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Conservation of spawning time between years in lumpfish *Cyclopterus lumpus* and potential impacts from the temporal distribution of fishing effort

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Abstract
Lumpfish, *Cyclopterus lumpus* L., has an extended ovary development period and a relatively long spawning season. It therefore seems unlikely that individuals spawning later in the season would be able to recover from spawning and develop their gonads in time to spawn during the early part of the season the following year. The hypothesis that individuals spawning early or late in a spawning season would spawn early or late the following year was tested using fish tagged in Iceland between 2008 and 2017. The tagging date and recapture date the following year were positively correlated with an average of 356 days at large (DAL). Fish sampled from the fishery indicate that tagging/recapture date gives an indication of spawning time. From this, it was concluded that spawning time in the current year can be used to predict spawning time the following year. As fishing effort was greatest at the end of April/beginning of May, it seems likely that fish that come to spawn at this time will be subject to a higher fishing mortality. Therefore, they will be less likely to spawn successfully than fish spawning earlier or later in the year. If spawning time is under genetic control, then this could have consequences for the spawning phenology of lumpfish.

KEYWORDS
coastal fishery, Iceland, ovary development, reproduction, reproductive phenology, roe fishery

1 | INTRODUCTION

The timing of reproduction has evolved to maximise the number of surviving offspring over the lifetime of the parent. At the population level, reproductive events may occur over a short period of time to take advantage of specific environmental conditions or may be protracted over several months (Sadovy, 1996). The temporal spread of these events is a product of both the number of reproductive events of an individual within a year, and the degree to which individuals across the population synchronise their reproduction. The timing of spawning is partially under genetic control (Otterå et al., 2012), but it can be influenced by the environment, nutritional status (Kennedy et al., 2010; Rideout & Tomkiewicz, 2011; Skjæraasen et al., 2009) and (or) social cues (Koizumi & Shimatani, 2016).

In many fish species, feeding and spawning areas are spatially segregated. Therefore, fish must migrate to spawn, which may bring them to areas more accessible to fishers (Jørgensen, Dunlop, Opdal & Fiksen, 2008). In addition, fish may form dense aggregations that are attractive targets for fishers (Claydon, 2004; Domeier, 2012; Sadovy de Mitcheson & Erisman, 2012). As the distribution of fishing effort is rarely homogeneous, there is the potential for selection that could impact the reproductive phenology of a population (Tillotson & Quinn, 2018). Management systems that lead to bias in fishing effort towards a specific period in the spawning season could potentially be problematic. The fishery for Pacific halibut *Hippoglossus stenolepis* (Schmidt) in the eastern Pacific Ocean is closed during the spawning season. However, in some years, the fishery reopens before spawning is complete. This results in late spawners suffering a greater fishing mortality than early spawners and could potentially result in the spawning season shifting to earlier in the year (Loher, 2011). If the majority of the fishing mortality of a species occurs during non-breeding times, when the populations consist of fish that spawn at different times, then the overall impact of bias during the spawning season is likely to be low. However, the effect of differential mortality in relation to spawning time is likely to be much greater for species in which a significant portion of mortality occurs during the spawning migration, for example Atlantic salmon *Salmo salar* L. (Consuegra, De Leániz, Serdio & Verspoor, 2005), or they are exclusively targeted during the spawning season, for example fish targeted primarily for their roe.

Lumpfish, *Cyclopterus lumpus* L., is a semi-pelagic (Kennedy, Jónsson, Ólafsson & Kasper, 2016) species that inhabits Arctic and sub-Arctic waters in the Northern Atlantic. Lumpfish spend their juvenile period in open water far from land. After reaching maturity and as the breeding season approaches, they migrate to coastal areas to spawn. When they migrate to the coast, their gonads are well developed, and they are targeted by fishers for their roe. In Iceland, female lumpfish are exclusively targeted by small coastal boats (<15 gross tonnage), which use large-mesh, bottom-set gillnets that are set in coastal areas with a depth generally <50 m and could be in areas as shallow as <10 m (Kennedy et al., 2019). Lumpfish in Iceland is documented to spawn from late March until mid-July, but as the fishery extends into August in some years, it is likely that spawning extends further (Kennedy, 2018). Divers have also observed lumpfish spawning in September (E. Bogason, personal communication, Strýtan Divecenter).

