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Intra- and interannual variation in fecundity and egg size of lumpfish (*Cyclopterus lumpus*) in Iceland

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Abstract—Intra- and interannual variability of fecundity and egg size of lumpfish (*Cyclopterus lumpus*) were assessed for 2009 and for 2014–2019 and compared with fecundity estimates from 1967 and 1969. Downregulation of fecundity was apparent throughout ovary development, but the intensity was reduced close to spawning. The fecundity of fish spawning later in the year was higher than that of fish that spawned earlier. Carcass weight was a better predictor of fecundity than length. The model was improved through the addition of liver weight, but this led to an increase of <1.0% in the explained variance in fecundity. Variation in fecundity between the periods studied (2009 and 2014–2019) was low; however, fecundity in these study periods was higher than in 1967 and lower than in 1969. Whether these differences were due to differences in methods could not be ruled out. Average egg diameter was positively correlated with fish size and decreased from the first to the second batch, and only limited variation between years was observed in this characteristic.

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The number of eggs produced by an individual fish influences the reproductive potential of the population (Trippel, 1999); however, information on fecundity and the temporal and spatial variability in this trait is lacking for many fish species. Collection of information on fecundity is not routine for most fish stocks, and spawning stock biomass is generally used as a proxy for total egg production and reproductive potential, despite indications that total egg production and reproductive potential may not be proportional to spawning stock biomass (Marshall et al., 1998). Because fecundity is not routinely estimated, fecundity estimates from a single year, or a small number of years, may be used to estimate annual changes in total egg production (Gundersen et al., 2000; Blanchard et al., 2003; Mehault et al., 2010). This use of temporally limited fecundity data may be problematic because of potential variability in fecundity between years (Rideout and Morgan, 2007).

The lumpfish (*Cyclopterus lumpus*) (Fig. 1) is a semi-pelagic species that inhabits temperate and Arctic regions of the North Atlantic Ocean. In the eastern Atlantic Ocean, it ranges from 80°N, around Svalbard, Norway (Eriksen et al., 2014), to 50°N in the English Channel (Ellis, 2015). In the western Atlantic Ocean, this species ranges from 56°N on the western coast of Greenland to around Newfoundland, Canada, and as far south as New England at about 42°N (Gregory and Daborn, 1982; Rackovan and Howell, 2017). Outside of the spawning period, juveniles and adults are distributed over open water, generally in the upper 50 m of the water column (Holst, 1993; Rosen and Holst, 2013) with adults migrating to coastal areas to spawn as the spawning period approaches.

Male lumpfish migrate to the coast before females, presumably to seek out and establish territory and spawning sites in preparation for the arrival of females. In Iceland, males arrive in January–February, and most females appear in March. Lumpfish spawn around Iceland from January through August; however, an individual fish will spawn only 2 batches of eggs with approximately 10–14 d between spawning events (Fulton, 1907; Bolton-Warberg[1]; Kennedy, 2018). Although

[1] Bolton-Warberg, M. 2018. Personal commun. Ryan Inst., Natl. Univ. Ireland, University Rd., Galway H91 TK33, Ireland.

Figure 1

Photograph of a female lumpfish (*Cyclopterus lumpus*) collected at Skagaströnd, Iceland, in 2014 from the landings of the female lumpfish fishery that operates in Húnaflói Bay.

females approach the coast of Iceland in spring, they remain in deeper water (~50–300 m) until they are very close to spawning (Kennedy and Jónsson, 2017). Lumpfish spawn as deep as ~40 m to as shallow as a few meters below the low tide mark (Fulton, 1907; Todd et al., 2018). When ready to spawn, a female seeks out a male and lays her eggs in its nesting site. A male will then care for and defend the eggs until they hatch (Fulton, 1907). It is during this time, when they are in coastal areas, that females are targeted by a commercial fishery for their roe.

The precise timing of when ovary development begins in lumpfish is not known. However, vitellogenesis in preparation for spawning the following year is already underway in July (Kennedy, 2018). Therefore, ovary development takes at least 8 months to complete. During early vitellogenesis, there is a single mode of oocytes within the ovary. When the oocyte diameter of the leading cohort (LC) reaches approximately 2.0 mm, a hiatus forms in the oocyte distribution creating 2 groups of oocytes. One group consists of small oocytes (diameters <1800 µm) that are not spawned and presumably become atretic and are reabsorbed; this group is referred to as the *non-spawning group* (Kennedy, 2018). The other group comprises large oocytes (diameters >1800 µm) and is considered the *spawning group* because its oocytes will be spawned during the current spawning season. A second hiatus forms within the spawning group, creating 2 batches of oocytes that are spawned separately. Because no oocytes are recruited into the vitellogenic pool after spawning has begun, the lumpfish is considered a determinate spawner (i.e., the maximum potential fecundity is set before spawning has begun). Therefore, it is possible to determine potential fecundity of lumpfish by estimating the number of oocytes within the spawning group. However, this maximum potential fecundity may not represent realized fecundity (the actual number of eggs spawned) because fecundity may be reduced as a result of downregulation, the process whereby the number of developing oocytes is reduced as ovary development progresses.

The aim of this study was to assess the potential fecundity of lumpfish in Iceland and how it varies with ovary development, within the spawning season and between years. The fecundity estimates from this study were compared with historical estimates made in 1967 and 1969. Because lumpfish spawn only 2 batches of oocytes and the batches are easily distinguished and do not hydrate their eggs, we took the opportunity to assess variation in egg size between individuals, batches, and years.

Materials and methods

Collection of samples

Lumpfish were sampled during scientific surveys and from landings of the commercial fishery for female lumpfish during 2009 and 2013–2019 (Table 1, Fig. 2). The Icelandic groundfish surveys took place annually during autumn (September–October) and spring (February–March). The samples collected from the commercial fishery were landed in 3 harbors: Skagaströnd, Stykkishólmur, and Þórshöfn. The fish landed at these harbors are caught in Húnaflói Bay, in Breiðafjörður, and on the northern coast of Langanes, respectively (Fig. 2). Fish landed in Skagaströnd accounted for 96% of the fish sampled from the commercial fishery. Lumpfish are known to move between these areas during the spawning season; therefore, taking fish from different areas likely did not affect results of this study (Kennedy et al., 2015).

During surveys, ovaries were sampled from fish within 1 h of capture. Fish collected from the fishery were covered in crushed ice upon landing, and ovaries were sampled within 24 h. For each fish, total length (to the nearest centimeter) and total body, carcass, liver, and gonad mass (with a precision of 2 g) were measured. For fish caught in the fishery, mass of the stomach contents and mass of the stomach and intestines were measured. A macroscopically assessed ovary developmental stage (Kennedy, 2018) (Table 2) and a *spawning year*, the calendar year in which it was next expected to spawn, was assigned to each fish.

Ovary sampling

All tissue and oocyte samples were placed in 45-mL tubes containing 10% buffered formalin, but the sampling varied depending on the developmental stage assigned because of differences in the organization of the ovary. Ovaries at the *developing* stage are homogeneous, and ovaries at the stage called *spawning 1* are not. At the developmental stage spawning 1, ovulation of the first batch of eggs has occurred; therefore, both developing oocytes and ripe eggs are present within the ovary (Kennedy, 2018). The developing oocytes are located in the dorsal area of the ovary, while the eggs are located in the ventral area. For fish classified as in the developing stage, 4–6 g of ovarian tissue was taken from the caudad area of the ovary. For fish at the stage spawning 1,

Table 1

Summary of information for female lumpfish (*Cylopterus lumpus*) collected around Iceland from groundfish surveys conducted in spring (February–March) and autumn (September–October) and from landings of the commercial fishery in 2009 and 2013–2019 and for lumpfish examined during previous studies in 1967 and 1969 (Schopka, 1970; Myrseth, 1971). Information includes year, source of fish sampled or of data, start and end dates of sampling, mean size and size range of fish sampled in total length (TL), number of lumpfish sampled (n), and the number of lumpfish with ovaries assigned to each stage of oocyte size frequency distribution (OSFD). The sum of the number of lumpfish with ovaries at each OSFD stage is not always equal to the total number of sampled fish because some fish had ovaries for which the OSFD stage was ambiguous and, therefore, were excluded from all analyses. No lumpfish had ovaries at OSFD stage 1.

Year	Sample or data source	Start date	End date	Mean size (cm TL)	Size range (cm TL)	n	OSFD stage				
							2	3	4	5	6
1967	Schopka	7 April	28 April	42	37–51	48		48			
1969	Myrseth	1 May	1 May	42	35–48	50		50			
2013	Autumn	2 Oct.	9 Oct.	39	32–45	16	12				
2014	Autumn	5 Oct.	18 Oct.	39	32–47	30	29				
2015	Autumn	09 Oct.	1 Nov.	39	31–51	54	50				
2014	Spring	1 Mar.	16 Mar.	40	34–49	50	29	19			
2015	Spring	4 Mar.	15 Mar.	40	34–48	65	37	28			
2016	Spring	26 Feb.	18 Mar.	40	34–49	92	63	29			
2017	Spring	27 Feb.	13 Mar	41	34–53	198	99	94		3	
2018	Spring	10 Mar.	21 Mar	40	33–47	84	44	38		2	
2009	Fishery	5 May	3 June	38	31–48	172		172			
2014	Fishery	10 April	3 July	40	30–47	71	3	32	20	8	7
2015	Fishery	24 Mar.	22 May	41	34–48	120	5	77	26	5	7
2016	Fishery	21 Mar.	30 May	40	34–48	221	8	118	70	9	14
2017	Fishery	31 Mar.	7 June	41	34–50	200	1	76	88	15	17
2018	Fishery	3 April	16 May	39	35–46	159		93	47	13	6
2019	Fishery	4 April	21 May	41	35–51	242		154	60	11	12

a sample of ovarian tissue containing developing oocytes and a sample of eggs were taken and stored in separate tubes. A sample of eggs and a section of ovarian tissue were taken from fish at developmental stage *spawning 2* and were stored in the same tube. At the stage spawning 2, the second batch of eggs has been ovulated, and the ovary is again homogenous.

