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Gonadal maturation of the female smooth lumpsucker (*Aptocyclus ventricosus*)

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Abstract—Features of oogenesis, ovarian maturity phases, and fecundity of the smooth lumpsucker (*Aptocyclus ventricosus*) are described here for the first time. Gonadal development was examined by histological methods and the morphological features and size of germ cells at various stages was determined. These features were used to more accurately define morphological criteria of 7 histological and macroscopic maturity phases. The smooth lumpsucker is an iteroparous gonochoristic species with determinate fecundity, group-synchronous ovary organization, total spawning (release of 1 batch of eggs per breeding season), and external fertilization.

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The family Cyclopteridae is represented by about 16 genera and 28 species (Eschmeyer et al., 2017) that inhabit the cold waters of the northern hemisphere (Nelson et al., 2016). The lumpfish (*Cyclopterus lumpus*) is a commercial fish and the most studied member of this family (Goulet et al., 1986; Goulet and Green, 1988). Other members of this family have been studied less frequently, and information about their reproductive biology is fragmentary and scarce.

The smooth lumpsucker (*Aptocyclus ventricosus*) is a widely distributed marine fish species that is endemic to the North Pacific. It inhabits both near bottom and mid-water layers at depths ranging from 5 to 1700 m (Hart, 1973; Eschmeyer et al., 1983; Orlov and Tokranov, 2008). It is a common species that is ecologically relevant to local food webs throughout its distribution. It is a major consumer of gelatinous planktonic animals, such as jellyfishes and comb jellies (Yoshida and Yamaguchi, 1985) and an important source of food for some fish species, marine mammals, and birds (Kato, 1982; Orlov, 1997; Zeppelin and Ream, 2006; Anthony et al., 2008; Sinclair et al., 2008).

There is little information available on the spawning features (e.g., behavior, physical changes) or embryonic, and larval development of the smooth lumpsucker. It is only known that this species performs spawning migrations from deep water to coastal zones, where breeding occurs over a rocky bottom at depths shallower than 10 m. Eggs are demersal and adhesive and have an average diameter of 2.4 mm. The incubation time between fertilization and hatching is more than 40 d. Reportedly, females die after spawning and males continue to protect the egg clusters (Kyûshin, 1975; Ilynsky and Radchenko, 1992; Mecklenburg et al., 2002; Fadeev, 2005). Spawn-

ing times in different parts of the North Pacific vary but generally occur from February through May (Vinogradov, 1950). There are no data on the development of the reproductive system, oogenesis, ovary organization, and spawning pattern of this species.

Our main goal was to provide the first description of 1) oogenesis, 2) type of fertilization, 3) gonadal differentiation and development, and 4) an estimation of fecundity in female smooth lumpsuckers and to define both macroscopic and microscopic maturity phases. Macroscopic staging is much quicker and less expensive than histological staging; however, microscopic analysis provides a more precise determination of phases and was used to evaluate the efficacy of macroscopic maturity scales. Understanding the reproductive cycle of the smooth lumpsucker will help to elucidate the biology of other members of the Cyclopteridae family.

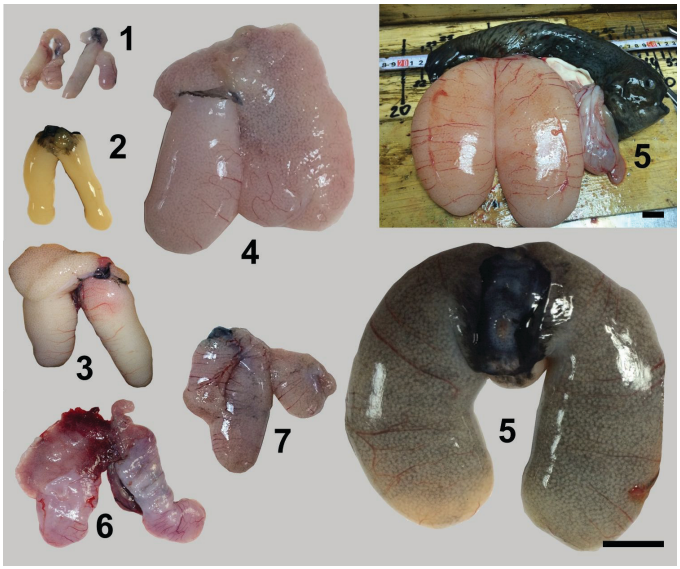

Figure 1

Photographs of ovaries of the smooth lumpsucker (*Aptocyclus ventricosus*) in different phases of gonadal maturation: 1) immature; 2) early developing; 3) developing; 4) spawning capable; 5) actively spawning subphase; 6) regressing; and 7) regenerating. The length of the scale bars represents 2 cm.