As vitellogenesis takes at least 8 months in lumpfish (Kennedy, 2018), this long development period could place a constraint on the spawning time the following year. If a fish spawns late in the season of the current year, then it seems unlikely it could recover from spawning and develop its gonads for spawning early in the season the following year. This suggests that fish that spawn early and late in the season will spawn early and late, respectively, the following year. The aim of the present study was to test this hypothesis using data from fish tagged during the lumpfish fishing season and recaptured the following year. A key assumption in the present study was whether capture in the fishery is indicative of spawning time as the ovary development stage of tagged or recaptured fish could not be assessed directly. Whether capture by the fishery is indicative of spawning time was assessed by examining the maturity stage of fish caught in the fishery using data from Kennedy (2018) along with additional sampling. In addition, the temporal distribution of fishing effort through time was examined and it is discussed how this may impact the spawning phenology of the population and how it influences the best time to tag to maximise recaptures the following year.

2 | MATERIALS AND METHODS

2.1 | Tagging of fish

Between 2008 and 2017, 10,700 female lumpfish between 29 and 56 (mean = 39.7, *SD* = 2.8) cm were tagged with Petersen disc tags (Figure 1) during 49 tagging events and released (Figure 2, Figure S1). These fish were caught during the commercial female gillnet fishery, or from commercial fishing vessels that were fishing outside the regulated period with permission from the Icelandic Directorate of Fisheries. As the nets were brought aboard, the fish were removed and placed in a water tank with flow-through sea water. Fish that showed no signs of damage and could swim normally were tagged and total length measured before release. Up until 2014, nickel pins were used to attach the tags. Between 2015 and 2017, approximately half of the fish were tagged with nickel pins and half with titanium pins.

The tags were printed with a contact phone number and a unique tag number, and when a recapture was reported, the fisher was asked for details on the capture date and location (latitude and longitude). The days at liberty (DAL) was defined as the number of days between release and recapture. The shortest distance between release and recapture, without crossing land, was measured using the distance tool in Google Earth (www.google.com/earth/) and termed displacement distance. This study is concerned with fish that were recaptured in the fishing season following the one in which they were tagged. Thus, fish with a DAL <300 days were excluded with exception of the analysis looking at recapture rate versus fishing effort (see below).

It was assumed that the tagging and recapture date are indicative of the spawning period of the fish in question. The specific date when these fish spawned, or would have spawned, either in the year they were tagged or recaptured, could not be determined. However, based upon data from Kennedy (2018), and through the additional sampling documented in the present study (see below), a significant portion of the fish captured in the fishery had ovulated oocytes (Results2.1), indicating they would spawn within hours of capture (Bobe, Jalabert & Fostier, 2008). In addition, many had almost

FIGURE 1 Female lumpfish with Petersen disc tag attached [Colour figure can be viewed at wileyonlinelibrary.com]

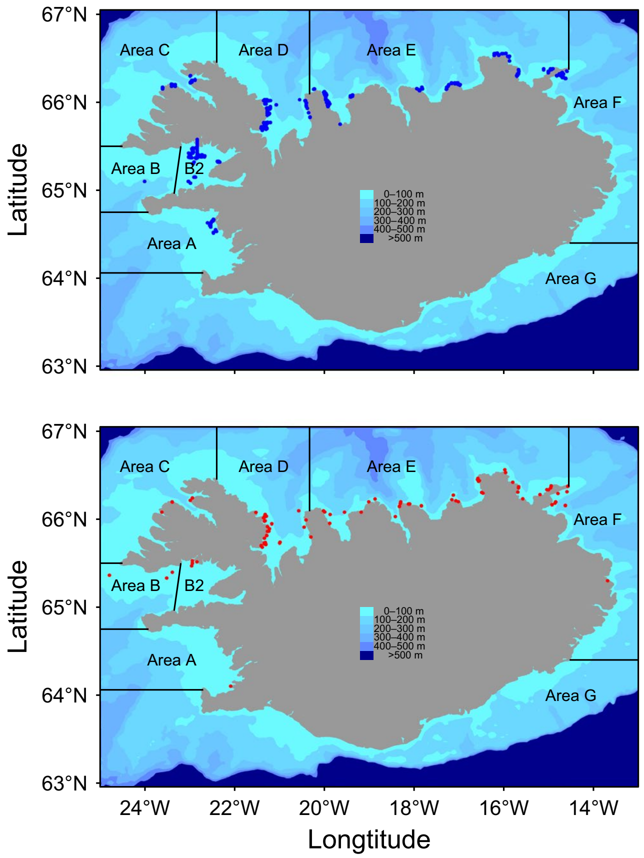

FIGURE 2 Map showing all fish tagged between 2008 and 2017 (top) and all fish recaptured >300 days at large between 2009 and 2018 (bottom). Lumpfish fishery management areas are shown [Colour figure can be viewed at wileyonlinelibrary.com]

