Abstract—A nursery site for the Alaska skate (Bathyraja parmifera) was sampled seasonally from June 2004 to July 2005. At the small nursery site (~2 km²), located in a highly productive area near the shelf-slope interface at the head of Bering Canyon in the eastern Bering Sea, reproductive males and females dominated the catch and neonate and juvenile skates were rare. Seasonal samples showed summertime (June and July) as the peak reproductive time in the nursery although some reproduction occurred throughout the year. Time-series analysis of embryo length frequencies revealed that three cohorts were developing simultaneously and the period of embryonic development was estimated at 3.5 years and average embryo growth rate at 0.2 mm/day. Estimated egg case deposition occurred mainly during summertime and hatching occurred during winter months. Protracted hatching times may be common for oviparous elasmobranch species and may be directly correlated with ambient temperatures as evident from a meta-data analysis. Evidence indicates that the Alaska skate uses the eastern Bering Sea outer continental shelf region for reproduction and the middle and inner shelf regions as habitat for immature and subadults. Skate nurseries may be vulnerable to disturbances because they are located in highly productive areas and because embryos develop slowly.

Elasmobranchs are of growing concern worldwide because they are threatened by increased fishing and habitat disturbances (Musick et al., 2000; Stevens et al., 2000). Characteristic life history traits of these fish include slow growth rates, late maturation, low fecundity, and long life-spans, all of which make them extremely vulnerable to increased fishing-induced mortality (Dulvy, 1999; Frisk et al., 2002). Species with these life history patterns depend on high juvenile survival and recruitment for population stability. An adequate understanding of reproduction dynamics and habitat requirements are lacking for most species, yet these may be the most critical biological criteria for successful reproduction.

Oviparous species such as skates (Rajidae) use nursery areas for egg deposition, embryo development, and hatching (Hitz, 1964; Hoff, 2007). They produce relatively large collagen egg cases (Knight et al., 1996) which contain a large yolk mass and developing embryo. The egg cases are deposited directly onto the seafloor and embryos develop independent of maternal care (Hamlett and Koob, 1999). The embryonic developmental period is unknown for most species of skates, but evidence indicates that it may exceed one year for temperate and deepwater species (Berestovskii, 1994). The Alaska skate (Bathyraja parmifera) represents >95% of estimated skate biomass on the eastern Bering Sea shelf (20 to 200 m) (Lauth and Acuna, 2007), and estimates of biomass and population numbers have indicated nearly a fourfold increase since 1975 (Hoff, 2006). Skates at all life stages are encountered in the shelf environment and the species range is limited to depths of <400 m on the slope (Hoff and Britt, 2003, 2005; Stevenson et al., 2007). The Alaska skate reaches a large size (153 cm) and can be locally abundant (Hoff and Britt, 2005). Its distribution pattern and accessibility in relatively shallow waters make the species a likely candidate in target fisheries, and its life history characteristics make it susceptible to population decreases (Matta, 2006; Matta and Gunderson, 2007). A nursery site for the Alaska skate was identified in June 2004 (Fig. 1) where significant numbers of skate egg cases were previously reported by commercial fishing crews and fisheries observers. The nursery exists in an area that has been heavily fished for walleye pollock (Theragra chalcogramma) and Pacific cod (Gadus macrocephalus) for many years, and the site is frequently disturbed by bottom trawls.

Understanding reproductive characteristics and essential habitat requirements are necessary to accurately predict population stability under changing conditions for elasmobranch species worldwide. The recent discovery of a nursery site for the Alaska skate allowed a first look at the reproductive details of the species. Specifically, this study estimates the timing of egg deposition and duration of embryonic development through length-frequency mode tracking from a seasonal sampling of embryos. In addition, the habitat of the Alaska skate is examined with respect to nursery site use and life-stage distribution patterns.