Materials and methods

Sampling for this study was carried out during an expedition on board of the research vessel *Professor Kaganovsky* (gross tonnage: 2508) of the Pacific Scientific Research Fisheries Center (TINRO-Center), Vladivostok, Russia, in the spring (16 March–30 May) of 2014. An RT/TM 57/360 midwater trawl net with 30-mm mesh was used. A total of 130 female smooth lumpsuckers were collected for analysis from the Sea of Okhotsk and near the southern Kuril Islands (43–60°N, 139–159°E). Total length (TL, in millimeters), body weight (BW, in grams), and gonad weight (GW, in grams) of each female were measured. The stomachs of smooth lumpsuckers typically were filled with water when the fish were brought on board, as is characteristic of this species and other Cyclopteridae (Ilynsky and Radchenko, 1992; Orlov, 1994). In this study, BW was measured after water had been expelled from the stomach. To analyze gonadal development, photographs were taken of the different maturity phases and then examined under magnification (Fig. 1). Gonadosomatic index (GSI) was calculated (Barrett and Munkittrick, 2010; Bahamonde et al., 2013) according to the following formula:

$$GSI = \frac{GW \times 100}{BW}, \quad (1)$$

where GW = gonad weight (in grams); and
BW = fish body weight (in grams).

Histological analysis was performed on 31 gonads that represent the different phases of development: 3 gonads for the immature phase, 12 gonads for the early developing subphase, 6 gonads for the developing phase, 4 gonads for the spawning-capable phase, 2 gonads for the regressing phase, and 1 gonad for the regenerating phase. Gonads were dissected and fixed in a 10% formalin solution in the field. The samples were then dehydrated, cleared with xylol, embedded in paraffin, sectioned (4 µm thickness), and stained with hematoxylin and Ehrlich's eosin. An Olympus BX45[1] microscope (Olympus Corp., Tokyo, Japan) and Leica DC 100 digital camera (Leica Microsystems,Wetzlar, Germany) were used for microscopy and photography. The image processing and data analysis program ImageJ, vers. 1.34e (Schneider et al., 2012) was used for measuring the diameters of oocytes and visualizing their structures. The ovarian phases of each gonad were classified on the basis of the most advanced oocyte stage observed in the histological sections according to the scale described in Brown-Peterson et al. (2011) (Table 1).

Absolute and relative fecundity were estimated by using 46 freshly caught females determined to be at the spawning-capable phase and at the actively spawning subphase by using the gravimetric method of Murua et al. (2003). A piece of ovarian tissue was taken from the median portion of the gonad from each specimen. The subsample of each ovary, representing 1.1–5.5% (about 10 g) of the GW, was weighed, and all advanced oocytes (diameter: 1.6–2.0 mm) in the subsample were counted by using an optical microscope MBS-9 (LZOS, Lytka-

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Macroscopic maturity scale for ovaries of the smooth lumpsucker (*Aptocyclus ventricosus*), with corresponding histological gonadal phases and oocytes stages (Brown-Peterson et al., 2011). Histological features include primary growth (PG) oocytes; cortical alveolus stage (CA) oocytes; primary (Vtg1), secondary (Vtg2), and tertiary vitellogenic (Vtg3) oocytes; atretic (A) follicles or eggs; oocyte maturation (OM); germinal vesicle maturation (GVM); germinal vesicle breakdown (GMBD); and postovulatory follicles (POFs). GSI=gonadosomatic index.