completed vitellogenesis and that final maturation and spawning were imminent.

2.2 | Ovary development and maturity stages

To assess the composition of maturity stages of lumpfish captured by the commercial fishery, data presented in Kennedy (2018) (years 2014–2016), together with additional sampling (2017–2018), were used. This consisted of ovary samples collected from the commercial fishery (Table 1). Upon landing of the fish, they were stored on ice and dissected within 24 hr. Total length, and total body, liver, ovary and eviscerated carcass weight were measured for each fish. The ovary

TABLE 1 Year, time period in which samples were taken (D1, D2), the number of fish sampled (*n*) and minimum and maximum total length (*L*) of fish sampled

Year	D1	D2	*n*	*L*. min	*L*. max
2014	10/04	03/07	71	30	47
2015	24/03	22/05	120	34	48
2016	21/03	30/05	221	34	48
2017	31/03	07/06	200	34	50
2018	03/04	16/05	159	35	46

stage for each fish was assessed macroscopically using the maturity scale from Kennedy (2018) (Table S1), and ≈ 5 g of ovary tissue was preserved in 10% formalin. If the ovary was at macroscopic stage 3, then both a sample of ovary tissue and a sample of the ovulated eggs were taken and stored in separate tubes.

For each ovary sample, after separating the oocytes from the connective tissue, they were photographed under a dissecting microscope at ×7.0 magnification. The images were analysed using ImageJ software (v. 1.49b, National Institute of Health, http://imagej.nih.gov/) and ObjectJ plug-in (v. 1.03 s, University of Amsterdam, http://simon.bio.uva.nl/objectj/), which measured the diameter of all oocytes >400 μm present in the image. Based upon the oocyte size distribution, the ovaries were assigned an oocyte size frequency distribution (OSFD) maturity stage described in Kennedy (2018) (Table S1) and the leading cohort (LC) oocyte diameter, the average diameter of the largest 10% of oocytes, was calculated according to the methodology in Kennedy (2018).

2.3 | Distribution of fishing effort

The lumpfish fishery is regulated with both spatial and temporal restrictions. Iceland is divided into seven regions (A–G) with region B, which covers Breiðufjórður, divided into two sub-regions, the outer (B1) and inner (B2) areas (Figure 2). The skipper of a boat selects a fishing region before their fishing period begins and cannot fish outside of the region they select, but they can cross between B1 and B2 assuming both areas are open. The opening season and closing season differ between areas. While the specific opening and closing dates of the fishery differ between years, in general, regions D-F open late March, regions A and G and sub-region B1 open at the beginning of April and sub-region B2 opens late May. Each region is open for ≈90 days. Each boat can only fish for a limited number of consecutive days within the opening and closing dates of the chosen region and must notify the Directorate of Fisheries when they will begin fishing. The number of consecutive days varies between years: between 2008 and 2017, this has been between 32 and 62 days.

A typical fishing pattern for a lumpfish boat is that the fisher will lay all the nets, which in most cases is the maximum number allowed by the regulations, on the first day of their fishing period. The fisher will then check approximately one half of the nets after 2–3 days, and the rest of the nets will then be checked 2–3 days after this. This pattern will continue throughout the fishing period of that boat. All of the nets will then be hauled on the last day of the boats fishing period. All the nets will be in the water for the entire fishing period unless bad weather is predicted; in this case, the nets will be hauled and redeployed after the bad weather has passed. A fisher may take up all the nets and stop fishing before they have used all of their allocated days if the catch has been low and they no longer consider it economically viable to continue fishing.

