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Description of embryonic development of Atka mackerel (*Pleurogrammus monopterygius*)

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Atka mackerel (*Pleurogrammus monopterygius*) is a hexagrammid fish that inhabits the temperate and subarctic North Pacific Ocean and neighboring seas (Fig. 1). This highly abundant fish is a critically important prey species (Sinclair and Zeppelin, 2002; Zenger, 2004) that supports a directed commercial trawl fishery (Lowe et al., 2006). Atka mackerel is a demersal spawner and males provide parental care to eggs (Zolotov, 1993). During breeding periods, sexually mature males aggregate on the bottom at nesting sites where they establish territories (Lauth et al., in press). Sexually mature females periodically visit male nesting territories from July to October to spawn batches of demersal egg masses (McDermott and Lowe, 1997; McDermott et al., 2007). Individual nests may consist of multiple egg masses deposited by different females, and males defend nesting territories for a protracted period lasting from the time territories are being established until all eggs within the territory are completely hatched (Lauth et al., 2007). Knowledge about the timing of the reproductive cycle and the use of spawning habitat are important for understanding population structure and the dynamics of stock recruitment, which in turn are important factors in the management of Atka mackerel populations.

The male brooding phase of the reproductive cycle has not been a focus of studies despite its critical importance in the propagation and survival of Atka mackerel. The incubation period from fertilization to hatching is a good proxy for determining the time that nest-guarding males stay at nesting sites once spawning has ended. There is one published study describing embryonic development of Atka mackerel at 11°C (Gorbunova, 1962); however the results are incomplete and provide only a partial description of embryonic development. An accurate and complete timetable of embryonic development is essential for determining how temperature affects the incubation period and the timing of the reproductive cycle in the North Pacific Ocean (Lauth et al., 2007). The objective of this study was to determine the incubation period of Atka mackerel embryos by using a controlled water temperature, and to construct a complete embryonic development series, from fertilization to first hatching, with particular reference to morphological features and pigmentation for categorizing preserved egg specimens.

Materials and methods

Eggs used to construct the embryonic development series were obtained by scuba divers from a nearshore Atka mackerel nesting site at Seguam Island in the Aleutian archipelago (Fig. 1) on 7 August 2002. The *in situ* egg mass was deposited and fertilized on a nest at an unknown time between two scuba dives at 1115 and 1720 Alaska Daylight Time (ADT). For the purpose of this experiment, the time of egg fertilization was assumed to be 6 hours before egg mass collection. The bottom water temperature at the time of the collection dive was 4.1°C

The egg mass was brought to the surface, separated into two halves, and each half was placed in a four-liter glass jar with seawater and an air stone. The jars with incubating egg masses were secured in a refrigerator set at 6.0°C and water temperature was monitored with a Tidbit Datalogger (Onset Computers, Bourne, MA) that recorded temperature once every minute. On 16 August 2004, eggs were transported inside thermoses and coolers with ice by air to the Alaska Fisheries Science Center (AFSC) in Seattle, WA. Upon arrival, the egg masses were placed in two 38-L aquaria housed in a temperature-controlled room maintained at 6.0°C. Each aquarium was equipped with air pumps, air stones, and a water circulation pump and water flow directed at the eggs. Seawater for the aquaria was pumped from Puget Sound, WA, run through 1-μm filters, sterilized with ultraviolet light, and stored in 200-L plastic barrels. The seawater in the barrels was adjusted to 32–33 ppt by using aquarium salt, and the barrels were kept inside the temperature-controlled room at the AFSC to maintain the same water temperature as that of the aquaria. Half the water volume in the aquaria was changed on a daily basis and incandescent lights were set on automatic timers to simulate daylight from 0600 to 1800 Pacific Daylight Time (PDT). Five to ten eggs were sampled every 1–3 days from 16 August to hatching and preserved in phosphate-buffered 5% formalin solution. Chorions were removed from eggs to facilitate examination of development with a stereo dissecting microscope. Descriptions of obvious morphological features or pigmentation were recorded for each