A nursery site of the Alaska skate (Bathyraja parmifera) in the eastern Bering Sea

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Materials and methods

Sampling at the nursery site

The Alaska skate nursery site was sampled by methods and gear similar to those used by the annual Alaska Fisheries Science Center (AFSC) standard eastern Bering Sea bottom trawl survey (see Lauth and Acuna, 2007). The samples were collected with an 83-112 eastern otter trawl with a 25.3-m headrope and 34.1-m footrope. The footrope consisted of a single firehose-wrapped chain lacking bobbins or discs, and bottom contact was monitored by using electronic tilt sensors designed by personnel at the AFSC. Towing speed varied from 2 to 3 knots and tows were made directly into prevailing currents and wind to help control towing speed. During each tow, starting and ending latitude, longitude, bottom depth, time, vessel speed, net height and width, and bottom temperatures were recorded with NETMIND (vers. 3.0, Northstar Technical Inc., St. John's, Newfoundland, Canada) acoustic trawl mensuration gear. Area swept was estimated from the average net width and distance fished during each tow. Egg case, fish, and invertebrate densities were estimated from the area swept and from the numbers within each category (egg case, fish, and invertebrate) caught in each trawl haul.

An initial exploratory trawl was conducted in June 2004 to locate the skate nursery. A subsequent survey to determine the spatial coverage of the nursery was conducted during July–August 2004. The extent of the nursery area was determined by using an adaptive trawling approach, where 1) trawls were conducted in each of four directions from 0.5 to 1.5 km apart and 2) a reduced egg case density of <500 eggs/km² was used as the criterion to indicate the farthest limits of the nursery (Fig. 1). The goal was to map the egg case distribution and estimate the size of the nursery area.

The Alaska skate nursery site was sampled a total of eight times over the 14-month period in June, July, September, and November of 2004 and January, April, June, and July of 2005. An index area was chosen during the July–August 2004 investigation and was sampled during each of the subsequent six seasonal sampling periods (September 2004 to July 2005). The index site was defined as an area where the skate eggs were pre-
dominately in early stages of development (newly de-
posited) and a large percentage were viable and at
high densities (>50,000 eggs/km²) to allow tracking
of embryonic development. The index site constituted
an approximate 1-km² area where the highest egg case
density trawls were located. During each seasonal sam-
pling period, a single 5 to 10 min bottom trawl targeted
the index site. The data collected from seasonal sam-
plings were similar to those previously described for the
July–August 2004 trawl investigation; however because
of time limitations, trawl data were limited to bottom
depth, temperature, distance fished, and start and end
latitude and longitude during seasonal sampling.

Collection of biological data

All skates were weighed and enumerated, or a weighed
numerical subsample was used to estimate total num-
ers from weighed samples. All egg cases were identified
to species and documented as empty (posthatching) or
full (prehatching), including eggs that may have been
damaged by the trawl. A random sample of full egg
cases was fixed in 10% formalin from each sampling
period for embryo measurements. Density estimates
for skates and egg cases were calculated as the number
of eggs encountered per km² by using area swept by
the net and the number of individuals encountered in
each trawl.

All skates encountered were identified to species and
sex, and total lengths (TL, to nearest cm) and weights
(to nearest 0.1 g) were recorded. Biological data were
collected on randomly selected Alaska skates during all
seasonal sampling to determine maturity state, repro-
ductive state, and diet composition. During the initial
July 2004 sampling, 67 female and 45 male Alaska
skates were examined and during all subsequent sam-
pling periods from 2 to 12 males and 5 to 17 females
were examined. For each skate sampled the species,
sex, total fish length, total fish weight, stomach content
weight, and general diet composition were recorded. Re-
productive state of males and females were determined
by following maturity stages detailed in Matta and
Gunderson (2007).

Embryo length-frequency measurements

Formalin-fixed egg cases were neutralized and soaked in
tap water for up to four days before measurements were
taken. Egg cases were cut open, embryos excised from
the yolk, and total lengths (TL) were measured to the
nearest 0.5 mm. For analysis, lengths were rounded to
the nearest millimeter. Measurements were taken from
the anterior tip of the snout or disc to the posterior tip
of the tail filament.