For fish sampled in 2009, fecundity was estimated by using the gravimetric method, and ovaries were not preserved in formalin. A single sample of ~5 g was weighed with a precision of 0.0001 g, and the number of oocytes within the sample was counted. These measurements were used to calculate the oocyte density, which was then used with the fresh ovary weight to calculate fecundity.

Calibration of an auto-diametric method

For fish sampled in 2013–2019, fecundity was estimated by using a combination of gravimetric and auto-diametric methods (Thorsen and Kjesbu, 2001). Calibration between the gravimetric and auto-diametric methods was done with samples collected during the autumn groundfish survey conducted in 2014 (number of fish sampled [n]=30) and the spring survey conducted in 2015 (n=65), along with samples collected from the fishery in 2015 (n=61). Because of the timing of sampling, few fish had oocytes with diameters of 0.8–1.2 mm; therefore, fish from the autumn groundfish survey conducted in 2015 with a gonadosomatic index >5 (n=12) were also included in the calibration.

The samples analyzed gravimetrically were collected in pre-weighed tubes, and as a result, the initial weight of the ovarian tissue was known. The ovarian tissue was blot-dried and weighed, and the decrease in weight due to preservation was calculated. Three subsamples were then taken and weighed, either at a precision of 0.0001 g for the samples taken from the autumn survey or to the nearest 0.001 g for samples taken from the spring survey and the fishery. The oocytes in each subsample were separated from the connective tissue by using fine paintbrushes and were photographed under a dissecting microscope; a magnification of 12.5× was used for the autumn survey samples, and a 7× magnification was used for samples from the spring survey and fishery. The images were then analyzed with ImageJ software (vers. 1.49b; Rasband, 2014) and the ObjectJ plug-in (vers. 1.03s, University of Amsterdam, available from website), which were used to measure the diameter of all oocytes present in each image. Light level was standardized by using distilled water and a gray level set at 207 (±2). Ovaries were

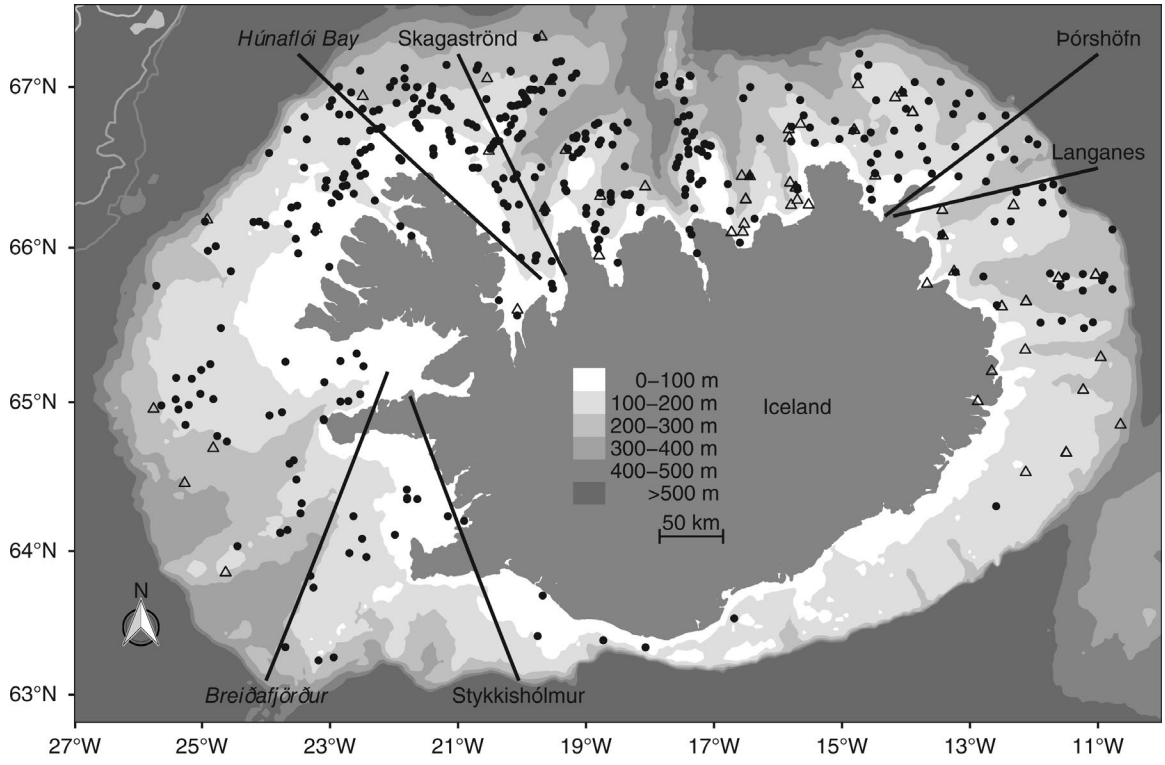

Figure 2

A map of locations where lumpfish (*Cyclopterus lumpus*) were sampled during groundfish surveys conducted around Iceland in the spring (circles) and autumn (triangles) in 2013–2018. Fish also were sampled in 2009 and 2014–2019 from landings of the commercial fishery at 3 harbors: Skagaströnd, Stykkishólmur, and Þórshöfn. Other locations mentioned in the main text are marked. The shades of gray indicate depth contours in 100-m intervals around the island nation.

assigned a stage of oocyte size frequency distribution (OSFD) (Kennedy, 2018) (Table 2). An OSFD stage could not be assigned to a small number of ovaries because the OSFD was ambiguous; these fish were excluded from all analyses. By using the data from the image analysis, several characteristics were calculated for each subsample and ovary, including average oocyte diameter, LC oocyte diameter, and oocyte density.

Average oocyte diameter For ovaries assigned to OSFD stage 2, the average diameter was calculated from all oocytes ≥400 µm. For ovaries assigned to OSFD stages 3, 4, and 5, average diameter was calculated for all the oocytes in the spawning group. Average oocyte diameter was not calculated for oocytes at OSFD stage 6. No lumpfish had ovaries at OSFD stage 1.

Leading cohort oocyte diameter For ovaries assigned to OSFD stage 2, the LC oocyte diameter was calculated from the largest 10% of oocytes ≥400 µm. For ovaries assigned to OSFD stages 3 and 5, LC oocyte diameter was calculated from the largest 10% of oocytes in the spawning group. Leading cohort oocyte diameter was used as an indicator of the progression of ovary development (Kjesbu, 1994). Leading cohort oocyte diameter was not calculated for ovaries at OSFD stages 4 or 6.

Oocyte density of subsamples For ovaries assigned to OSFD stage 2, the oocyte density of the subsamples was from the number of oocytes ≥400 µm in the subsample divided by the weight of the subsample. For ovaries assigned to OSFD stages 3, 4, and 5, the oocyte density of the subsamples was calculated from the number of oocytes in the spawning group divided by the weight of the subsample. Oocyte density of each ovary was estimated by taking the average oocyte density of the 3 subsamples. Oocyte density of the developing oocytes of ovaries at OSFD stage 4 (in which the ovary contains developing oocytes and ripe eggs) was estimated to investigate whether the number of batches present within the spawning group affected the relationship between oocyte diameter and oocyte density. Oocyte density was not calculated for ovaries at OSFD stage 6.

Some ovaries from the autumn survey contained a small number of residual eggs that were not spawned; these samples were excluded from the calibration between

Table 2

Descriptions of the macroscopically determined stages of ovary development, or maturity, and the stages of oocyte size frequency distribution (OSFD) used to assess lumpfish (*Cyclopterus lumpus*) collected around Iceland from groundfish surveys and from landings of the commercial lumpfish fishery during 2009 and 2013–2019. This table essentially is reproduced from Kennedy (2018).