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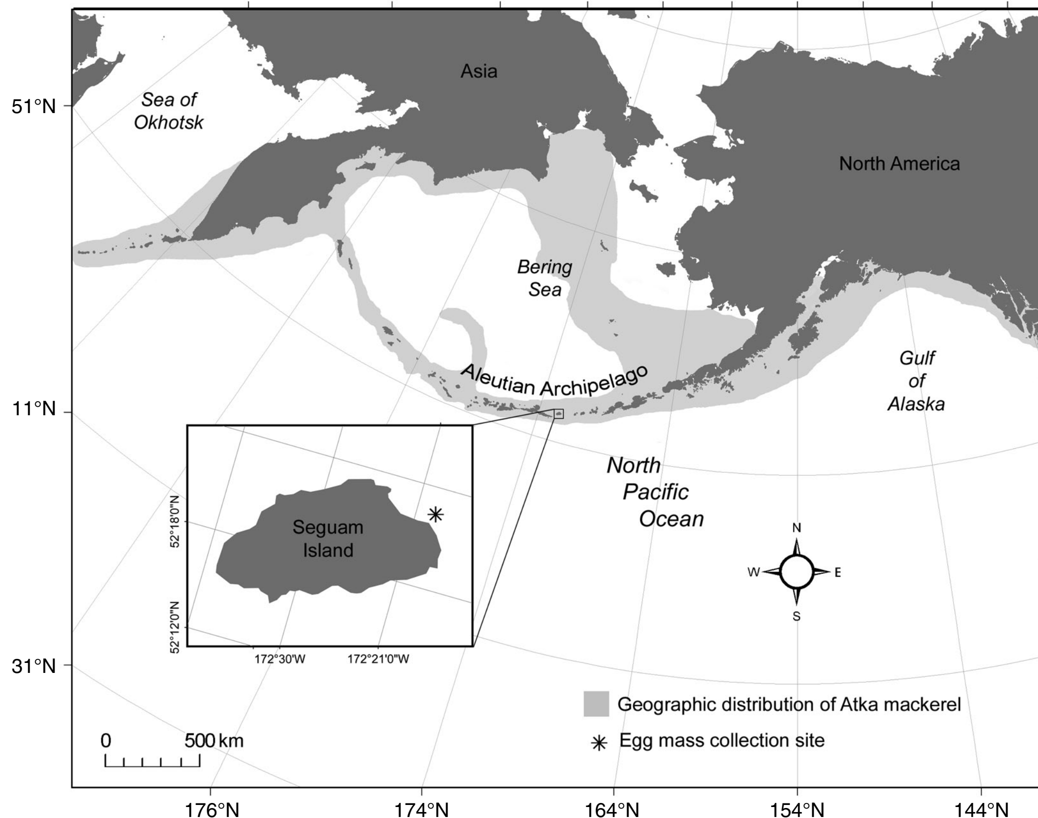

Figure 1

Map showing the geographic distribution of Atka mackerel (*Pleurogrammus monopterygius*; light gray shading) in the North Pacific Ocean and adjoining seas. Also shown is the location (*) near Seguam Island where a newly fertilized Atka mackerel egg mass was obtained for an incubation experiment.

preserved embryo and the observations from the entire progression were used to construct a chronological series describing embryonic development at 6.0°C.

Results

The newly fertilized eggs were collected from a nest containing several separate egg masses. The eggs were light green and were relatively soft and loosely clumped, in contrast to their character in the following days when they became more firm, rubbery, and tightly attached to one another. As the eggs aged, their color turned reddish brown. The original egg mass had approximately 1500 eggs that ranged in diameter from 2.5 to 2.8 mm. The average daily water temperature during the incubation ranged from 5.42° to 6.57°C and the mean and standard deviation were 6.2° and ±0.3°C, respectively. Incubated eggs began hatching on day 74 and preserved length of yolksac larvae was 9.4–10.9 mm SL.

Embryonic development

The description of embryonic development was divided into two sections: the first section is a description of the development of morphological features, and the second is a description of the development of pigmentation. For brevity, each paragraph in the pigmentation section describes one or more pigment type from the time they first appear until they are fully developed. Table 1 provides descriptive summaries for the progression of both morphological features and pigmentation.

