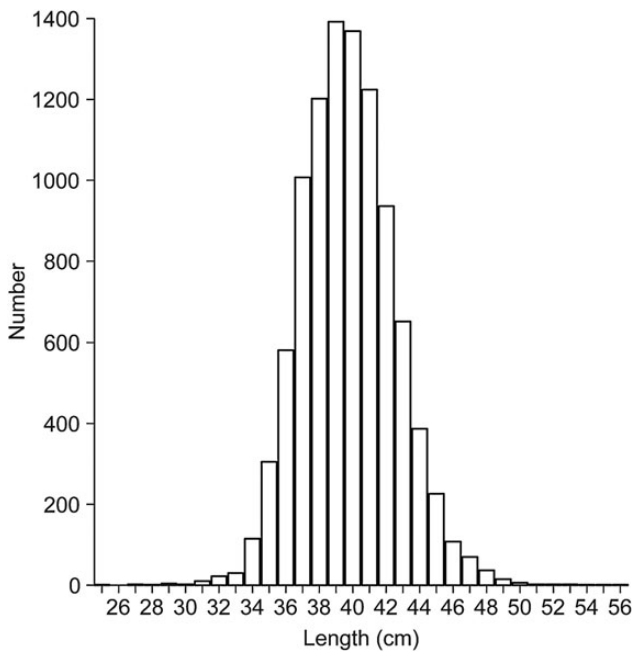
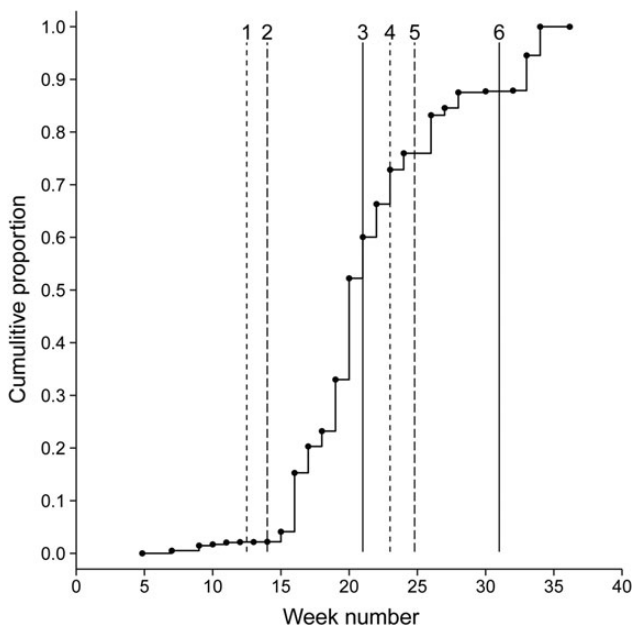**Figure 2.** Number of female lumpfish tagged at length.

Figure 3. Distribution of tagging by week number for all years (2008–2014) combined. Lines represent the opening of the fishery in areas D, E, F, and G (1), A, B, and C (2) and B2 (3) and the closing of the fishery in areas D, E, F, and G (4), A, B, and C (5), and B2 (6).

rate after 1 year was defined as the percentage of fish caught after 250 DAL (r_1) and was calculated using the formula

$$r_1 = \frac{R_1}{T - R_0},$$

where R_1 is the number of fish caught after 250 DAL, T is the number of fish tagged the previous year, and R_0 is the number of fish tagged

and recaptured the previous year. The value of 250 days was used to define 1 year at liberty as there was a hiatus in the distribution of DAL with no fish being recaptured between 150 and 250 DAL (see Results).

Results

Of 9710 tagged female lumpfish, 880 fish were recaptured giving a return rate of 9.1% (Table 3). DAL varied between 0 and 396 (Figure 5). Of the fish tagged in coastal areas which were at liberty <150 days, average DAL was between 6.9 (area B) and 12.7 (area E1) with a maximum of between 24 (area B) and 45 (area F) (Table 4). Eighty-two fish were at liberty for >250 days (0.8%) (Table 3; Figure 5), with an average of 354 days. Sixty fish were captured and re-released. Tagged fish varied between 25 and 56 cm total length with an average of 39 cm (Figure 2) while fish which were recaptured varied between 31 and 55 cm (when tagged) with an average of 39 cm. The rate of recaptures was significantly related to length at tagging for fish between 34 and 48 cm (linear regression; $R^2 = 0.86$, $P > 0.001$) (Figure 6). As the number of fish tagged at each centimetre length class <34 and >48 cm was low, a single recapture gave a relatively high return rate in comparison with other size classes.