To assess the distribution of fishing effort through the fishing season, the number of fishing boats that were actively fishing is calculated for each day of the year. A boat was considered to be actively fishing between the date it gave to the Directorate of Fisheries as

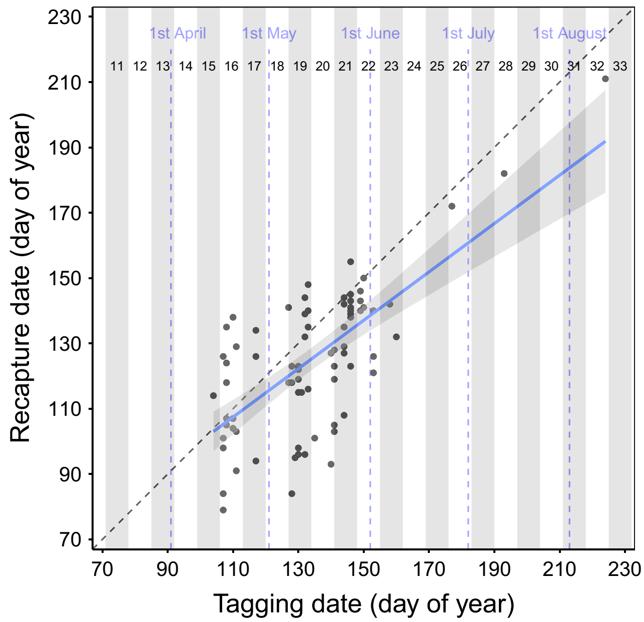

FIGURE 3 Recapture date versus tagging date of tagged fish recaptured >300 days at large. Solid line shows linear regression line; dashed line shows 1:1. Week numbers with 1 January as a Monday are shown [Colour figure can be viewed at wileyonlinelibrary.com]

its start date and the date of its last landing using lumpfish nets of that year.

To maximise the number of recaptures the following year, it would appear prudent to tag close to the end of the fishing season to avoid tagged fish being recaptured within a short time of being released. To evaluate whether this is correct, the recapture rate for each tagging event was calculated. Recapture rate at differing levels of fishing effort on the day of release and at 356 days after release (mean DAL for fish >300 DAL) was investigated using linear regression or generalised, least squares models (using nlme package in R [Pinheiro, Bates, DebRoy & Sarkar, 2011]) if heteroscedasticity violations occurred when using linear regression.

3 | RESULTS

A total of 89 fish were recaptured >300 DAL, with a mean DAL of 356 days. Recapture date was positively correlated with tagging date (linear regression $F = 75.3$, $n = 89$, $r^2 = 0.55$, $p < 0.001$) (Figure 3). The slope of the regression analysis was close to, but significantly different from, 1 (one-sample Students' *t* test, $df = 87$, $t = -2.12$, $p = 0.04$). Mean displacement distance was 69 km (min–max = 1–447).

Owing to the small number of fish that were released/recaptured later than week 24, there is the possibility these few fish could be highly influential within the linear model applied. To ensure that this was not the case, the five fish tagged/recaptured after week 24 were omitted from the analysis and the model parameters recalculated. In addition, Cook's distance was calculated for each point (which included the five fish previously mentioned) and fish with a Cook's distance > N/4 were omitted ($n = 6$). Neither of these tests significantly impacted the resultant model, and the significance value was of a similar level to the original model, that is $p < 0.001$.

In the fish sampled from the commercial fishery, a mean of 52% (min–max, 10%–86%) had ovulated eggs in their ovary or had spawned at least one batch of eggs (Figure 4). The LC of fish at OSFD maturity stage 3 was similar to that of fish with ovulated eggs in their ovary (Figure 5).

Fishing effort from 1980 until 1997 had a unimodal distribution, and the distribution of effort before and after the peak was roughly symmetrical (Figure 6, Figure S1). Fishing effort tended to peak between days 130 and 145 (Figure 7). From 1998, the distribution of fishing effort shifted to a more asymmetrical distribution and tended to peak earlier, between days 110 and 130. The shift in the distribution of fishing effort was not due to an earlier opening of the fishery as the opening date was generally later between 1998 and 2017 than the period between 1980 and 1997 (Figure 7).