Maturity phases	Main histological features of each phase	Main macroscopic features of each phase
Immature	Oogonia, PG	Ovaries small, translucent, gray, white, milky, or pink, occupy less than 1/5 of the body cavity. In some cases, ovary envelope is characterized by black color. GSI<0.6%.
Early developing subphase	PG, CA	Ovaries yellow, milky, pink, or reddish, occupy about 1/4 the volume of the body cavity. No eggs are visible to the eye. GSI 2.7–5.6%.
Developing	PG, CA, Vtg1, Vtg2	Ovaries opaque, orange, milky, pink, or reddish, occupy about 1/3–2/3 the volume of the body cavity. Small eggs are visible to the eye, with diameter <1 mm. GSI 3.7–39%.
Spawning capable	PG, CA, Vtg3, OM	Ovaries gray, milky, or pink, occupy about 2/3 the volume of the body cavity. Eggs are visible to the eye and had diameter >1 mm. GSI 31–45%
Actively spawning subphase	PG, GVM, GVBD, hydration, ovulation	Ovaries occupy all the volume of the body cavity, opaque, gray, or pink. Visible eggs (diameter >2 mm) are presented. Oocytes are 2 times larger than in the spawning-capable gonads. GSI 31–56%.
Regressing	POF, PG, some CA or Vtg, residual eggs present	Ovaries red or black, flaccid, with enlarged blood vessels. Gonads are reduced in size, occupy less than 1/3 of the body cavity. GSI 5.5–10.5%
Regenerating	PG, A, some CA, gamma/delta atresia and old POFs may be present	Ovaries occupy about 1/3 the volume of the body cavity, gray or reddish, with distinguished blood vessels. GSI 6%.

rino, Russia) at 8×2 zoom. Absolute (F_{abs}) and relative fecundity (F_{rel}) were estimated as

$$F_{abs} = \frac{n \times GW}{w}; F_{rel} = \frac{n \times GW}{w \times BW}, \quad (2)$$

where n = the number of advanced oocytes in subsample;
w = the weight of the subsample (in grams);
GW = the gonad weight (in grams); and
BW = the fish body weight (in grams).

Results

Immature ovaries were observed in the smallest females, which had a mean TL of 159.0 mm (standard deviation [SD] 55.2), a mean BW of 305.4 g (SD 228.0), and a mean GW of 6.2 g (SD 5.6). The most advanced germ cells in immature ovaries were represented by primary growth oocytes. Also observed were early primary growth (chromatin nucleolar) oocytes, which are characterized by a basophilic cytoplasm stained with hematoxylin and a large round nucleus with the nucleolus arranged at the periphery. Their diameters ranged from 46 to 101 µm (Fig. 2A). Advanced primary growth (perinucleolar) oocytes had diameters from 93 to 188 µm. Primary growth oocytes were characterized by the presence of oil droplets at the oocyte cytoplasm periphery. The GSI of the immature female was 3% (SD 0.6).

Gonads in an early development subphase were found in larger females, which had a mean TL of 220.5 mm (SD 39.9), a mean BW of 362.3 g (SD 150.7), a mean GW of 19.1 g (SD 9.7), and a mean GSI of 4% (SD 0.7). Cortical alveoli oocytes, as the most developed oocyte present, were diagnostic of this subphase. Their diameters at the early stage ranged from 218 to 359 µm and had a zona radiata width of 2–3 µm (Fig. 2B).

Gonads of the developing phase, observed in still larger females that had a mean TL of 257.2 mm (SD 35.1), a mean BW of 828.5 g (SD 193.6), were the most variable in terms of the size and weight of the gonads, and having a mean GW of 213.5 g (SD 142.5) and a