Macroscopic stage	Description	OSFD stage	Description
Immature	Ovary is small, and no developing oocytes are visible.	1	Ovary contains only previtellogenic oocytes.
Developing	Ovary has increased in size and is easy to distinguish in the body cavity. Oocytes within the ovary are clearly visible. Ovary can be orange, purple, or green. A small amount of fluid may be close to the oviduct on the ventral area of the ovary; this fluid should not be confused with the large amount of viscous ovarian fluid and eggs seen in the spawning stage.	2	The oocyte size frequency distribution indicates a single group of oocytes within the ovary with diameters of almost all oocytes <1800 µm. Distribution is unimodal and, as ovary development progresses, becomes negatively skewed.
		3	A hiatus has formed in distribution at diameters around 1400–1600 µm, separating oocytes into 2 distinct groups. The group of large oocytes (with diameters typically >1800 µm) has a bimodal distribution, and the distribution of the group with small oocytes (≤1800 µm) is variable. In a small number of cases, the small oocytes may not be present.
Spawning 1	Separation in the ovary is clear. There are developing oocytes in the dorsal area of the ovary and ripe eggs in the ventral area of the ovary. The developing oocytes are connected to ovarian tissue. The eggs look "wet," are not connected to the ovarian tissue, flow freely within the ovary, and are bathed within a viscous ovarian fluid.	4	Ovary contains developing oocytes and ripe eggs. The eggs are larger than the developing oocytes. Both the eggs and developing oocytes have a unimodal size distribution. There may also be a group of small oocytes (diameters <1800 µm) with a variable size frequency distribution.
Partially spent	Ovary is similar in appearance to, and difficult to discern from, an ovary in the developing stage.	5	There may be 1 or 2 groups of oocytes present within the ovary. A group of large oocytes (with diameters typically >1800 µm) has a unimodal distribution, and the size frequency distribution of the group with small oocytes (≤1800 µm) is variable. In a small number of cases, the small oocytes may not be present.
Spawning 2	Ovary is flaccid and contains mostly ripe eggs, which flow freely within the ovary. The eggs are not connected to ovarian tissue and are bathed within a viscous ovarian fluid. The dorsal area of the ovary wall has a "banded" appearance.	6	Ovary contains a single group of ripe eggs that have a unimodal distribution. There may also be a group of small oocytes (diameters <1800 µm), with a variable size frequency distribution.
Spent	Ovary is flaccid, and a small number of residual eggs may be visible.	7	Ovary may contain a small number of residual eggs or oocytes with a size distribution similar to that of oocytes at stage 2, 3, or 6.

gravimetric and average oocyte diameter, as well as from all fecundity analyses, because of concerns about nonhomogeneity of the ovary.

Measurements of oocyte size and oocyte density were $\log_{10}$-transformed, and general linear models were fitted by using R (vers. 3.6.1; R Core Team, 2019). These models were used to estimate oocyte density from measurements of oocyte size.

Estimation of fecundity with the auto-diametric method

Fecundity was estimated by using the auto-diametric method for fish with ovaries at OSFD stages 2, 3, and 5. For each fish, a small piece of preserved ovary was blotted to remove excess formalin; then the oocytes were separated and photographed. Images were analyzed and average oocyte diameter was calculated in a manner similar

to that described previously. For each fish, a minimum of 150 oocytes ≥400 µm were measured. Oocyte density was estimated from average oocyte diameter by using the relationships described previously (see the "Results" section). Fecundity could then be estimated by multiplying oocyte density by weight of preserved ovary (see the "Results" section). Fecundity was estimated only for fish with an average oocyte diameter >550 µm, the minimum average oocyte size used in the oocyte diameter–oocyte density calibration. Leading cohort oocyte diameter was calculated for each fish in a similar manner to that previously mentioned.

Because oocytes were not measured for samples collected in 2009, the LC oocyte diameter for these samples was calculated on the basis of a linear relationship between $\log_{10}$-transformed oocyte density (calculated as fecundity divided by ovary weight) and $\log_{10}$-transformed LC oocyte diameter. From this relationship, LC oocyte density was calculated with this equation:

$$\log_{10}(\textit{LC oocyte diameter}) = 3.94 + \log_{10}(\textit{oocyte density}) \times -0.27. \quad (1)$$

Eighty eggs were measured from ovaries at the developmental stages spawning 1 or spawning 2. Preservation in formalin does not affect diameter of oocytes because lumpfish lay demersal eggs that are not hydrated (senior author, unpubl. data).

Effects of preservation

Because the auto-diametric method was calibrated by using ovaries preserved in 10% formalin, the effect of preservation on fresh ovary weight was examined by using the same ovaries used in the auto-diametric calibration. On the basis of these results, preserved ovary weight was estimated by using a combination of average oocyte diameter and fresh ovary weight (see the "Results" section).

Historical estimates

Data on fecundity for 1967 and 1969 were extracted by using digitized images of plots of fecundity versus length from Schopka (1970) and Myrseth (1971). A sampling date was assigned to the data from each study. Schopka (1970) sampled fish during 7–28 April 1967; because it was not possible to assess a specific sampling date to each fish, they were all assigned a day midway through the sampling period: 16 April. Myrseth (1971) collected samples on 1 May 1969.

Statistical analysis

General linear models were fitted to the data, and the best models were chosen on the basis of the coefficient of determination (r^2) and the Akaike information criterion (AIC). Variables included in the models were length, carcass weight, liver weight, date of capture (expressed as day of year), and spawning year. Carcass weight was included in the models, as opposed to whole body weight, because part of whole body weight was composed of ovary weight, which was used to estimate fecundity. In addition, large amounts of water and food (up to 800 g or 23% of total body mass) were present in many stomachs from the fish caught during the spring and autumn surveys but not in those from fish sampled from the commercial fishery. Date of capture was converted to a numerical number (1–365), with 1 September rather than 1 January as day 1 because fish in the same ovary development cycle were captured before and after 1 January.

Expected fecundity before spawning of the first batch was calculated for fish with ovaries at OSFD stage 5 by using the general linear model of *fecundity=length+date of capture*, fitted to data from fish with ovaries at OSFD stage 3. The date of capture of the fish with ovaries at OSFD stage 5 was set as 14 d prior to their date of capture on the basis of the assumption of 14 d between the spawning of the first and second batches of eggs (Fulton, 1907). The result of actual fecundity divided by expected fecundity for fish with ovaries at OSFD stage 5 gives an indication of the proportion of eggs spawned in the first batch of eggs (e.g., a value of 0.50 would indicate that approximately half of the eggs were spawned in the first batch and the remaining half would have been spawned in the second batch). The resultant values of proportion of eggs spawned were tested, with a 1-sample Student's *t*-test, to determine whether the mean proportion of eggs spawned for all ovaries assigned to OSFD stage 5 was significantly different from 0.50. Carcass weight was not used to predict fecundity for fish with ovaries assigned to OSFD stage 5 because carcass weight at length was lower for fish at this stage than for fish with ovaries at OSFD stage 3, indicating carcass weight decreased during the time between these stages. Length was not expected to change between stages.

Ovaries containing eggs

Because of the heterogeneous nature of the ovary, fecundity could not be estimated for ovaries that contained ripe eggs (i.e., ovaries at stages spawning 1 and spawning 2). Average diameter of the developing oocytes and eggs was measured in a manner similar to that described previously. The effect of carcass weight and batch number was investigated by using general linear models, with oocyte diameter and carcass weight $\log_{10}$ transformed. Possible effects of spawning year were investigated by using a Tukey's honestly significant different (HSD) test.

Results

Calibration of the auto-diametric method

For ovaries at OSFD stage 2 (on the basis of $\log_{10}$-transformed data), there was a significant negative linear correlation between average oocyte diameter and oocyte density (linear regression: n=88, r^2=0.99, P<0.001) (Fig. 3).