Lumpfish caught <150 DAL

After excluding fish which were at liberty for <3 days and where location of recapture was not known or the location was unreliable (e.g. the position was on land), movement data were available for 730 fish (Table 3). Average displacement distance was 41 km but this varied between areas (Table 4) and was positively correlated with DAL for fish caught <150 DAL (Pearson's correlation; $R^2 = 0.10$, $P < 0.0001$) (Figure 5). The maximum displacement distance for fish recaptured <150 days from release was 587 km; this fish was at liberty for 18 days giving a displacement rate of 33 km^{-1} day. Mean displacement rate was 4 km^{-1} day with a maximum of 49 km day^{-1}, the maximum displacement rate was from a fish which travelled 298 km in 6 days. Fish were most frequently caught in the area they were tagged with decreasing recapture rates as distance from the tagging area increased (Table 4) except areas E1 and E4. The week number in which the fish were tagged had no significant effect on the total distance travelled for fish tagged on the coastal areas (linear regression; $R^2 = 0.002$, $P > 0.05$). Maturity status was recorded for 5009 fish tagged on or before Week 20, of which 96, 3, and 1% were at Stages 2, 3, and 4, respectively. The return rate did not vary between stages (χ^2 test; $\chi^2 = 4.6$, d.f. = 2, $P > 0.05$); the return rate was 10.7, 8.3, and 1.8% for Stages 2, 3, and 4, respectively.

Only 2 of 503 fish tagged in area A were recaptured in other areas; one was recaptured in area B and one in area E5. The fish recaptured in area E5 had the largest displacement distance of all tagged fish (587 km), travelling from Faxaflói (area A) around the Westfjords to the west side of Melrakkaslétta peninsula (Figure 1). The recapture rate of area B (2.5%) was the lowest of any area and also had the highest number of fish which were recaptured in the area in which they were tagged. The fish which was recaptured in area A was found dead on a beach 9 days after tagging. Fish tagged in area C showed a tendency to move south with 18.8% of the fish recaptured in area B while two fish travelled around the Westfjords and moved east. One tag from a fish tagged in area C was found attached to a piece of lumpfish in the catch of a prawn trawler 18 months after tagging (not shown in Figure 1). Fish tagged in areas D, E1, and E2 moved both east and west in roughly

**Table 1.** Number of fish tagged in each year and area.

| Year | Tagging area | | | | | | | | | | | |
	A	B	C	D	E1	E2	E3	E4	E5	F	Off	Total
2008				1243	399	386						2028
2009		701		450	364		241		470	243		2469
2010	280	648	282	381	307			280	279	280		2737
2011	223	516	225	825	39							1828
2012		421				14					94	529
2013			8		35			27			20	90
2014											29	29
Total	503	2286	515	2899	1144	400	241	307	749	523	143	9710

Off, fish which were tagged during the Icelandic groundfish survey.

Table 2. Maturity stages with external appearance used for lumpfish.

Maturity stage	External appearance
(2) Early	Abdomen (belly) greatly distended, no swelling in the urogenital region, sphincter muscle and ovarian membrane not visible.
(3) Medial	Abdomen greatly distended, moderate swelling in the urogenital region, sphincter muscle visible, ovarian membrane not visible.
(4) Advanced	Abdomen greatly distended, exaggerated swelling in the urogenital region, sphincter muscles and ovarian membrane visible.
(5) Spawning	Abdomen greatly or moderately distended, exaggerated or moderate swelling in urogenital region usually accompanied by haemorrhaging at the oviduct.
(6) Spent	No distention of the abdomen; no swelling in the urogenital region; ovarian membrane is healing or has completely healed (i.e. sphincter muscle not visible).

Description from Grant (2001).
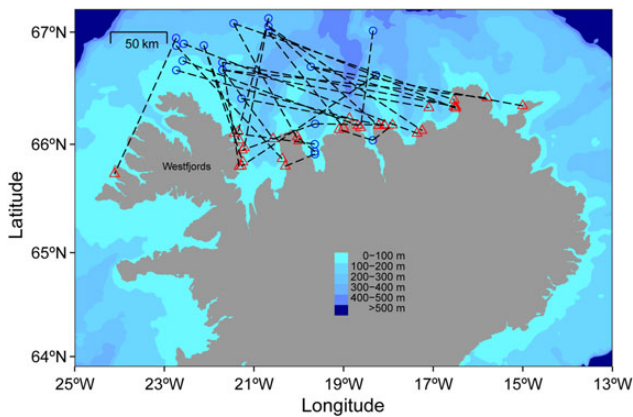
Figure 4. Release (circles) and recapture (triangles) locations of lumpfish tagged during the Iceland groundfish survey 2012–2014. Dashed lines are for illustrative purposes only and do not represent the route used to calculate displacement distance.