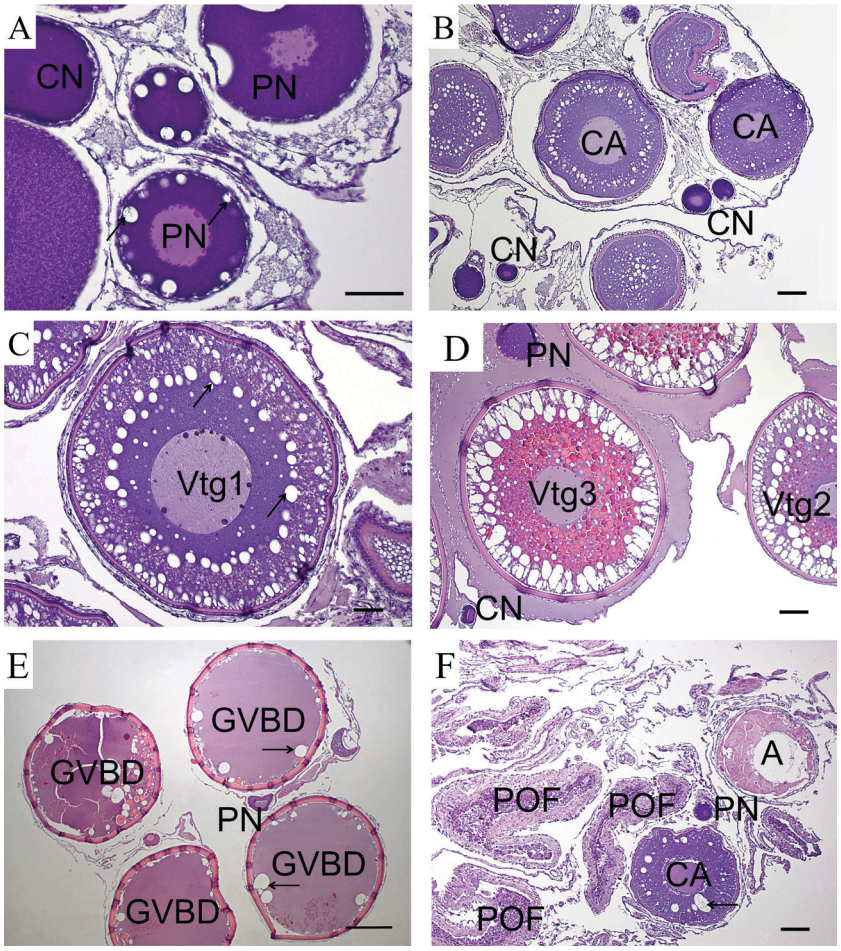

Figure 2

Photographs of ovaries of the smooth lumpsucker (*Aptocyclus ventricosus*) showing the microscopic characteristics of different gonadal phases: (**A**) immature; (**B**) early developing subphase; (**C**) developing; (**D**) spawning capable; (**E**) actively spawning subphase; and (**F**) regenerating. Microscopic characteristics include chromatin nucleolar (CN), perinucleolar (PN), cortical alveoli (CA), primary (Vtg1), secondary (Vtg2), tertiary vitellogenic (Vtg3), germinal vesicle breakdown oocytes (GVBD), postovulatory follicles (POF), atretic eggs (A), and oil droplets (arrow). The lengths of the scale bars represent (A–C) 50 µm, (D and F) 100 µm, and (E) 600 µm.

mean GSI of 28.9% (SD 7.6). The most advanced germ cells in this phase were primary and secondary vitellogenic oocytes, which increased in diameter because of increased yolk in the cytoplasm. Oocytes were from 360 to 448 µm, and the number of oil droplets increased during the later stages. In cortical alveoli oocytes, the zona radiata became thicker (7–9 µm), and delicate striations appeared. The process of yolk filling the cytoplasm began at the periphery and progressed toward the central areas of the oocytes, whose diameters ranged from 447 to 512 µm (Fig. 2C).

Females with ovaries at the spawning-capable phase had a mean TL of 263 mm (SD 45.9), a mean BW of 944 g (SD 186.4), a mean GW of 330 g (SD 131), and a mean GSI of 36% (SD 7.4). In the ovaries of these females, vitellogenic oocytes (diameter varied from 525 to 960 µm) had developed simultaneously (Fig. 2D). Only minor asynchrony was visible in the development of the advanced cohort of oocytes. The degree of oocyte cytoplasm filled with yolk was slightly different. However, these deviations disappeared by the completion of vitellogenesis. The zona radiata became thicker (13–17 µm), and radial striations appeared.

Females with gonads at the actively spawning subphase had a mean TL of 297.4 mm (SD 31.6), a mean BW of 1284.8 g (SD 313.2), a mean GW of 590.7 g (SD 149.3), and a mean GSI of 45% (SD 7.2). In gonads of these females, the stage of "germinal vesicle break-