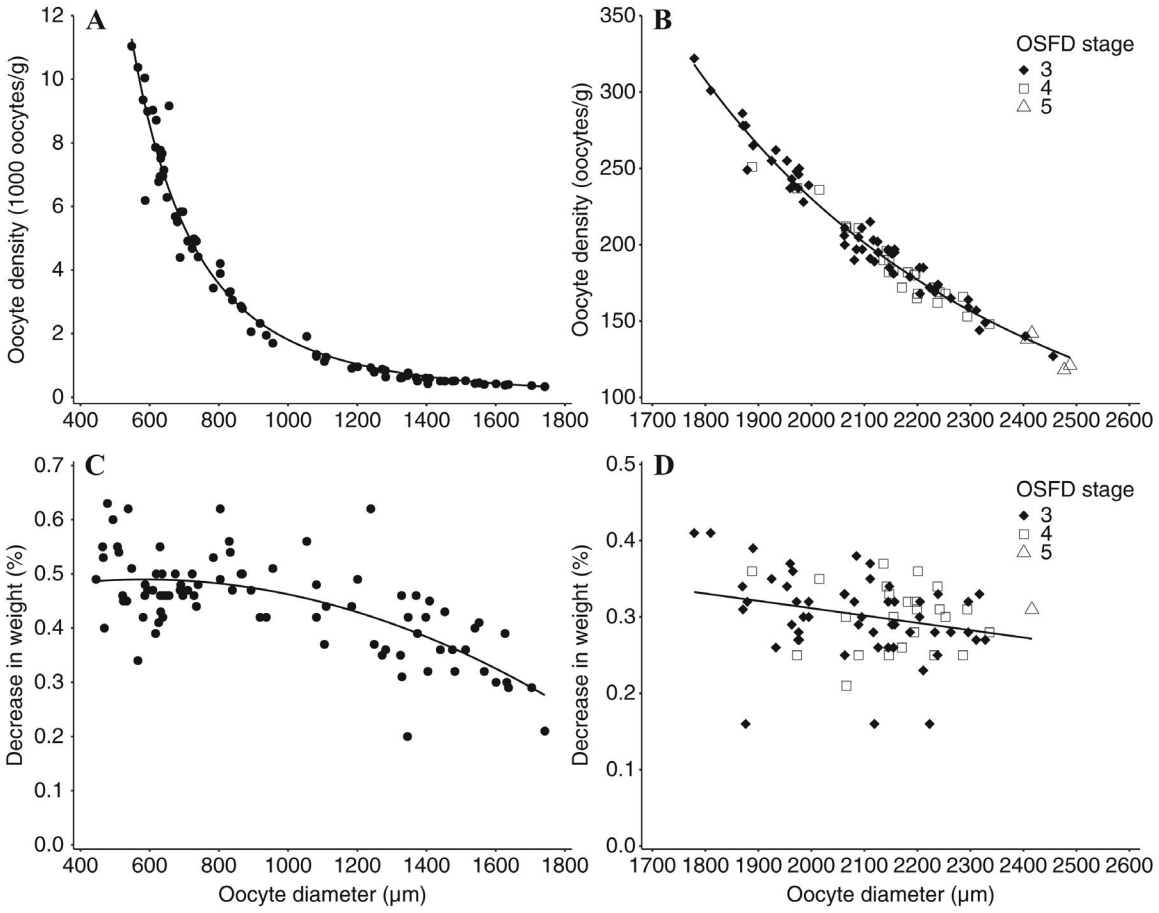

Figure 3

Relationships between oocyte diameter and oocyte density of lumpfish (*Cyclopterus lumpus*) with ovaries at oocyte size frequency distribution (OSFD) (**A**) stage 2 and (**B**) stages 3 (diamonds), 4 (squares), and 5 (triangles) and relationships between oocyte diameter and the decrease in weight of ovaries due to preservation in 10% formalin for lumpfish with ovaries at (**C**) stage 2 and (**D**) stages 3, 4, and 5. Lines indicate the power regression in panels A and B, polynomial regression in panel C, and linear regression in panel D. Ovaries classified as at OSFD stage 2 contain a single group of oocytes between 400 and 1800 µm with a unimodal size frequency distribution. In ovaries classified as at OSFD stage 3, a break in size frequency distribution separates oocytes into a group of large oocytes (diameters >1800 µm) that have a bimodal distribution and a group of small oocytes (diameters ≤1800 µm) that have a variable distribution; the oocyte diameter and oocyte density refer to the group of large oocytes. At OSFD stage 4, ripe eggs and developing oocytes have a unimodal distribution; the oocyte diameter and oocyte density refer to the developing oocytes. At OSFD stage 5, a group of large oocytes has a unimodal distribution and, if present, a group of small oocytes has a variable distribution. Lumpfish were sampled around Iceland in 2009 and 2013–2019 during groundfish surveys and from commercial fishery landings.

By using these data and the following equation, oocyte density was estimated for ovaries at this stage:

$$Oocyte\ density = 10^{-3.15\ \log_{10}(oocyte\ diameter)+12.68}. \quad (2)$$

There was no significant difference in the relationship between average oocyte diameter and oocyte density for fish with 2 batches of oocytes in the spawning group (ovaries assigned to OSFD stage 3) and fish with 1 batch of oocytes in the spawning group (ovaries assigned to OSFD stage 4 or 5) (general linear model: $P>0.05$); therefore, the data from these 3 stages were combined. The $\log_{10}$-transformed data indicate that there was a significant negative linear correlation between average oocyte diameter and oocyte density (linear regression: $n=85$, $r^2=0.97$, $P<0.001$) (Fig. 3). By using these data and the following equation, oocyte density was estimated for ovaries at the OSFD stages 3–5:

$$Oocyte\ density = 10^{-2.79\ \log_{10}(oocyte\ diameter)+11.57}. \quad (3)$$

Effects of preservation

The decrease in weight of ovarian tissue after fixation in formalin for ovaries in OSFD stage 2 was correlated with average oocyte diameter, and on the basis of AIC values, a second order polynomial regression gave the best fit to the data (polynomial regression: n=86, r^2=0.46) (Fig. 3). The weight of ovaries, adjusted for the effect of preservation, was calculated by using this equation:

$$\textit{Preserved weight} = \textit{fresh weight}\ (1 - [(1.87 \times 10^{-4}\ \textit{oocyte diameter}) + (-1.6 \times 10^{-7}\ \textit{oocyte diameter}^2) + 0.44]). \quad (4)$$

The decrease in weight of ovarian tissue after fixation in formalin for ovaries in OSFD stages 3 and 5 was negatively and linearly correlated with average oocyte diameter (linear regression: n=78, r^2=0.06) (Fig. 3). The weight of ovaries, adjusted for the effect of preservation, was calculated by using this equation:

$$\textit{Preserved weight} = \textit{fresh weight} \times (1 - [-9.6 \times 10^{-5}\ \textit{oocyte diameter} + 0.5]). \quad (5)$$

Fecundity and ovary development

It is common to $\log_{10}$ transform fecundity and body size data for fish in order to satisfy the assumptions of linear regression. However, general linear models of untransformed data gave a better fit than $\log_{10}$-transformed data, with coefficients of multiple determination (R^2) of 0.42 and 0.38 for the general linear model of fecundity and carcass weight with untransformed and transformed data, respectively. All assumptions of linear regression were met when untransformed data were used; therefore, untransformed data were used throughout the data analysis.

For fish with ovaries at OSFD stage 2, the best model for the prediction of fecundity included carcass weight, LC oocyte diameter, and spawning year (Table 3, Suppl. Table 1) with fecundity being positively correlated with carcass weight and negatively correlated with LC oocyte diameter (Fig. 4). Fecundity was significantly lower in 2014 than in all other years, and in 2015 it was significantly higher than in all other years, as indicated by results from the Tukey's HSD test. Carcass weight was a better predictor of fecundity than length.

For fish with ovaries at OSFD stage 3, carcass weight was a better predictor of fecundity than length. The best model for the prediction of fecundity included carcass weight, liver weight, date of capture, and LC oocyte diameter (Table 4, Suppl. Table 2). In this model, fecundity was positively correlated with carcass weight, liver weight, and date of capture and negatively correlated with LC oocyte diameter (Fig. 5). The addition of liver weight and LC oocyte diameter to the model, although both statistically significant, increased the explanatory power of the model by <1.0% each (Suppl. Table 2). There was no significant difference in fecundity between years in the study period 2014–2019 (Fig. 6). Mean relative fecundity was 34,700 oocytes/kg body weight (standard deviation [SD] 5900).

Potential fecundity of fish with ovaries at OSFD stage 5 was, on average, 0.54 (SD 0.19) of the fecundity expected of fish with ovaries classified as in OSFD stage 3 on the basis of length (Fig. 7). These values were not significantly different from the expected value of 0.50 (Kennedy, 2018) (Student's t-test: t=1.7, df=63, P=0.09). On removal of 4 outliers (Fig. 7), the average potential fecundity decreased to 0.50 (SD 0.12) of the fecundity expected of fish with ovaries classified as at OSFD stage 3 on the basis of length.

When data from 2009 were included in the general linear model of *fecundity=carcass weight+liver weight+date*

Table 3

Estimates of fecundity from the best general linear model for lumpfish (*Cylopterus lumpus*) with ovaries at oocyte size frequency distribution (OSFD) stage 2. This model included carcass weight, leading cohort (LC) oocyte diameter, and spawning year. Ovaries classified as at OSFD stage 2 contain a single group of oocytes between 400 and 1800 µm with a unimodal size frequency distribution. Fecundity estimates, obtained by using gravimetric and auto-diametric methods, are given in number of oocytes. The model was fit to data from fish sampled around Iceland during 2013–2019. SD=standard deviation.

Term	Estimate	SD	t	P
(Intercept)	51,5269.9	38589.3	3.4	<0.0001
Carcass weight	123.2	11.7	0.5	<0.0001
Spawning year: 2015	−17,0746.5	25,611.0	6.7	<0.0001
Spawning year: 2016	−84,873.4	21,797.4	3.9	<0.001
Spawning year: 2017	−81,345.8	22,167.5	−3.7	<0.001
Spawning year: 2018	−51,092.5	25,423.5	2.0	<0.05
LC oocyte diameter	−244.8	15.0	−16.3	<0.0001