equal numbers with some migrating as far as areas B and F (Table 5, Figure 1). One fish tagged in area E1 was caught by a trawler in area F in September 2009, 122 days after tagging (Figure 1). One fish tagged

Table 3. The total number of recaptures (TR), recapture rate (r_0), the number of tags where DAL was 3 or greater (R_{3d}), and the number of fish recaptured after >250 DAL (R_1) for each area.

| Year | Tagging area | | | | | | | | | | | |
	A	B	C	D	E1	E2	E3	E4	E5	F	Off	Total
TR	28	57	50	264	104	88	51	54	71	80	33	880
r_0	5.6	2.5	9.7	9.1	9.1	22.0	21.2	17.6	9.5	15.3	23.1	9.1
R_{3d}	18	38	48	214	93	71	31	52	61	71	33	730
R_1	1	6	6	32	5	6		5	12	9		82

in E1 was recaptured at the island of Grímsey on 9 May 2008, 27 days after tagging and 107 km from its tagging location; Grímsey is ~42 km from mainland Iceland (shortest distance). Fish tagged in area E3 showed a tendency to move west with almost 26% of the fish being recaptured in areas D–E2. Fish tagged in area E4 were the group least likely to be recaptured in the same area with over 80% recaptured in area E5 on the west of the Melrakkaslétta peninsula (Figure 1). Fish tagged in area E5 moved both east and west along the coast with many being recaptured on the west coast of the Melrakkaslétta peninsula (Table 5. Figure 1). Most of fish tagged in area F were recaptured in area F but 45% were recaptured in areas to the west.

Many of the fish which were captured and re-released spent only 1–2 DAL, either after their first or second capture, or both, thus did not travel far (<25 km). However, there were five fish which travelled >25 km both after tagging and after being released for a second time (Figure 7).

Fish tagged offshore were at liberty for between 20 and 61 days (Table 4) and showed no clear pattern in their migration in terms of which area they would be recaptured in. There were two opposing examples: two fish which were released in proximity were caught over 200 km from each other, whereas two fish released at the same time were caught by the same fisherman on the same day (Figure 4).