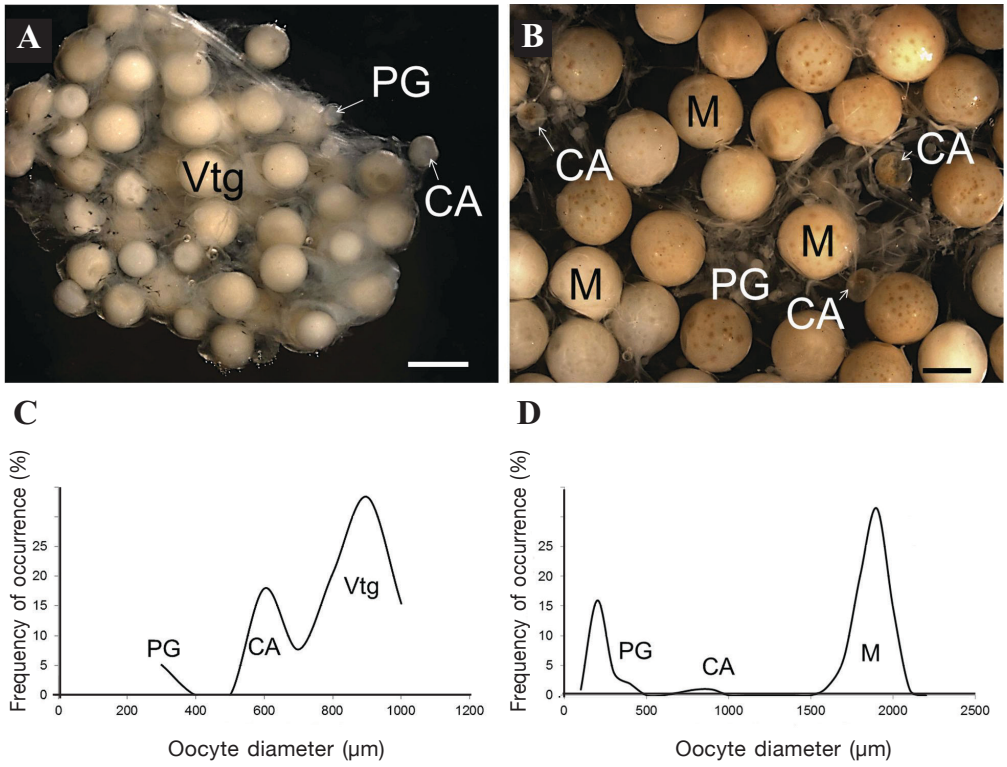

Figure 3

Photographs of the ovaries of smooth lumpsucker (*Aptocyclus ventricosus*) in the (**A**) developing phase and (**B**) actively spawning subphase and the oocyte size frequency in ovaries of the (**C**) developing phase and (**D**) actively spawning subphase. The following features are indicated: primary growth (PG); cortical alveoli (CA); vitellogenic (Vtg); and mature (M) oocytes. The length of the scale bars in the photographs represents 1 mm.

down oocytes" (Brown-Peterson et al. [2011]) with yolk homogenization was present in the ovary. The diameter of advanced oocytes increased by about 2.5 times (1401–1658 µm), and the thickness of their zona radiata ranged from 39 to 61 µm. Primary growth oocytes and oogonia, which served as the reserve fund of germ cells, occurred among mature oocytes (Fig. 2E).

Regressing and regenerating gonads were detected in 3 females, which were caught at depths of 86–138 m at distances of 26–58 nmi from the coast. The TL of these spent fish ranged between 261 and 300 mm, body weight varied between 523 and 615 g, gonadal weight varied between 32 and 64 g, and mean GSI was 7.4% (SD 4.7). Ovaries at the regressing phase were identified in 2 of these females by the presence of postovulatory follicles; primary growth oocytes were located among them. In gonads of 1 of the 3 females, we found late-stage atretic eggs, postovulatory follicles, and early primary vitellogenic oocytes that indicate a regenerating phase (Fig. 2F). No sperm were found in any of the ovaries.

The results from examination of oocyte diameters indicated group-synchronous oocyte development. In developing ovaries (Fig. 3, A and C), 3 groups of oocytes were clearly distinguishable on the basis of size. The first group was characterized by primary growth oocytes of 250-µm diameter, the second by cortical alveolus oocytes of 600-µm diameter, and the third by vitellogenic oocytes of 850-µm diameter. In actively spawning subphase gonads (Fig. 3, B and D), the majority of germ cells were in the germinal vesicle breakdown stage and ranged in diameter from 1800 to 2000 µm. There were also a reserve fund of oocytes, including primary growth and cortical alveolus oocytes of the same size as developing gonads.

Gonad maturation begins in individuals longer than 129 mm TL. Spawning and spent fish range from 218 to 300 mm TL. Therefore, mature individuals have dominated trawl catches during research surveys and commercial fishing operations in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka (Orlov and Tokranov, 2008).

Our histological study on the smooth lumpsucker has shown a discontinuous type of oogenesis or determinate type of fecundity, which is characterized by 2 oocyte generations (vitellogenic oocytes and reserve fund of sex cells) in ovaries at the developing and spawning-capable phases. The reserve fund of sex cells

was represented by oogonia, primary growth oocytes, and cortical alveoli oocytes in all examined ovaries.