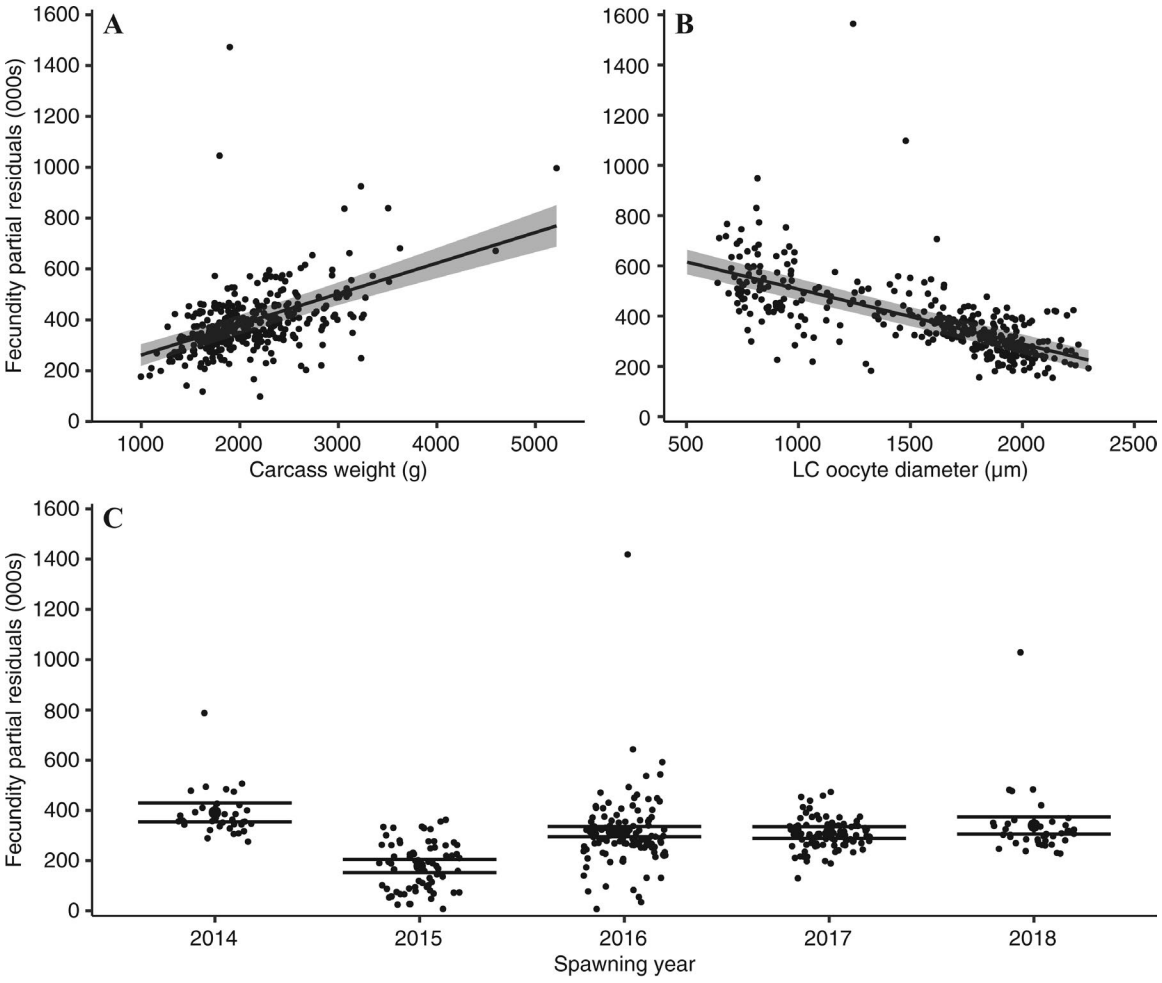

Figure 4

Plots of partial residuals for (**A**) carcass weight, (**B**) leading cohort (LC) oocyte diameter, and (**C**) spawning year, from the model that best explains the variability of fecundity in lumpfish (*Cyclopterus lumpus*) with ovaries at oocyte size frequency distribution (OSFD) stage 2. Ovaries classified as at OSFD stage 2 contain a single group of oocytes between 400 and 1800 µm with a unimodal size frequency distribution. In panels A and B, the linear regression line is shown, and the gray shaded area indicates 95% confidence intervals. In panel C, the horizontal lines indicate 95% confidence intervals. Fecundity estimates, obtained by using gravimetric and auto-diametric methods, are given in number of oocytes. The model was fit to data from fish sampled around Iceland during 2009 and 2013–2019.

of capture+year, spawning year was a significant factor in the model with fecundity significantly lower in 2009 than in 2015 *(*P<0.01), 2016 (P<0.05), 2017 (P<0.01), and 2019 (P<0.05) (Fig. 8). The result was similar when the data for back-calculated LC oocyte diameter was included in this general linear model. The biggest difference was between 2009 and 2017, with fecundity being ~8.7% lower in 2009 than in 2017 for a fish with an average carcass weight (1860 g), average liver weight (111 g), average date of capture (day 106), and average LC oocyte diameter (2306 µm).

Fecundity estimates from 1967 and 1969 were significantly lower and significantly higher, respectively, than in all the years in our study when we used the model of *fecundity=length+date of capture+year* (P<0.001) (Figs. 8 and 9). It should be noted that the use of length rather than carcass weight in the model gave a slightly different result in regard to differences in fecundity between 2009 and 2014–2019, with this difference no longer apparent when length was used as the covariate (Fig. 9).

Egg size

The general linear model revealed that $\log_{10}$-transformed average egg diameter was significantly correlated with $\log_{10}$-transformed carcass weight (P<0.001). In addition,

Table 4

Estimates of fecundity from the best general linear model for lumpfish (*Cyclopterus lumpus*) with ovaries at oocyte size frequency distribution (OSFD) stage 3. This model included carcass weight, liver weight, day of year captured, and leading cohort (LC) oocyte diameter. In ovaries classified as at OSFD stage 3, a break in size frequency distribution separates oocytes into a group of large oocytes (diameters >1800 µm) that have a bimodal distribution and a group of small oocytes (diameters ≤1800 µm) that have a variable distribution. Fecundity estimates, obtained by using gravimetric and auto-diametric methods, are given in number of oocytes. The model was fit to data from fish sampled around Iceland during 2009 and 2014–2019. SD=standard deviations.

Term	Estimate	SD	*t*	*P*
(Intercept)	−3497.5	13,717.1	0.3	0.80
Carcass weight	37.4	2.4	5.7	<0.0001
Liver weight	76.6	30.8	2.5	<0.05
Day of year 2	301.7	28.8	0.5	<0.0001
LC oocyte diameter	−14.1	6.2	2.3	<0.05

average egg diameter was significantly lower (approximately 1.6%) for fish with ovaries at developmental stage spawning 2 than for fish with ovaries at the stage spawning 1 ($P<0.01$). Average egg diameter was significantly different between years ($P<0.001$) (Fig. 10); however, results of the Tukey's HSD test indicate that the only significant difference was between 2014 and 2016 ($P<0.05$).

Discussion

Lumpfish add to a growing list of diverse fish species for which downregulation of fecundity, the process whereby the number of developing oocytes are reduced as ovary development progresses, has been documented (Vladykov, 1956; Kurita et al., 2003; Saborido-Rey et al., 2015; Flores et al., 2017). In many determinate spawners, there are several months between the commencement of ovary development, with the recruitment of previtellogenic oocytes to the developing pool of vitellogenic oocytes, and the spawning of these oocytes (Rijnsdorp, 1989; van Damme et al., 2009; Skjæraasen et al., 2017). Because the actual energy available for reproduction is difficult to forecast at this early stage of ovary development, more oocytes are recruited to the developing pool than could be taken to full development. As ovary development proceeds, the number of oocytes can be reduced, meaning they can be fine-tuned to the actual energy available through reabsorption of a portion of oocytes through atresia (Kraus et al., 2008; van Damme et al., 2009; Nissling et al., 2016). The energy that was invested into those oocytes can then presumably be made available for other purposes. This process, therefore, maximizes the number of eggs spawned given the amount of energy available.

This downregulation has an implication for the method used when investigating fecundity in fish. If a fish is sampled before downregulation is complete, then realized fecundity (number of eggs actually spawned) will be overestimated. Downregulation in lumpfish takes place mostly during OSFD stage 2. Fecundity decreases at OSFD stage 3, and this decrease is relatively small. Therefore, fecundity of lumpfish can be reliably estimated when ovaries are in OSFD stage 3.

Carcass weight was the best predictor of fecundity and notably outperformed length. This result is consistent with findings from other studies of fish fecundity that indicate that body weight is generally a better predictor of fecundity than length (Koops et al., 2004; Rideout and Morgan, 2010; Tanaka et al., 2017). The addition of liver weight explained only a small percentage of the variation in fecundity. This finding corresponds with those of previous studies in which characteristics intended to measure "condition," or energy reserves, added little in comparison to the factors reflecting body size (Alonso-Fernández et al., 2009; Rideout and Morgan, 2010; Rogers et al., 2019). The reason that such indices of energy reserves have a minor effect on explained variance is likely that, when sampling fish close to spawning, the energy to be used for ovary development has already been transferred from storage to the gonads. Therefore, the remaining energy at the time of sampling consists mainly of the energy required to complete and survive spawning and would not be expected to correlate with fecundity.

It is interesting to note that fish spawning later in the year had a higher fecundity than fish spawning earlier. Intra-annual variation in batch fecundity of indeterminate spawners is well documented (Alheit, 1993), but such variation has rarely been documented in determinate spawners. One of the few examples was reported by