Lumpfish caught >250 DAL

Of the 82 fish caught >250 days after release (Table 3), 50% were caught within 30 km from the site in which they were tagged and 75% were within 80 km (Figure 8). The displacement distance of fish which were recaptured after 250 DAL was between 1 and 447 km, with an average of 65 km. Two fish tagged in area D were recaptured by a trawler north of the Westfjords in January 2009 and January 2012, 274 and 261 days after tagging, respectively. The percentage of fish caught >250 DAL, r_1, varied by year (min
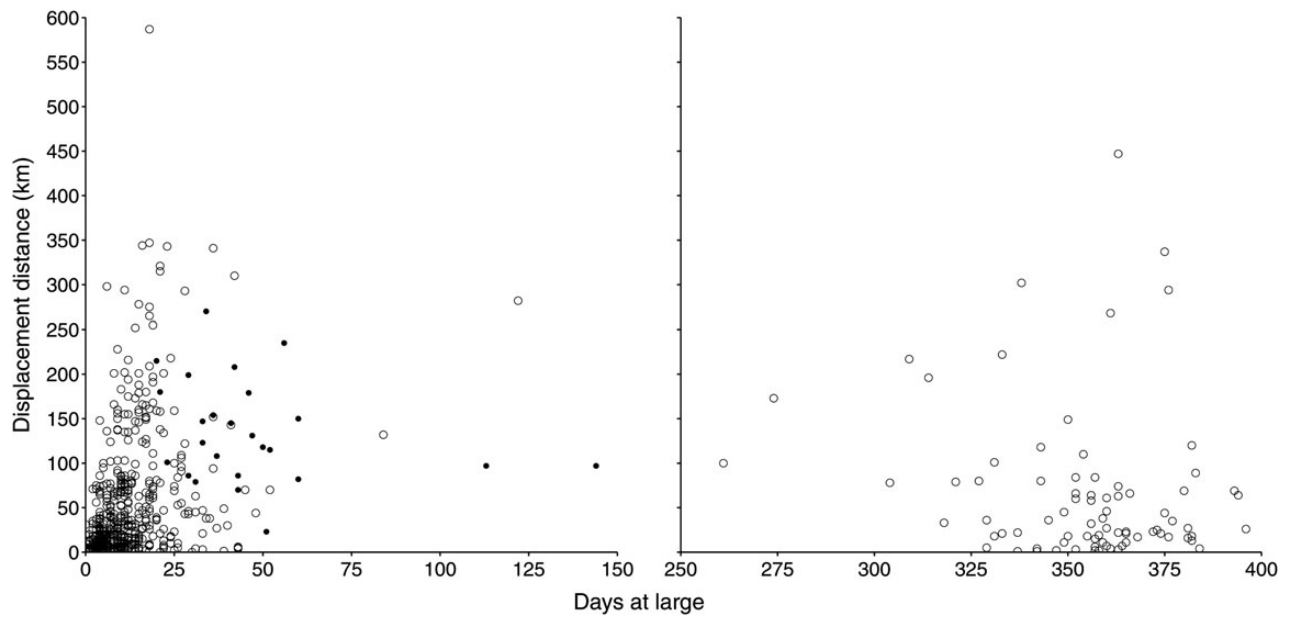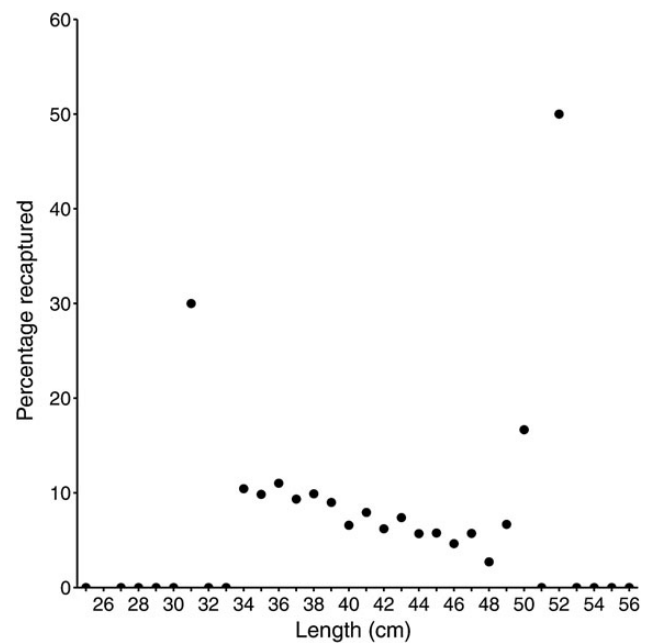
Figure 5. DAL vs. displacement distance for all lumpfish tagged and recaptured between 2008 and 2014. Fish tagged during the Icelandic groundfish survey are shown by filled circles, all other fish shown by open circles.

Table 4. Summary statistics of days at liberty (DAL) (a) and displacement distance (km) (b) for fish tagged in the different areas and during the Iceland groundfish survey (Off).

Area	Min	1st Qu	Median	Mean	3rd Qu	Max.
(a)						
A	0.0	0.0	8.0	7.0	10.0	30.0
B	0.0	1.0	5.0	6.9	11.0	24.0
C	0.0	7.8	8.5	10.7	12.5	28.0
D	0.0	3.0	5.0	8.2	9.0	84.0
E1	0.0	7.0	10.0	12.7	17.0	122.0
E2	0.0	4.0	4.0	7.0	9.0	37.0
E3	0.0	2.0	8.0	8.5	12.5	36.0
E4	0.0	4.0	4.0	7.3	8.0	39.0
E5	0.0	4.5	11.0	12.3	13.0	43.0
F	0.0	3.0	10.0	10.0	15.0	45.0
Off	20.0	33.0	41.0	40.6	50.0	61.0
(b)						
A	<1.0	1.0	5.0	36.5	11.0	587.0
B	<1.0	3.5	10.0	14.1	15.0	228.0
C	<1.0	3.5	26.0	57.3	57.5	293.0
D	<1.0	1.0	7.0	30.6	23.0	344.0
E1	<1.0	16.0	60.0	59.4	79.5	347.0
E2	<1.0	1.0	1.0	38.6	68.0	265.0
E3	<1.0	1.0	3.0	23.2	22.0	173.0
E4	<1.0	19.0	23.0	31.3	36.0	166.0
E5	<1.0	4.0	18.0	35.8	42.5	298.0
F	<1.0	3.0	17.0	50.1	76.5	275.0
Off	23.0	97.0	134.0	138.8	180.0	270.0

Includes only fish which were at liberty for <150 days.