Recapture rate of fish <300 DAL and >300 DAL was positively correlated with fishing effort on the day they were released (linear regression, $F = 27.75$, $n = 49$, $r^2 = 0.15$, $p < 0.01$) and the fishing effort 356 days after they were released (generalised least

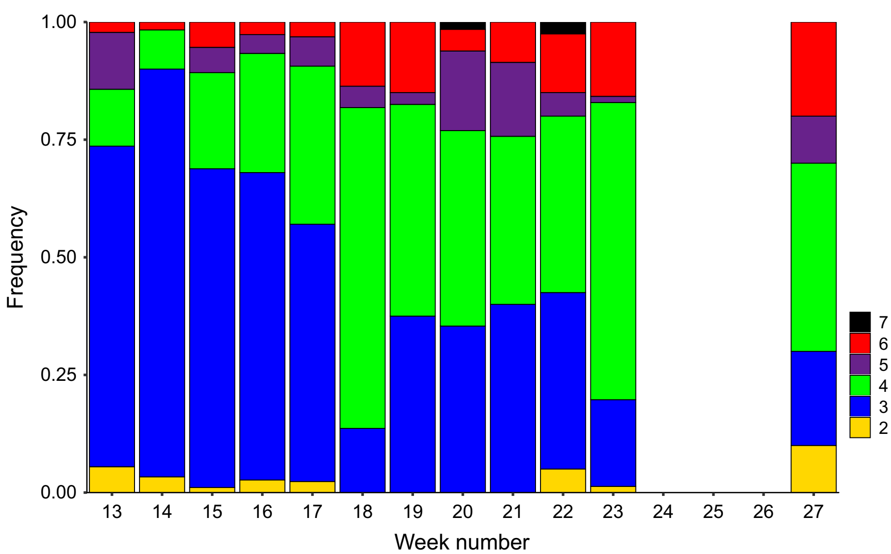

FIGURE 4 Proportion of fish sampled in the commercial female lumpfish fishery at each oocyte size frequency distribution (OSFD) maturity stage versus week of sampling [Colour figure can be viewed at wileyonlinelibrary.com]

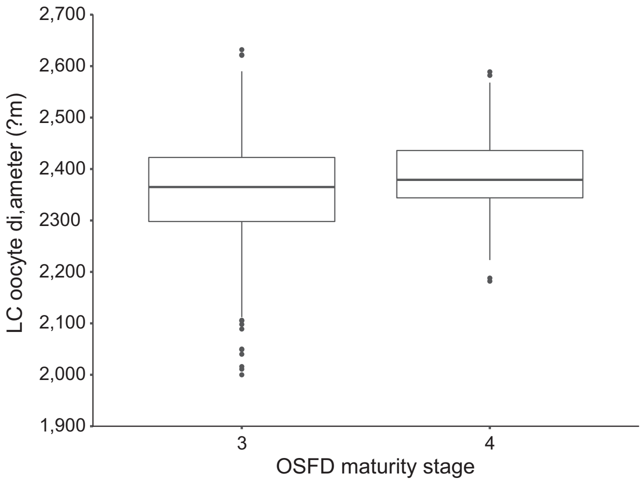

FIGURE 5 Boxplot of LC oocyte diameters for fish caught in the commercial female lumpfish fishery at oocyte size frequency distribution (OSFD) maturity stages 3 and 4

squares linear regression, $F = 9.18$, $n = 48$, $p < 0.001$), respectively (Figure 8).

4 | DISCUSSION

Lumpfish are not only known to return to areas close to where they spawned the previous year (Kennedy, Jónsson, Kasper & Ólafsson, 2015), but as demonstrated by the present study, they will also return at a similar time. This is likely to be partly a consequence of the time needed for vitellogenesis. Spawning is an energy intensive activity with lumpfish losing 30%–35% of their weight due to the expulsion of the eggs themselves (Hedeholm, Post & Grønkjær, 2017). Thus, time will be needed for the fish to recover and rebuild reserves. At least, a further 8 months are then needed for vitellogenesis. As a consequence, a fish spawning in August is unlikely to be ready for spawning until a similar time the following year.

It could be argued that spawning takes place every 2 years, that is they skip spawning (Rideout & Tomkiewicz, 2011), which would give lumpfish ample time to rebuild reserves and spawn at an earlier date during its next spawning event. However, the present study exclusively deals with fish that were recaptured 1 year after they were tagged. From this, it can be concluded that if a lumpfish spawns in two consecutive years, then spawning time will be similar. However, this conclusion cannot be drawn for individuals that skip a year. The current data set is based upon >10,000 fish tagged over a period of 10 years, and not a single fish was recaptured >2 years after having been tagged. This could mean that spawning over more than 2 years is extremely rare and that skipped spawning is rare or that almost all tags are lost after 2 years.