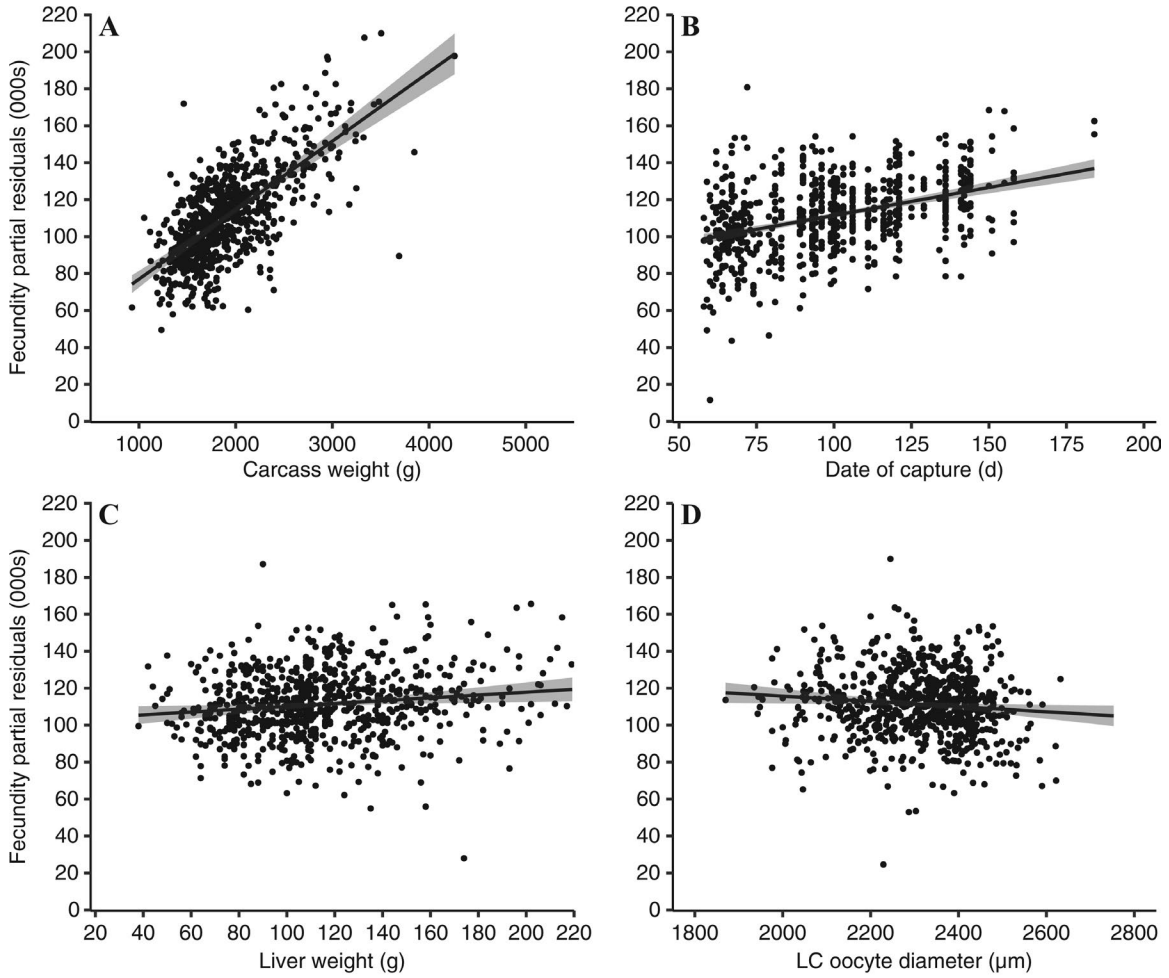

Figure 5

Plots of partial residuals for (**A**) carcass weight, (**B**) date of capture, (**C**) liver weight, and (**D**) leading cohort (LC) oocyte diameter, from the model that best explains variability in fecundity of lumpfish (*Cyclopterus lumpus*) with ovaries at oocyte size frequency distribution (OSFD) stage 3. In ovaries classified as at OSFD stage 3, a break in size frequency distribution separates oocytes into a group of large oocytes (diameters >1800 µm) that have a bimodal distribution and a group of small oocytes (diameters ≤1800 µm). In each panel, the linear regression line is shown, and the gray shaded area indicates 95% confidence intervals. For date of capture, 1 January was set as day 1 to aid interpretation. Fecundity estimates, obtained by using gravimetric and auto-diametric methods, are given in number of oocytes. The model was fit to data from fish sampled around Iceland during 2009 and 2013–2019.

Kjesbu et al. (1998), who found that fecundity was higher for Atlantic cod (*Gadus morhua*) that had already begun spawning than for fish that had not (i.e., early spawners had a higher fecundity than late spawners). The reason for this pattern in Atlantic cod was not clear, but Kjesbu et al. (1998) speculated that it was due to differences in sea temperatures between the timing of vitellogenesis of early and late spawners or was a result of the 2 groups belonging to different subpopulations. The results of our study and the fact that this aspect is rarely addressed in fecundity studies of determinate spawners highlight that a lack of variation in fecundity through the spawning season should not be assumed. Failure to investigate whether this variation indeed occurs in other species and populations could lead to bias when estimating the total egg production of a population or when using the annual egg production method for estimating spawning stock biomass.

What are the potential causes of this intra-annual variation in fecundity of lumpfish? Although the extent of the feeding area of lumpfish from Iceland is not fully known, there are indications that it may cover the Irminger Sea from southeastern Greenland, over the Denmark Strait and into the Norwegian Sea (Nøttestad

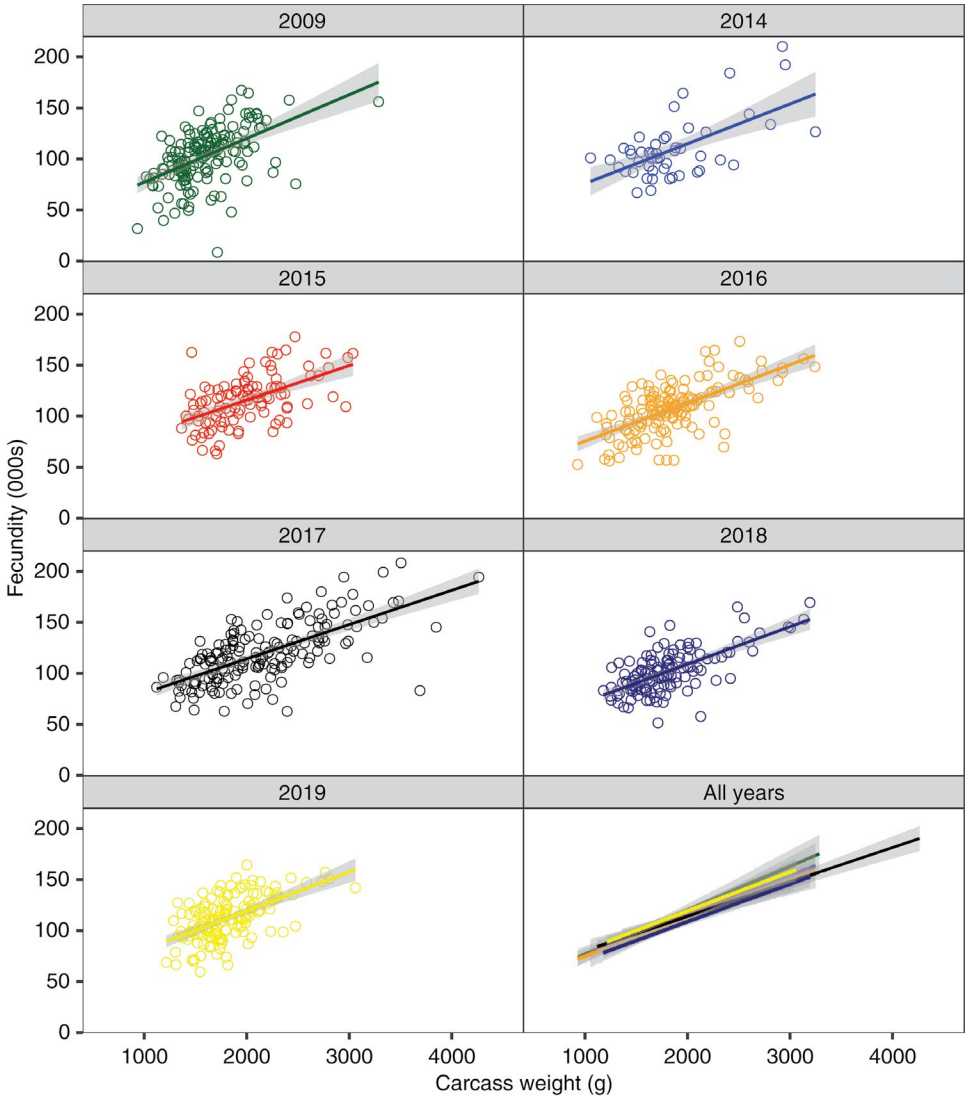

Figure 6

Relationships between carcass weight and fecundity for lumpfish (*Cyclopterus lumpus*) that had ovaries at oocyte size frequency distribution (OSFD) stage 3 and were sampled from the spring groundfish survey and landings of the commercial fishery at harbors around Iceland in 2009, 2014, 2015, 2016, 2017, 2018, and 2019 and in all years. In ovaries classified as at OSFD stage 3, a break in size frequency distribution separates oocytes into a group of large oocytes (diameters >1800 µm) that have a bimodal distribution and a group of small oocytes (diameters ≤1800 µm). In each panel, the linear regression line is shown, and the gray shaded area indicates 95% confidence intervals. Fecundity estimates, obtained by using gravimetric and auto-diametric methods, are given in number of oocytes.

et al.[2]). Over this large area, there will be differences in biotic and abiotic conditions that could drive differences in fecundity and spawning time in different parts of the population. In addition, if early and late spawners begin ovary development at different times of the year, the environmental conditions during vitellogenesis will differ, and that difference could also affect the resultant fecundity (Kjesbu et al., 2010). This aspect of fecundity of lumpfish is interesting in the context of the premise that lumpfish that spawn early or late in a spawning season will spawn early and late in the following season, respectively (Kennedy and Ólafsson, 2019). This intra-annual

[2] Nøttestad, L., V. Anthonypillai, S. Vatnehol, A. Salthaug, Å. Høines, A. H. Ólafsdóttir, J. Kennedy, E. Homrum, L. Smith, T. Jansen, et al. 2019. Cruise report from the International Ecosystem Summer Survey in the Nordic Seas (IESSNS) 28th June–5th August 2019. Working document to ICES Working Group on Widely Distributed Stocks (WGWIDE, No. 5), Spanish Institute of Oceanography (IOE), Santa Cruz, Tenerife, Canary Islands, 28 August–3 September 2019, 48 p. [Available from website.]