Morphological features

Preserved eggs from the day of collection (fertilization) had a single blastomere sitting on a yolk containing a group of >50 oil globules varying in size (0.08–0.20 mm). After 72 hours of meroblastic cleavage, a blastodermal cap formed on top of the yolk. Over the next four days, the blastodermal cap flattened and increased in diameter as the edge began folding under (gastrulation) to form a germ ring that started moving downward over the yolk (epiboly; Table 1). The embryonic shield formed as the germ ring advanced over the yolk. The blastopore closed on day 15 when the germ ring completely enveloped the yolk. During days 17–21, the optic capsule and eye lenses formed, the head and anterior body became thick and more defined, and the notochord, myomeres, and Kupffer's vesicle became visible (Table 1).

One week after blastopore closure (day 22), the tail region began lifting away from the yolk, and within two days, the length of the embryo was 50% of the circumference of the yolk. As the tail grew longer, it curved further away from its longitudinal axis, causing the embryo to curl around the top quarter of the yolk rather than at the equator. The tail was 75% of its way around the yolk by day 29 and touched the snout by day 36. Lengthening further, the tail extended past the anterior edge of the eye (day 40) and past the posterior edge of the head (day 48); the maximum length was reached on day 64 when it was 1.75 times the circumference of the yolk.

Pigmentation

Embryo pigmentation first appeared on day 31. Sparse melanophores appeared in the eye surrounding the lens and along the dorsal midline, nape, and gut (Table 1; Fig. 2). The eye became completely pigmented and much darker by day 38. The beginning of the dorsal midline series was observed as scattered melanophores in the area between 20% body length (BL) and 50% BL. By day 44 the dorsal midline series extended as a double row anterior to the nape and posterior to 50% BL where it joined to form a single row of irregularly spaced melanophores that continued to 70% BL. On day 49, the single row of dorsal midline pigment extended to 5–6 myomeres anterior to the caudal peduncle. At hatching, the dorsal midline series was a double row of continuous pigment extending from the nape to three myomeres anterior of the caudal peduncle (Fig. 3). Dorsal gut pigment first appeared halfway along the gut where the pigment progressively spread posteriorly toward the anus, and then anteriorly toward the head. On day 42, the dorsal gut pigment extended the full length of the gut, excluding the anus. During subsequent development, a few melanophores migrated ventrally onto the lateral gut wall and others moved close to the newly developed pectoral fin buds. By the last week of development (day 71), there was heavy dorsal gut pigment, moderate pigment on the lateral gut, and no pigment on the ventral gut or anus (Fig. 3).

The head remained unpigmented until day 36 when melanophores appeared on the snout, forebrain, midbrain, and nape (Fig. 2). Initially, head pigment was scattered lightly across the dorsal surface except where it outlined the posterior edge of both lobes of the nape. The nape pigment converged toward the double row of melanophores extending anteriorly from the dorsal midline series. During days 37–61, the dorsal midbrain and nape pigment increased, leaving an unpigmented area along the midline (Fig. 2) and several melanophores also became visible on the opercle between the eye and pectoral-fin base. By day 61, opercular pigment concentrated into one dark spot and a second smaller spot appeared on the opercle below the right lower quadrant of the eye (Fig. 3). Head pigmentation was complete by day 64; stellate melanophores coalesced on the midbrain and nape and heavy pigment covered the nape and mid-

Table 1

Description of embryonic development by day for Atka mackerel (*Pleurogrammus monopterygius*) eggs incubated at 6.2°C.

Day	Description
0	Single blastomere; yolk contains group of >50 oil globules; meroblastic clevage begins
1	4 blastomeres
2	32 blastomeres
3	64–28 blastomeres
4	Blastodermal cap; individual cells indistinguishable and begin to flatten
7	Gastrulation, epiboly, and formation of embryonic shield begin
9	25% epiboly
11	50% epiboly
12	75% epiboly
15	Blastopore closed
17	Optic vesicles begin to form
18	Myomeres visible on anterior body behind nape
19	Kupffer's vesicle visible; optic vesicles formed; myomeres visible on central 60% of body
21	Posterior 50% of body thick and raised from surface of yolk; eye lenses are formed
22	Midbrain enlarges to form bump; tail region lifts away from yolk
23	Midbrain differentiates and forms a bump behind eyes
24	Embryo arches over 50% of the yolk
25	Tail curves away from longitudinal axis
26–27	Otic capsules formed
28	Dorsal finfold on posterior 1/3 of body extends anteriorly to 60% BL
29	Dorsal finfold extends anteriorly to nape; embryo 75% of the way around yolk
31	Pigmentation first appears in eye and along dorsal midline, posterior dorsolateral nape, and dorsal gut
35	Pectoral fin buds formed
36	Head pigment on snout, midbrain and nape; embryo tail touches snout
40	Nares visible; embryo tail extends past anterior edge of eye
41	Nares formed
42	Lower jaw beginning to form
48	Embryo tail extends past posterior edge of head
51	Postanal ventral midline pigment appears
55	Nape enlarges to form hump
58	Opercular pigment; lower jaw fully formed
62	Internal notochord pigment visible
64	Embryo tail length is 1.75× circumference of yolk
65	External lateral pigment visible
71	Pigmentation indistinguishable between embyros and hatched larvae
74	First hatching