One question arises: how does the timing of the first spawning come about? Is it genetic, or a result of environmental conditions? Spawning time of individuals in several species is known to be influenced by genetics (Otterå et al., 2012; Quinn, Peterson, Gallucci, Hershberger & Brannon, 2002; Su, Liljedahl & Gall, 1999). However, the decision about when to initiate oogenesis is under the influence

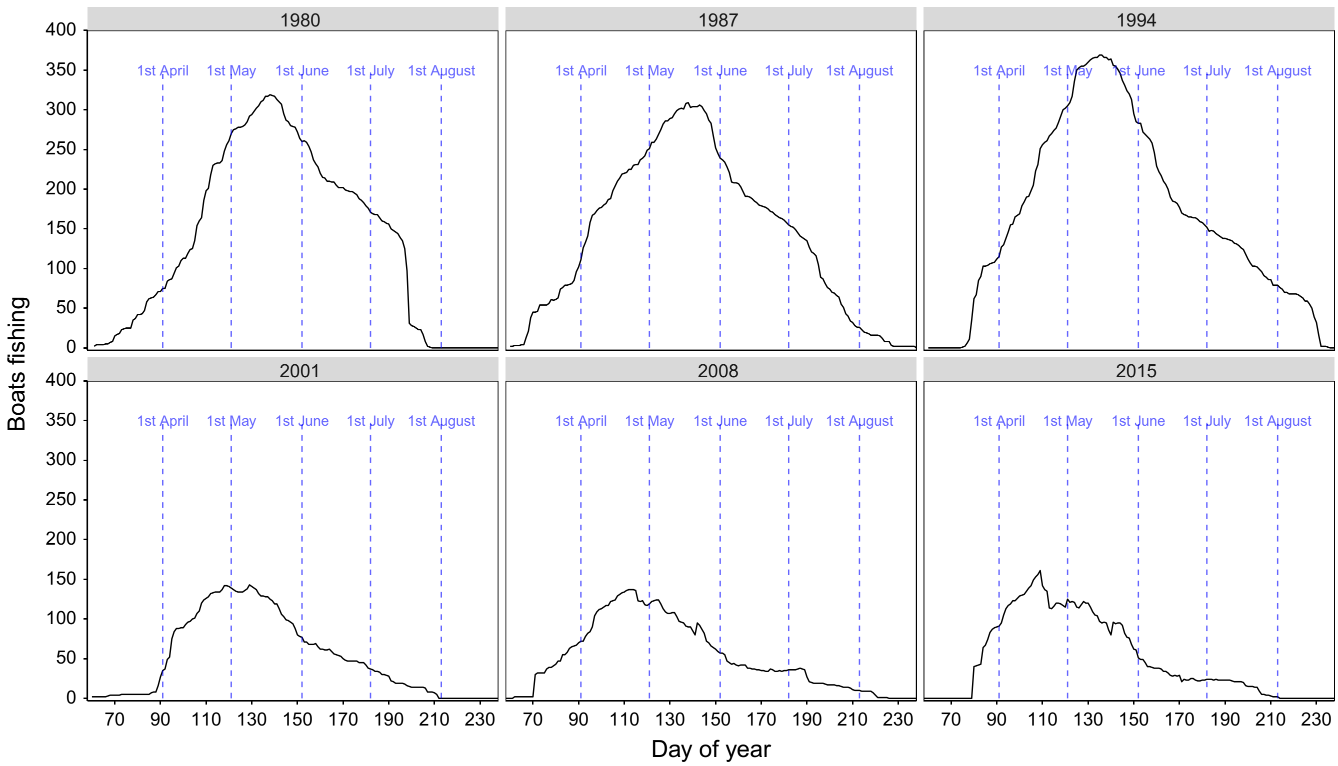

FIGURE 6 The distribution of fishing effort, measured as number of boats fishing, through the fishing season for selected years between 1980 and 2017. All years can be found in Figure S1 [Colour figure can be viewed at wileyonlinelibrary.com]