Figure 6. Percentage of fish recaptured (<250 DAL) vs. length at tagging.

0.2%, 2012; max 1.8%, 2008) and area (min 0.2%, area A; max 1.9%, area E2). Of the fish which were caught after 250 DAL and caught >50 km (n = 33) from their tagging location, 47% of these fish were caught in areas E1–E3, whereas only 6% of the fish caught <50 km (n = 49) from their tagging location were recaptured in areas E1–E3 (Figure 8).

Discussion

The results confirm the findings of previous tagging studies that lumpfish migrate large distances from their offshore feeding grounds to coastal areas during March and April (Schopka 1974; Holst, 1993; ICES, 2012) and that they will also migrate large distances in coastal areas (Bagge, 1967; Schopka, 1974; Blackwood, 1983: Grant, 2001; Fréchet et al., 2011). Many fish were tagged on, what are thought to be, spawning grounds, deduced from the presence of large concentrations of mature females, but migrated to

Table 5. Area of tagging vs. final area caught for female lumpfish at liberty for at least 3 days.

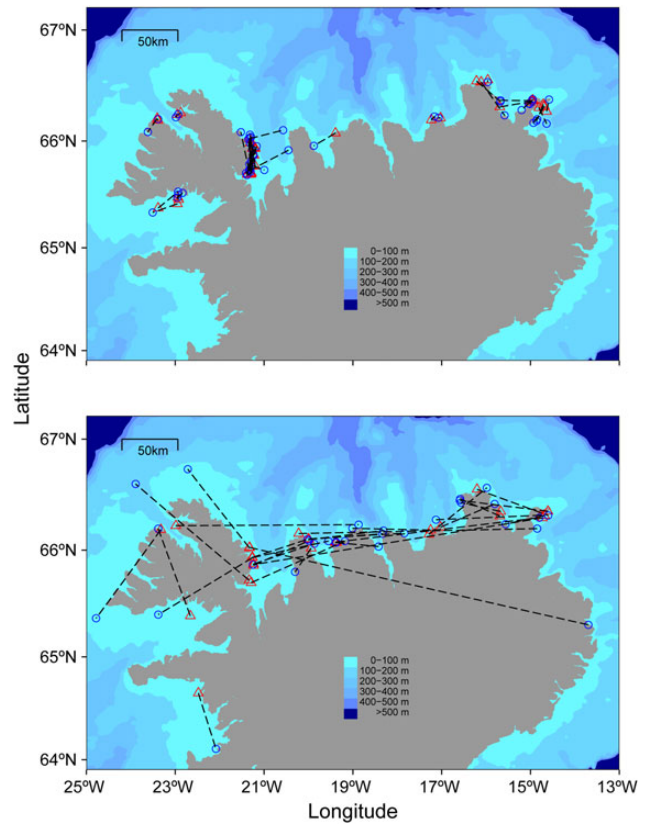| Tagging area	Recapture area										
	A	B	C	D	E1	E2	E3	E4	E5	F	Off
A	88.9	5.6							5.6		
B	2.6	94.7	2.6								
C		18.8	75.0	2.1		2.1			2.1		
D		3.7	6.1	79.9	7.0	1.4	0.9			0.5	0.5
E1		1.1	5.4	34.4	36.6	8.6	9.7		2.2	2.2	
E2				2.8	5.6	63.4	8.5	7.0	8.5	4.2	
E3				6.5	6.5	12.9	71.0		3.2		
E4					1.9	3.8	1.9	9.6	82.7		
E5				3.3				1.6	80.3	14.8	
F				1.4	1.4		8.5	4.2	29.6	54.9	
Off			3.0	24.2	15.2	18.2	12.1	9.1	18.2		

Numbers are percentage of the total number of fish recaptured from each tagging area.
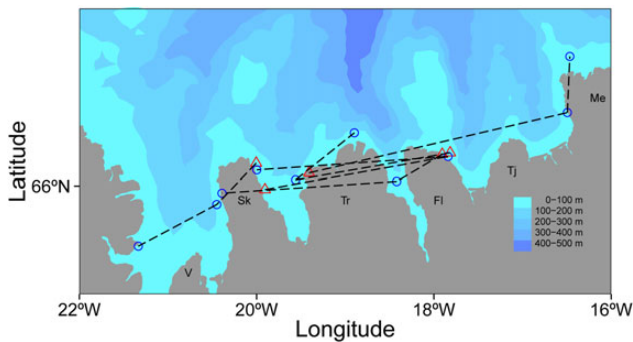
Figure 7. Location of tagging (X), location of first capture and re-release (Y), and position of final capture (O) for five female lumpfish. Lines are for illustrative purposes only. The peninsulas mentioned in the text are marked V, Vatnsnes; Sk, Skagi; Tr, Tröllaskagi; Fl, Flateyjarskagi; Tj, Tjörnes; Me, Melrakkaslétta.