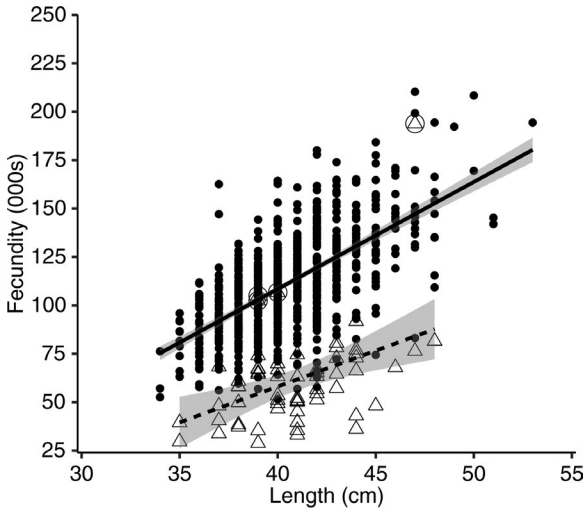

Figure 7

Relationship between total length and fecundity for all lumpfish (*Cyclopterus lumpus*) that had ovaries at oocyte size frequency distribution (OSFD) stages 3 (circles) and 5 (triangles) and were sampled from the spring groundfish survey and landings of the commercial fishery at harbors around Iceland during 2009 and 2014–2019. In ovaries classified as at OSFD stage 3, a break in size frequency distribution separates oocytes into a group of large oocytes (diameters >1800 µm) that have a bimodal distribution and a group of small oocytes (diameters ≤1800 µm). At OSFD stage 5, a break in size frequency distribution separates oocytes into a group of large oocytes (diameters >1800 µm) that have a unimodal distribution and a group of small oocytes (diameters ≤1800 µm). Linear regression lines are shown for OSFD stages 3 (solid) and 5 (dashed), with 95% confidence intervals represented by the gray shaded areas. Outliers are circled. Fecundity estimates, obtained by using gravimetric and auto-diametric methods, are given in number of oocytes.

difference in fecundity means that late-spawning fish, assuming similar spawning mortality, will have greater lifetime fecundity than early-spawning fish. However, greater lifetime fecundity may not translate into greater numbers of surviving offspring because mortality of lumpfish in early life stages may not be equal through the spawning season as a result of differing environmental conditions, prey availability, or predation (Methot, 1983; Narimatsu and Munehara, 1999; Voss et al., 2006).

Although there was interannual variability in the fecundity of lumpfish, the variability during 2009–2019 was low in comparison with the variability observed in other long-term studies of fish fecundity (Kjesbu et al., 1998; Kennedy et al., 2007; Rideout and Morgan, 2007). The extent to which fecundity varies between years in fish species is poorly understood because of a limited number of multiyear studies. Knowledge of what drives variability, or the lack thereof, is also limited, but there is some evidence that levels of specific prey items and abiotic conditions can play a role (Kjesbu et al., 1998). The reasons for the limited variability in fecundity between years observed in our study are unclear. It may be a result of stable environmental conditions and food availability in the years studied, or it may be that lumpfish place a high priority on reproduction and will maintain a similar level of fecundity from year to year at the expense of growth or energy reserves.

There were clear differences in fecundity in our study compared with historical estimates from Schopka (1970) and Myrseth (1971). Both studies used different methods in order to estimate fecundity. Schopka (1970) preserved the gonads in Gilson's fluid and used an automatic egg counter, and Myrseth (1971) froze ovaries and then used the gravimetric method. How the authors of the previous studies accounted for fish that had already spawned one batch differed. Schopka (1970) did not take it into account, and Myrseth (1971) included only fish in which the ovary filled the body cavity down to the abdomen in order to exclude any fish that had spawned one batch. Bear in mind that the number of fish that were caught in the commercial fishery and had ovaries at OSFD stage 5 in our study was low, approximately 7%.

Inclusion of fish with ovaries assigned to OSFD stage 5 in fecundity estimates will lower the estimated population fecundity; however, exclusion of fish with small gonads has the potential to exclude fish with low fecundity and, therefore, lead to an overestimation of population fecundity. The fecundity estimates of 1969 are almost all within the upper range of expected values based on estimates from 2009 and 2014–2019. In contrast, the variability was lower in 1969, and there is a notable lack of fecundity values within the lower range of values seen in 2009 and in 2014–2019. This lower variability and lack of fish within the lower range of fecundity values in 1969 indicates that the difference in fecundity between 1969 and the fecundity estimated in our study is largely driven by the bias in sampling in Myrseth (1971); therefore, the difference between the fecundity in 1969 and in 2009–2019 is likely a result of a difference in method.

In our study, no fish at OSFD stage 3, and approximately one third of fish at OSFD stage 5, had a fecundity <50,000 oocytes. Only one fish from Schopka (1970) had a fecundity <50,000 oocytes, indicating that the occurrence of OSFD stage 5 was lower in the study of Schopka (1970) than in our study. This low occurrence of fish at OSFD stage 5 in Schopka (1970) indicates that not accounting for fish at this stage had no significant influence on the estimation of fecundity in 1967 and does not explain the low fecundity observed by Schopka (1970). However, because methods differed between studies (automatic egg counter, Parrish et al., 1960, versus auto-diametric method), it is not possible to state with certainty that there is a real difference in fecundity between

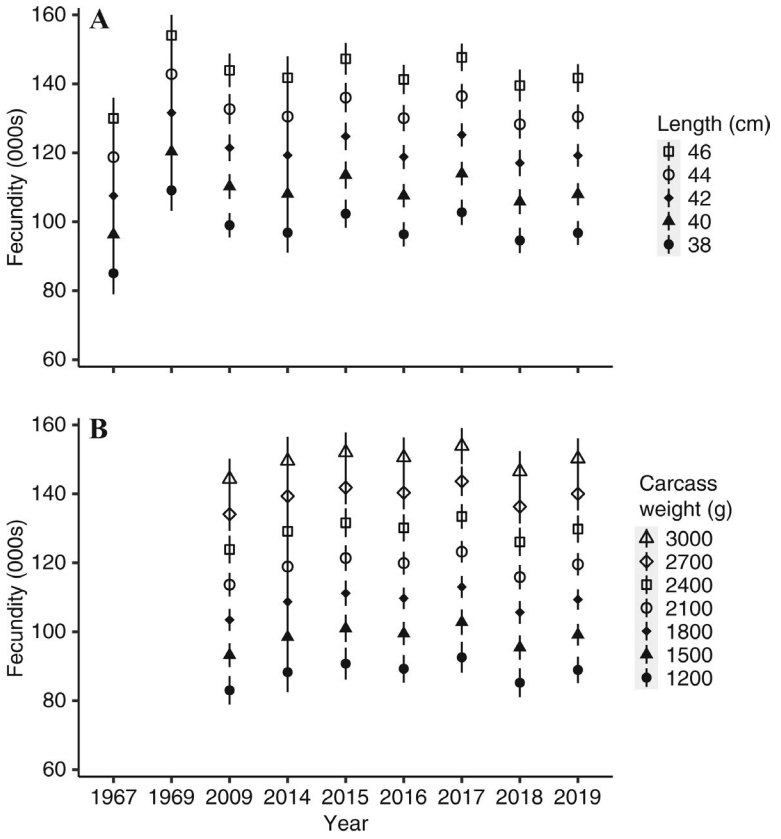

Figure 8

Values of fecundity predicted with a general linear model for lumpfish (*Cyclopterus lumpus*) at different (**A**) total lengths and (**B**) carcass weights. For each year, the average date of capture was set at 20 April in the model. For only analysis by carcass weight, the average liver weight used in the model was 111 g. Data used in the model are from fish sampled for this study around Iceland during 2009 and 2014–2019; data for 1967 and 1969 are from previous studies (Schopka, 1970; Myrseth, 1971).

1967 and 2009–2019. It must also be noted that, even if the difference is real, the historical estimate covers only a single year and it is not possible to know if this was typical of the population around that time. Therefore, we cannot conclude, on the basis of data from this study, that there have been any significant changes in the reproductive capacity of the population of lumpfish over the past 50 years.

There are a small number of studies on fecundity of lumpfish in other areas; however, differences in fecundity between areas needs to be carefully considered. Fecundity in fish is highly variable both within and between years, and it can also vary spatially within a population (Morgan and Rideout, 2008). In a study of lumpfish in Greenland in 2012 and 2014 (Hedeholm et al., 2017), a lumpfish with a carcass weight of 2 kg had a fecundity of 100,000–120,000 oocytes, a value that is broadly similar to fecundity observed in our study. Still, it is difficult to draw conclusions about whether fecundity of lumpfish in Greenland is lower, higher, or similar to that of lumpfish in Iceland. Hedeholm et al. (2017) did not consider temporal variations but did find spatial variation. In contrast, we did not investigate spatial variation but did find temporal variation. Therefore, differing conclusions could be drawn depending on how the comparison is carried out.

Fecundity has been estimated for lumpfish in Canada (Gauthier et al., 2017); unfortunately, the only information presented is fecundity versus ovary weight, making comparisons of the fecundity–size relationship difficult between fish from Iceland and those from Canada. The majority of the data from Gauthier et al. (2017) indicates that fecundity of lumpfish in Canada was 50,000–200,000 oocytes, similar to the range observed in our study; given the nature of the data presented, further comparisons between studies are not possible. Gauthier et al. (2017) also presented information on *hydrated* egg size, which probably refers simply to egg size because lumpfish do not hydrate their eggs. These egg size values ranged from ~1.0 to ~2.0 mm with a median around 1.7 mm. These sizes are considerably smaller than those of eggs sampled from fish captured in Iceland. Gauthier et al. (2017) measured eggs from histological sections, an approach that generally underestimates diameter in comparison with the methods employed during our study. Caution should be applied, therefore, when comparing the results of the 2 studies.