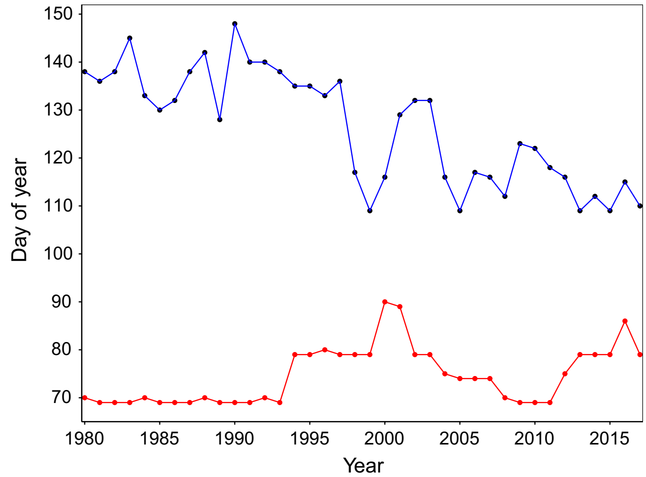

FIGURE 7 The date at which the fishing effort peaked each year (blue line) and the date at which the fishing season opened (red line) between 1980 and 2017 [Colour figure can be viewed at wileyonlinelibrary.com]

of a number of environmental cues, such as photoperiod and temperature, but can also be affected by the internal state of the individual (e.g., energy reserves). The actual date of spawning can then be affected by the rate of ovarian development, with both lower temperatures and lower food availability postponing spawning (Kjesbu, 1994). Juvenile lumpfish are distributed over a large area, from the southern tip of eastern Greenland to Svalbard in the Arctic (ICES, 2017). With such a wide distribution, there will be variability in the conditions encountered by individuals that could affect ovary developments rates and lead to a wide range in spawning time, but currently this remains poorly understood.

An important assumption in the present study is that capture in the fishery gives an indication of spawning time. Over the course of the season, a mean of 52% of fish had either ovulated oocytes in their ovary or were between batches. Thus, spawning would either take place imminently, or they had recently spawned one batch of eggs. The remaining proportion consisted of fish at OSFD stage 3. Oocyte size during vitellogenesis gives an indication of the progress through this process and when spawning will occur (Kjesbu, 1994). When vitellogenesis is complete, oocytes go through final maturation and ovulation (Tyler & Sumpter, 1996). After ovulation, the eggs of most species of fish go through a rapid (a few hours) decrease in quality (Bobe et al., 2008); thus, spawning would likely take place soon after ovulation. The LC oocyte diameter of fish at OSFD stage 3 was similar to the LC oocyte diameter of fish with ovulated eggs. This indicates that vitellogenesis was almost complete. Ovulation would then occur and spawning would soon follow. Based upon this information, the assumption that capture date gives an indication of spawning time is considered reasonable.

There is, however, substantial variation between the recapture dates of fish that were spawned at a similar time. This will be partially linked to capture date giving only an indication that spawning events are close, but it is not definitive. Some fish may have been tagged