Figure 8. Location of release (circles) and recapture locations (triangles) of tagged lumpfish which were at liberty for >250 days. Fish which were recaptured <50 km (top) and >50 km (bottom) from their tagging location are shown.

other areas, while others had a displacement distance of <50 km even after 50 DAL. The reasons for these movements, or lack thereof, are not entirely clear but could be related to the search for a suitable mate which is in possession of a suitable nesting site. In addition, and not mutually exclusive from the previous suggestion, this movement may be related to the possibility that they are batch spawners (Fulton, 1907) and have adopted a strategy of placing large distances between subsequent batches to spread the risk. However, detailed knowledge on the location and density of males when spawning actually takes place is lacking but it seems unlikely they need to travel hundreds of kilometres to find a mate. A more likely explanation is that these large-scale movements are related to homing behaviour, either natal homing or homing to where they had spawned previously (see below).

The movement of fish between different areas is likely to have been biased by the dates of the fishing season in different regions. Due to the restriction in relation to the breeding of eider ducks, fish were tagged later in the year in area B2 which meant that the fishing season was already over in the other areas so there was little chance of these fish being caught if they migrated away from this area. In addition, ~50% of the fish tagged in area B were

tagged after the season in that area had finished, in an attempt to estimate the number of fish which would return the following year. This probably explains why the recapture rate of area B was the lowest of any area and also had the highest proportion of fish which were recaptured in the area in which they were tagged. This difference in the timing of the fishing season may also have affected the number of fish which would have been recaptured in area B2 as the fish may have migrated to the area, spawned, and left before the fishing season would have begun.

It should be noted that no fish were tagged on the west coast of the Melrakkaslétta peninsula, thus all fish recaptured here would have migrated from other tagging locations, which suggests that this may be an important spawning area. The area of a high number of returns on the east coast of the Westfjords may also represent an important spawning area, with many fish recaptured in this area, which were both tagged here and had migrated from other areas. The high rate of recaptures in these area, may in part, be due to high fishing effort in the area, but areas of high fishing effort are usually due to high concentrations of fish.

A notable recapture was the fish which was recaptured at the island of Grímsey. This fish was tagged in area E1 then left the coastal area to make this journey. Unfortunately, no information on the spawning status of this fish was recorded on recapture. Had the fish spawned at Grímsey in a previous year (lumpfish aggregate in Grímsey during the spring so presumably they spawn here also) and was exhibiting homing behaviour? if so, why did it migrate to mainland Iceland before going on to Grímsey? Another

explanation may be that the fish had finished spawning and was migrating away from the coast via Grímsey. Fish which were recaptured and re-released demonstrate that lumpfish do not take the shortest route between their tagging and recapture position and may move in one direction and then double back. In fact for one fish, if the tagging and final recapture position were used, it would only have appeared to have moved <20 km; however, this fish moved from the eastern side of Skagi to the eastern side of Flateyjarskagi then back to the western side of Skagi, giving a total distance of over 200 km.

Most of the fish tagged were recaptured within ∼2 weeks of being released. This is similar to the results presented by Schopka (1974) and is unsurprising as the fish are released onto areas where they are being targeted by fishers. In contrast with the results from Schopka (1974), who reported that recaptures after 3 weeks were very low, in the present study, many fish were recaptured between 3 and 7 weeks after tagging. Very few fish were recaptured after 50 DAL but this is likely due to restrictions on the number of fishing days, which were either 50 or 62 days between 2008 and 2012. Schopka (1974) proposed that the fall in recapture rates after 3 weeks indicated the length of the spawning period for individual fish and thus fish would leave the spawning area after having completed spawning. However, it is difficult to conclude the length of the spawning period for lumpfish based upon tagging returns as the the length of time until spawning commences for the tagged fish is unknown. Most of the fish in Schopka (1974) were tagged from January to May; the maturity data collected during this study showed that a significant proportion (>10%) of fish at Stage 4 or 5 did not occur until mid and late May, respectively. This indicates that for many of the fish tagged in Schopka (1974), it would likely have been several months to weeks, depending on the month of tagging, before the fish would begin to spawn. In addition, there are indications that fish may remain in proximity to the spawning area for up to 2 weeks after spawning is completed (Grant, 2001). Thus the 3-week spawning period proposed by Schopka (1974) should be viewed with caution.