The estimated relative fecundity from our study (34,700 oocytes/kg body weight) was slightly lower than the estimate from Pountney et al. (2020) (40,400 oocytes/kg body weight). The reasons for this difference may be that Pountney et al. (2020) counted all the oocytes >370 µm, a threshold lower than that used in our study (~1600–1800 µm, depending on the oocyte distribution). Therefore, Pountney et al. (2020) likely included oocytes from the non-spawning group, meaning the group of oocytes between 400 and 1800 µm in ovaries classified as at OSFD stage 3 that would have become atretic and not spawned (Kennedy, 2018). In addition, the fish examined by Pountney et al. (2020) were captive bred and would have experienced conditions different than those experienced by the wild fish collected in our study.

Fish with ovaries at OSFD stage 5 had a fecundity roughly half that of fish with ovaries at OSFD stage 3

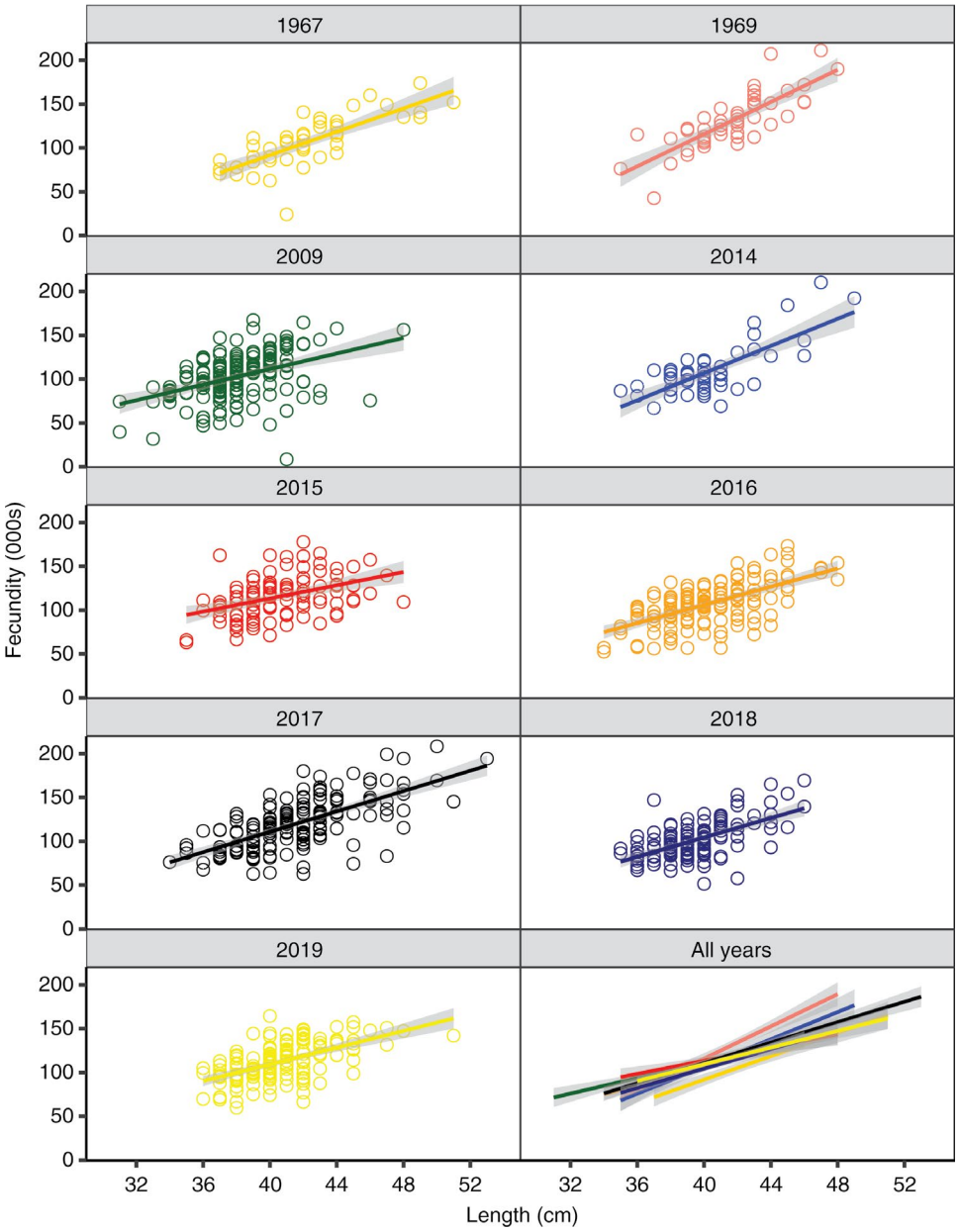

Figure 9

Relationships between total length and fecundity for lumpfish (*Cyclopterus lumpus*) that had ovaries at oocyte size frequency distribution (OSFD) stage 3 and were sampled around Iceland in 1967, 1969, 2009, 2014, 2015, 2016, 2017, 2018, and 2019 and in all years. In ovaries classified as at OSFD stage 3, a break in size frequency distribution separates oocytes into a group of large oocytes (diameters >1800 µm) that have a bimodal distribution and a group of small oocytes (diameters ≤1800 µm). In each panel, the linear regression line is shown, and the gray shaded area indicates 95% confidence intervals. Fecundity estimates, obtained by using gravimetric and auto-diametric methods, are given in number of oocytes. Data for 1967 and 1969 are from Schopka (1970) and Myrseth (1971).

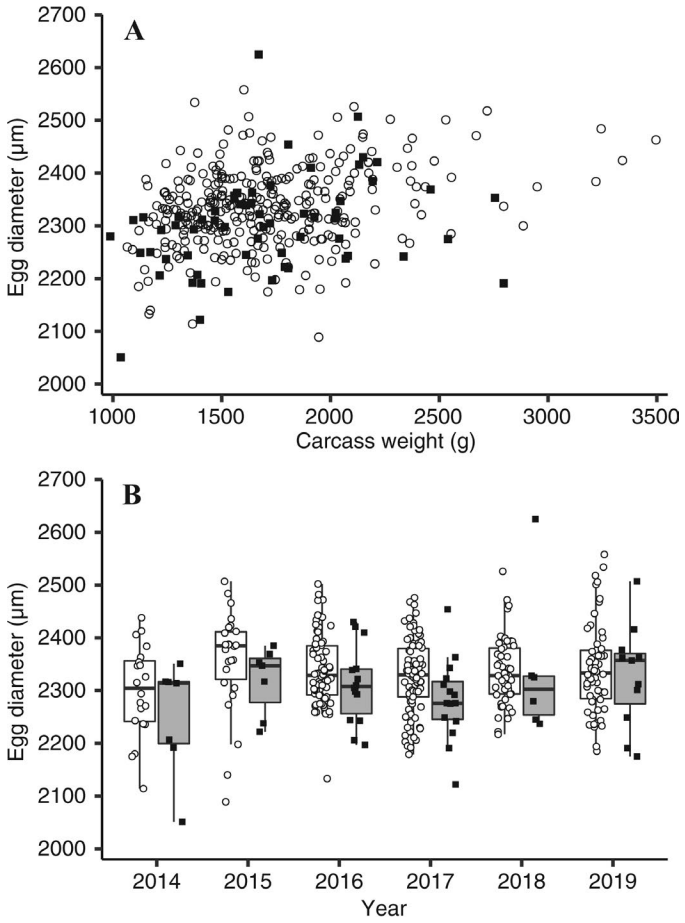

Figure 10

Average egg diameter as a function of (**A**) carcass weight and (**B**) year of capture for lumpfish (*Cyclopterus lumpus*) that were sampled around Iceland in 2014–2019 and had ovaries at the developmental stages spawning 1 (open circles) and spawning 2 (squares). At stage spawning 1, the first batch of eggs have been ovulated and the ovary also contains developing oocytes that will become the second batch. At stage spawning 2, the second batch of eggs have been ovulated. In panel B, the line within the box represents the median value. The bottom and top parts of the box represent the first and third quartiles (25th and 75th percentiles) of average egg diameter. Whiskers above and below the box correspond to 1.5 times the interquartile range.

irrespective of whether outliers were or were not excluded in the estimation of the average proportion of eggs spawned. This finding supports the conclusion of a previous study (Kennedy, 2018), based on oocyte size distributions, that lumpfish spawned 2 batches of eggs with a roughly equal number of eggs. However, in our study, there were 4 notable outliers with ovaries at OSFD stage 5 that had fecundity similar to fish with ovaries classified as at OSFD stage 3. The existence of these outliers indicates that there may be a small number of individuals (~0.5% in this study) that, without reduction in the total number of eggs spawned, will spawn only one batch of eggs. This phenomenon has been reported in lumpfish in an aquaculture scenario in which the incidence of single-batch production was higher than in our study, with estimates of 50% for fish kept at 6ºC and 9ºC and of up to 78% for individuals held at 14ºC (Pountney et al., 2020). The mechanisms behind this single-batch spawning remain unknown.

Egg size increased with carcass weight but decreased from the first batch to the second. This decrease from the first to second batch was investigated by Kennedy (2018), and with an additional 3 years of data from our study, this observation still holds. We also found low variation in egg size between years. Variability in egg size is a rarely investigated component of reproductive biology because of the number of confounding factors, such as fish size, progression through spawning for batch spawners, and the hydration of eggs for species with pelagic eggs. Although a few studies have investigated annual variation in egg size (Almatar and Bailey, 1989; DeMartini, 1990; Hinckley, 1990), a comprehensive investigation into annual variation across species is lacking. The information provided by this study should aid such a study in the future.

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