Values of F_{abs} ranged between 24,240 and 63,756 oocytes per female with a mean of 42,187 oocytes per female (SD10,246). The F_{rel} values ranged between 21 and 67 oocytes/g of body weight, with a mean of 36 oocytes/g of body weight (SD 9).

There was a stronger correlation between fecundity and body weight (regression equation: y=25.187x +10,365, coefficient of determination [r^2]=0.73 for F_{abs}; y=55.454x+24,823, r^2=0.76 for F_{rel}) than between fecundity and length (y=194.35x–15,374, r^2=0.62 for F_{abs}; y=469.3x–45,013, r^2=0.65 for F_{rel}).

Discussion

The results of our study prove that the smooth lumpsucker is an iteroparous, total spawning species according to the classifications of Murua and Saborido-Rey (2003), McBride et al. (2015), and Pavlov and Emel'yanova (2016). This reproductive strategy means that females of this species are multiple spawners and do not die after breeding, in contrast to previous opinions (Vinogradov, 1950; Fadeev, 2005). Some authors (Ilynsky and Radchenko, 1992; Orlov and Tokranov, 2008) have questioned this assertion, suggesting that a proportion of the females survive and are involved in repeated spawning. Although the scientific literature documents that a large number of dead smooth lumpsucker are found after spawning, these dead fish are actually mostly males that were protecting egg clusters (Ul'chenko and Orlov, 2001). In the closely related species of the lumpfish, females survive after spawning, exit the spawning grounds, and return offshore when oviposition is complete (Cox and Anderson, 1922; Kennedy et al., 2015). However, for the lumpfish, the results of Bagge[2] and Kasper et al. (2014) both indicate low levels of postspawning survival.

The presence of several clearly grouped oocytes in ovaries (Fig. 3) indicated discontinuous oogenesis (determinate fecundity) and group-synchronous development of vitellogenic oocytes; oocytes were released one during the spawning season (total spawning). Similar reproductive characteristics have been observed in other teleost fishes of the families Clupeidae, Cyprinidae, Salmonidae, Percidae, Scorpaenidae, and Cottidae (Muñoz et al., 2002; Petersen et al., 2004; TenBrink and Aydin[3]; McBride et al., 2015). In contrast, another member of the family Cyclopteridae, *Lethotremus awae*, is a multiple spawner during every mating season and is characterized by asynchronous development of vitellogenic oocytes (Abe and Sato, 2009) — a reproductive strategy that may be attributed to the more southern range of this species: eastern coast of central Japan and Yellow Sea near Chefoo (Pavlov and Emel'yanova, 2016).

The ovaries of the smooth lumpsucker are characterized by the absence of sperm in all gonads, indicating gonochorism, oviparity, and external fertilization (Devlin and Nagahama, 2002). The size of mature oocytes and thick zona radiata are similar to those of some members of the families Salmonidae, Pleuronectidae, Hexagrammidae, Hemitripteridae, Cottidae, and Clupeidae, which have adhesive demersal eggs that are deposited on a variety of substrates. A thick envelope protects these demersal eggs from mechanical damage during development in the coastal zone (Warfel and Merriman, 1944; Ivankov and Kurdyayeva, 1973; Stehr and Hawkes, 1979; Markevich, 2000; Kolpakov and Dolganova, 2006; TenBrink and Buckley, 2013). Oil droplets appear in the cytoplasm of chromatin nucleolar oocytes and are present until the embryonic stage (Kyûshin, 1975).

We found that smooth lumpsuckers from the Sea of Okhotsk and near the southern Kuril Islands had absolute fecundity values less than or equal to those reported elsewhere. Kyûshin (1975) reported absolute fecundity values ranging from 45,500 to 80,000 eggs for smooth lumpsucker collected in February off the Shikabe coast (Funka Bay, southern Hokkaido, Japan). Absolute fecundity values varying from 30,000 to 50,000 eggs were reported off the southeastern coast of the Kamchatka Peninsula (Vinogradov, 1950).

Our study has extended current knowledge on oogenesis, reproductive strategy, fecundity and has identified specific features of the reproduction of the smooth lumpsucker. Snailfishes (Liparidae) have some features, such as large eggs, low fecundity, the laying of eggs in sheltered locations with the use of the female ovipositor, and possibly the protection of clutches in species having a large sucking disk (Rass, 1950; Stein, 1980; Chernova, 2014), that are similar to features of the smooth lumpsucker, but members of Liparidae have not been studied in detail. The data from our study may help to elucidate the reproductive biology of this closely related group of fishes.

Acknowledgments

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