These results show that lumpfish are capable of swimming at speeds up to 49 km day^{-1}. Even though most of the estimated speeds were less than this, it must be considered that these swimming speeds were based upon the fish taking the shortest route between the two points. The fish which were recaptured and re-released show this is unlikely to be the case, it is also unlikely that the fish would have spent the entire time between tagging and recapture travelling between the two locations. Average swimming speeds have previously been estimated by Mitamura et al. (2011) who tracked lumpfish in Norway using acoustic transmitters and receivers. The maximum average swimming speed recorded was 1.7 km h^{-1} (40.8 km day^{-1}), which is similar to the results of the current study (49 km day^{-1}).

The tagging results support the findings from previous studies from Iceland and other areas, which indicate homing behaviour in lumpfish (Bagge, 1967; Schopka, 1974; Fréchet et al. 2011). The route taken by homing fish is unclear but this may be related to the movement of fish around the coast. The fish may migrate towards the closest land from their offshore feeding grounds and then migrate along the coast to their previous spawning area. It is interesting to note that fish recaptured after 250 DAL in areas E1–E3 were much more likely to be >50 km from their tagging location than fish recaptured in other areas. This suggests that areas E1–E3 may be utilized as a migratory pathway to a greater extent than as a spawning area. This is also supported by the fact that a higher proportion of fish tagged in area E1 and E3 (DAL <150)

were recaptured outside their tagging area in comparison with fish tagged in other areas. This is most notable in E4 where >90% of the tagged fish were recaptured in other areas. While this is an indication of habitat use, verification is difficult as this would require an estimate of the abundance of nests in the various areas, an estimate currently not available.

In Febuary–March, before arriving at the coast, female lumpfish are distributed throughout the continental shelf area north of 64°N. They are caught during the Icelandic groundfish survey with 95% being caught between 40 and 300 m (depth range of the survey is 20–500 m) (Sólmundsson et al., 2010). The fish which were tagged during this survey were recaptured in five of the seven different regions despite their tagging locations being in proximity of each other. This pattern is unsurprising given the migration of fish which were tagged on the spawning grounds which then proceeded to migrate around the coast. The results from the present study show similar results to Schopka (1974) who also tagged lumpfish in offshore areas of northern Iceland and found that lumpfish did not migrate to the closest spawning area but would sometimes be recaptured hundreds of kilometres from the tagging location.

The recapture rate vs. length at tagging shows that the fishery, as a whole, is selecting for smaller fish. The regulations in Iceland state the lumpfish can be targeted using nets with either a 267- or a 292-mm mesh size. The fishers may use all of one type or a mix of the two and this is recorded in the log books. In the years 2008–2013, 93.5% of fishers used 267 mm mesh size, 3.6% used 292 mm, and 2.9% used a mix (proportion of each net is unknown) (unpublished data, Marine Research Institute, Iceland). With such a high proportion using one net type, the selectivity presented here will closely resemble that of the 267 mm mesh size. However, the selectivity of the fishery has likely varied over time as the proportion of fishers using 267 mm mesh size in 1980 was ∼50% and gradually increased until ∼2008 where it has remained relativity constant (92–95%) until the time of writing (2014) (unpublished data, Marine Research Institute, Iceland).

There is now abundant evidence that lumpfish are capable of spawning on consecutive years (Schopka, 1974; Fréchet et al. 2011, Kasper et al. 2014); however, questions still remain of the proportion of the spawners which will do this and also if it is common for fish to spawn three times, or more. A single fish was reported by Schopka (1974) and two fish by Kasper et al. (2014) which had been recaptured after 2 years at liberty so these fish may have spawned twice or may have skipped a spawning season (e.g. Rideout and Tomkiewicz, 2011, Skjæraasen et al., 2012). There are anecdotal reports of dead lumpfish being caught by bottom trawls in spring after the spawning season, which is thought to indicate a high post-spawning mortality (Bagge, 1967). Two tags were returned from dead fish, one having been found on a beach and one being caught by a trawler; however, two dead fish tells us very little about post-spawning mortality. Thorsteinsson (1981) considered the low rate of return reported in Schopka (1974) to be a result of tagging mortality and tag loss. While the tags used in the current study were different from those used by Schopka (1974) (spun nylon vs. plastic disks attached with a nickel pin), tag loss is also suspected to be a problem here as there were signs of rusting on returned pins (Kasper et al., 2014), which has been reported previously (Forrester and Ketchen, 1955; Fréchet et al., 2011).