brain except for an unpigmented midline through the midbrain and anterior half of the nape. Internal pigment was also visible at the base of the midbrain near the nape and external pigment increased slightly on the forebrain and disappeared on the snout (Fig. 2).

Postanal ventral melanophores (pvm) became visible late during the embryonic development (day 51) along the ventral midline at 80% BL. By day 65, the pvm series extended anteriorly to 50% BL. At time of hatching, the completed series consisted of a light irregular line of melanophores at 50% BL, larger and more closely spaced melanophores at 60–80% BL, and ended 1–2 myomeres anterior to the terminus of the dorsal midline series (Fig. 3).

The internal and external lateral pigment series were the last two pigments to appear. On day 62, internal

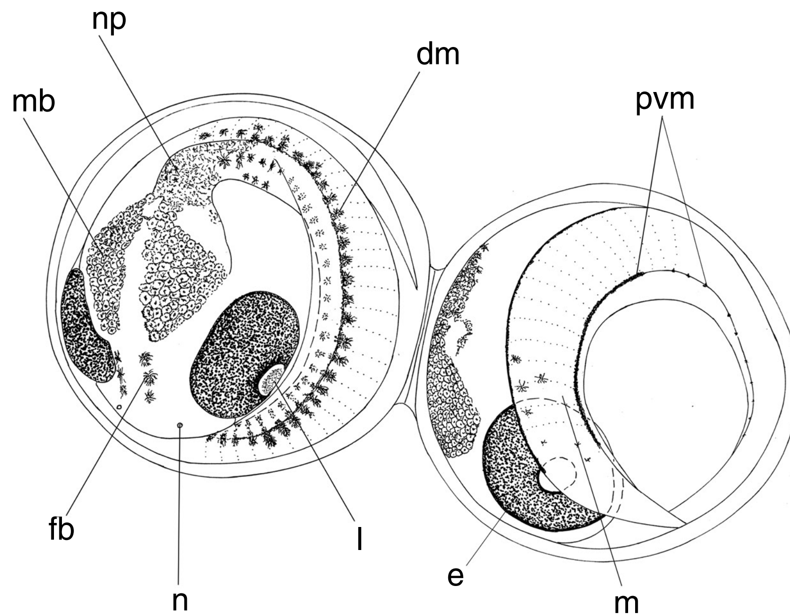

Figure 2

Drawing of two Atka mackerel (*Pleurogrammus monopterygius*) embryos with egg diameters of 2.5–2.8 mm after 11 weeks of development at 6.15°C (areas of pigment: fb = forebrain, mb = midbrain, np = nape, dm = dorsal midline, and pvm = postanal ventral melanophores; morphological features: n = nares, l = lens, e = eye, and m = myomere).