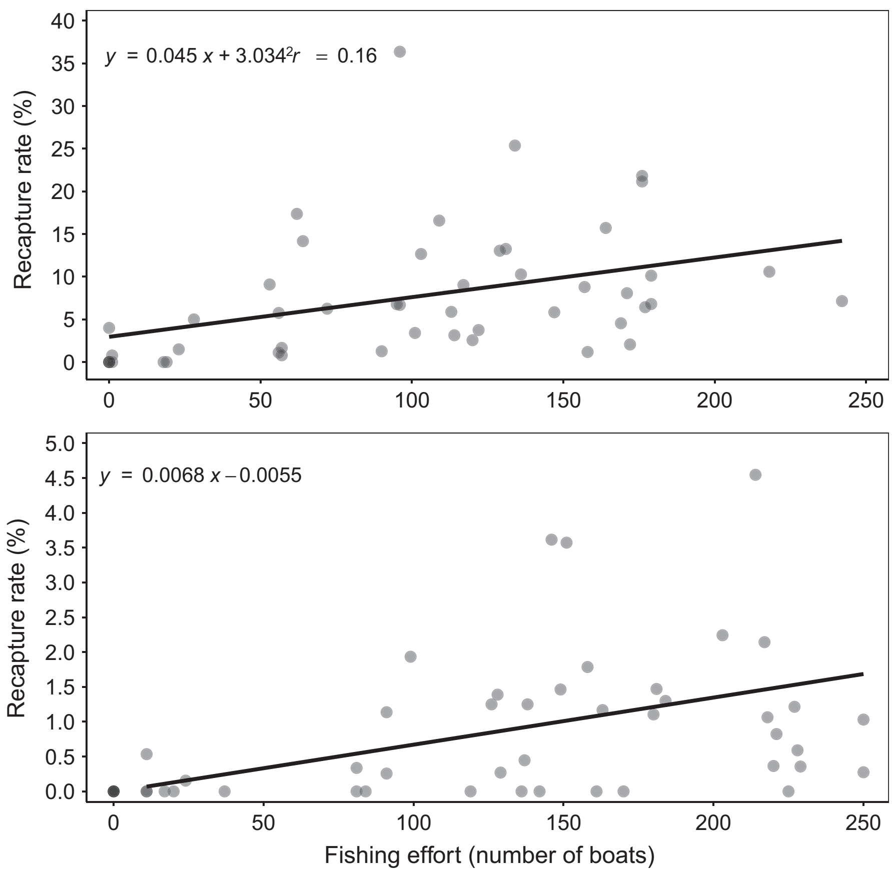

FIGURE 8 The recapture rate of tagged fish that were recaptured <300 days at large (top) and >300 days at large (bottom) vs. fishing effort on the day the fish were tagged and fishing effort 356 days after the fish were tagged, respectively. Line shows linear regression model (top) and linear model fitted using generalised least squares (bottom) along with the equation of the model and r^2 value for the linear regression model

several weeks from spawning their first batch, and others may have been tagged just before spawning their second batch. The same was true when they were recaptured. In addition, as spawning time is influenced by multiple factors, variations in the relationship are to be expected. Given the significant positive relationship, even after excluding fish tagged after week 24, suggests that spawning time in 1 year, even if it does not influence it directly, gives an indication of spawning time 1 year later.

Fishing effort over the fishing season is uneven with a peak around mid-May from 1980 to 1997, which shifted to the end of April/beginning of May in 1998. If spawning time is at least partially genetically determined, as is found in other fish species, then this uneven distribution of fishing effort could impact the temporal distribution of spawning in the population. The closer the time of spawning events and the time of peak fishing effort, the greater the chance a fish has of being caught in the fishery and not being able to spawn. To say it another way, fish with a greater temporal distance between spawning and the peak in fishing effort will have an increased likelihood of spawning successfully and passing on their genes to the next generation. Thus, over time, if spawning time is under genetic control, it is expected that spawning of the population will drift towards periods when fishing effort is low.

As lumpfish are only targeted by fishers during the spawning period, this bias in fishing mortality is likely to have a greater impact than on other species where only a small portion of fishing mortality occurs during the spawning period. However, the reason lumpfish spawn over such an extended period is in need of further investigation. For this reason, it is difficult to predict the implications of the current fishing pattern. While it would be possible to tailor management to spread fishing effort more evenly, this is unlikely to be popular amongst fishers. As the season progresses, the growth of seaweed becomes problematic as this becomes entangled on the net affecting its efficiency and fishers have to spend a greater amount of time cleaning their nets during hauling. Many fishers that participate in the lumpfish fishery also take part in the coastal jig fishery, which runs from May to August. Therefore, extensive overlap between the lumpfish fishery and the jig fishery is undesirable.

Several tagging events at the end of the fishing season yielded no recaptures, and the results of the present analysis reveal the likely reason for this. During mid-August in 2010 and 2011, a large number of lumpfish were tagged in Breiðufjörður, but the fishing season ended in early August in the following years. Given that lumpfish tend to return to areas where they spawned previously and at a similar time to the year before, the lack of recaptures is unsurprising.

Despite greater numbers of fish being recaptured within a short time if tagged during a period of high effort, recapture rate the following year is positively correlated with fishing effort 356 days after tagging. Given that the date of peak fishing effort has been relatively constant between years in the past decade, the best strategy to maximise recaptures the following year would be to tag fish when fishing effort peaks, that is around the end of April, beginning of May.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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