Using the same data as in the current study, Kasper et al. (2014) estimated post-spawning survival to be ∼10%; however, this estimate should be viewed with caution. In addition to the above-mentioned problem of tag loss, the growth of the fish will also

influence the return rate. With the fishery selecting for smaller fish (current study), the probability of the fish being recaptured is reduced due to growth. The age/spawning experience of the fish may also impact the results as post-spawning survival is likely to be lower for older/larger fish. There is also one order of magnitude difference between areas in the percentage of fish returning after 1 year at liberty making an estimation of survival rates difficult.

In considering an appropriate management strategy for a species, a good understanding of the population structure is essential, i.e. is the management unit a single population, several non-interbreeding populations or something in between? The lumpfish population is currently considered to be a single population. The question is, do the results from the current study support this single population hypothesis? With a significant proportion of fish moving from one area or region to another, this would seem to support the single population model. However, the homing behaviour noted may indicate some form of metapopulation (where there is significantly less interaction between patches than within a patch). There has been no investigation into the possibility of natal homing, and this homing behaviour may be where the fish had spawned previously rather than where they themselves hatched, so the juvenile stage may be a source of significant mixing between areas. As such, there is currently no evidence which supports the rejection of the single population hypothesis but the current study does not offer unequivocal evidence for the single population model.

If the current consideration of a single population is not correct and the lumpfish in Iceland is better described as a metapopulation, will the current management strategy have negative consequences on the population? If lumpfish in Iceland is made up of several subpopulations, then the fishing pressure would be spread across several of these subpopulations due to the following factors: (i) The lumpfish fishing season occurs from March until August, when many of the fish are migrating, thus catches likely consist of lumpfish which would have spawned in the area in which they were caught and also fish which would have migrated to other spawning sites. (ii) Due to the small size of the boats which participate in the fishery and as a result of the division of the coastal area, fishing will be spread along the coast. Due to the spreading of fishing effort over several subpopulations, the management of lumpfish as a single stock when in reality it is better described as a metapopulations is likely to have little detrimental impact on the population. However, as the catches from an area consist of fish from several of the subpopulations, decreases in specific subpopulations would be difficult to detect using catch data, and setting a TAC for each subpopulation would be unfeasible. Based upon the available information, the current practice of managing lumpfish as a single population is the most appropriate option.

The current study utilized data both from fish which were tagged during their migration to the coast, before the fishery had started, and fish that were tagged during the commercial fishery. The combination of this data produced a greater insight into the migration of lumpfish than would have been possible if only a single tagging source had been used. The fish tagged during the Icelandic groundfish survey gave an insight into how these fish dispersed around the coast and that the location of tagging seems to give no indication of where these fish will be recaptured. As these fish are not likely to be caught for at least 1 month giving the fish time to disperse, a low tagging effort can produce useful results. This tagging was however limited in its distribution covering only northwest Iceland. Future tagging studies should broaden the tagging effort to include west

and the north east Iceland. While tagging in the commercial fishery was disadvantaged by the high recapture rate during the first few days of release, thus requiring a high tagging effort, it did give insight into the movement of fish once they had reached the coast and how lumpfish, after reaching the coast, may still migrate several hundred km before they will spawn. This pattern would not have been obvious using the tagging data from the Icelandic groundfish survey alone.

The use of the Peterson disk tags appeared to be a suitable option for the tagging of lumpfish when recapture is expected within 1 year. However, due to corrosion, the nickel pins should be substituted with stainless steel (Forrester and Ketchen, 1955). There is currently a lack of knowledge on the juvenile phase of lumpfish. Tagging studies on juvenile lumpfish have been hampered by low return rates (Kasper *et al.*, 2014), which may be a result of low survival and(or) tag loss. Future studies should assess tagging methods on captive juvenile lumpfish as juvenile fish may "outgrow" the tag, which may result in the loss of the tag or have detrimental effects on the fish. Outgrowing of the tag may also be an issue with adult fish and may be also be factor in the low return rates after 1 year.

In conclusion, these results demonstrate that lumpfish are highly mobile fish capable of migrating large distances between offshore feeding areas and coastal spawning areas. When at the coastal area, they may migrate to other areas around the coast or remain close to the vicinity of tagging for up to 50 days. The extensive movements around the coast probably influenced the lack of genetic structure observed around Iceland (Pampoulie *et al.* 2014) and support the recommendation of a single TAC for lumpfish in Iceland.

Acknowledgements

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