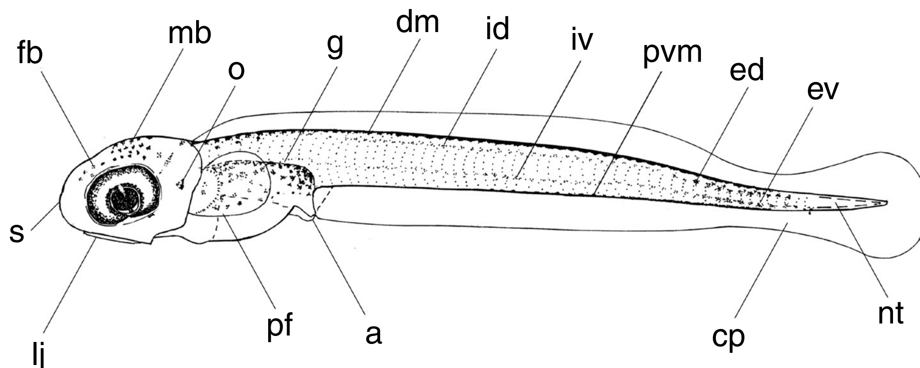

Figure 3

Drawing of a 10.9 mm Atka mackerel (*Pleurogrammus monopterygius*) larva one day after hatching (areas of pigment: fb = forebrain, mb = midbrain, o = opercular, g = gut, dm = dorsal midline, id = internal dorsal, iv = internal ventrolateral, pvm = postanal ventral melanophores, ed = external dorsolateral, and ev = external ventrolateral; morphological features: s = snout, lj = lower jaw, pf = pectoral fin, a = anus, cp = caudal peduncle, and nt = notochord).

pigment was observed above and below the notochord, posterior to the anus, and extending toward the tail; the ventrolateral series began 2–5 myomeres posterior to the start of the dorsolateral series. On day 65, the external lateral pigment appeared on the posterior 20% of the body above and below the notochord and on the ventrolateral caudal body. From day 71 to 74, there were no appreciable differences between hatched and unhatched embryos (Fig. 3). The internal dorsolateral series began just anterior to the anus and was spaced regularly with about one melanophore per myomere until termination at a point even with the dorsal midline series. The internal ventrolateral series began 10–12 myomeres posterior to the anus with similar spacing until 80% BL, where it became irregular until terminating three myomeres before the end of the pvm (postanal ventral melanophore) series. The external dorsolateral and ventrolateral pigment covered the posterior 25% of the body; dorsolateral pigment ended even with the dorsal midline series and the ventrolateral series extended halfway onto the caudal peduncle. Some larvae had one melanophore on the caudal peduncle midway between the last myomere and notochord tip.

Discussion and conclusions

This study provides a complete description of embryonic development that details the progression of morphological features and pigmentation in Atka mackerel embryos from fertilization to first hatching. Daily egg development did not deviate from known fish embryology, and the incubation period was 74 days at an average daily water temperature of 6.2°C. The formerly published incubation period of 40–45 days at an average water temperature of 11°C was based on a 19-day rearing experiment supplemented with data from *in situ* egg samples collected from nesting sites (Gorbunova, 1962). Additional imprecision may have been introduced by unregulated and widely varying water temperatures used during the incubation experiment (8–15°C; Gorbunova, 1962). Comparing our study with that of Gorbunova (1962), we found that incubation time was inversely related to temperature, which is commonly known to be true for fishes (Hempel, 1979).

A review of the scientific literature on near-bottom water temperatures at North Pacific Ocean nesting sites shows that temperatures are generally within several degrees of the incubation temperature used in our study (6.2°C). At western North Pacific Ocean nesting sites, water temperatures ranged from 2.5° to 8.2°C in 1958 (Gorbunova, 1962), and from 4.84° to 8.30°C in 1985 and 1992 (Zolotov, 1993). Similarly, across the central and eastern North Pacific Ocean, the mean and standard deviation of water temperature at 106 nesting sites was 5.4°±1.2°C and was as low as 3.9°C (Lauth et al., in press). It is apparent from our study that the use of nesting substrate by males increases substantially with the longer incubation periods caused by lower water temperatures. In such cases where males are guarding multiple egg masses at varying developmental stages, the brooding phase will be more protracted than that where there is only a single egg mass.

Additional controlled rearing experiments at a wider range of water temperatures are needed to determine more accurately how the rate of embryonic development, and hence male brooding period, is affected. The complete embryonic development series from this study and an empirically derived incubation rate can be used for modeling the relative spawning and hatching dates of egg masses collected from different nesting sites (Lauth et al., 2007). Such an incubation model would be useful for investigating the variability in timing of the reproductive cycle across the broad longitudinal range of Atka mackerel, which is important for conserving and managing Atka mackerel populations and nesting habitat.

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