Growth rates of Alaska skate embryos were estimated
by following methods similar to those used for the ju-
venile English sole (Plueronectes vetulus) off the Wash-
ington coast (Shi et al., 1996). Natural mode breaks
were used to demarcate cohorts from embryo length
frequencies. A mean embryo length was estimated for
each cohort at each sampling period and plotted along
with the corresponding sampling date. A best-fit linear
model was used to determine daily growth rates of
each cohort. Embryonic growth was assumed linear
throughout development, and the cohort data indicated
that the linear model was applicable. Hatching dates
were estimated by using a mean hatching size of 224
mm TL (mean of all near hatching embryos, n = 39)
and the average growth rate from the linear regres-
sion. Hatching-date estimates were defined as the time
required to reach 224 mm TL based on the length and
date of capture. Egg-deposition date was obtained for
each embryo measured by back-calculating the time
required to reach a size of 1 mm based on the length
and date of capture and the average growth rate. An
estimate of time between cohorts was calculated as the
difference between mean lengths for each cohort divided
daily growth rate to obtain average time between
each depositional event.

Analysis of developmental period determined
from the literature

A review of previously published studies on hatching
duration and rearing temperatures was synthesized for
comparison with hatching duration and rearing tempera-
tures obtained from this study. Species in this analysis
were limited to oviparous elasmobranchs, which encom-
passed a diverse group of 13 chondrichthyan fishes: a
chimera, the spotted ratfish (Hydrolagus coliei), two
catshark species (Scyllorhinus spp.), and ten species of
skates in three genera (Raja, Leucoraja, and Okamejei)
(Table 1). Species reviewed were found from subtropi-
cal to temperate waters spanning a range of tempera-
tures from 4.6°C to 24°C. Developmental periods and
rearing temperatures were obtained from the reported
literature for each study. When a range was reported
for either developmental period or rearing temperature,
an arithmetic mean was calculated from those values.
Temperature and embryonic development period were
plotted and a nonlinear regression algorithm was applied
to the data.

Habitat use

The distribution of life stages of the Alaska skate was
investigated by examining bottom trawl survey data
from the eastern Bering Sea summertime groundfish
survey of the AFSC for years 2000 through 2007 (Lauth
and Acuna, 2007). Alaska skate density for each sta-
tion was estimated as the summed catch per unit of
effort (CPUE, number of skates/km²) obtained at each
station for the eight years surveyed. Density estimates
were calculated at each trawl station for each life his-
tory stage of the Alaska skate: juvenile (<300 mm TL,
newly hatched to age +1); immature (301–920 mm TL);
and adults (>920 mm TL, average maturity size; Matta
and Gunderson, 2007). Distribution maps were produced
with ArcMap (vers. 8.3, Environmental System Research
Institute (ESRI) Redlands, CA).
Table 1
Data from reported embryonic developmental periods and developmental temperatures for oviparous elasmobranch species from previously published studies worldwide. Values are the arithmetic means of the reported values.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Mean developmental period (days)</th>
<th>Mean developmental temperature (°C)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thorny skate</td>
<td>Raja radiata</td>
<td>912</td>
<td>4.6</td>
<td>Berestovskii, 1994</td>
</tr>
<tr>
<td>Little skate</td>
<td>Leucoraja erinacea</td>
<td>279</td>
<td>10</td>
<td>Steele et al., 2004</td>
</tr>
<tr>
<td>Clearnose skate</td>
<td>Raja eglanteria</td>
<td>63</td>
<td>24</td>
<td>Libby and Gilbert, 1960</td>
</tr>
<tr>
<td>Clearnose skate</td>
<td>Raja eglanteria</td>
<td>82</td>
<td>21</td>
<td>Luer and Gilbert, 1985</td>
</tr>
<tr>
<td>Clearnose skate</td>
<td>Raja eglanteria</td>
<td>85</td>
<td>20</td>
<td>Luer et al., 2007</td>
</tr>
<tr>
<td>Clearnose skate</td>
<td>Raja eglanteria</td>
<td>368</td>
<td>9.1</td>
<td>Perkins, 1965</td>
</tr>
<tr>
<td>Big skate</td>
<td>Raja binoculata</td>
<td>277</td>
<td>11.5</td>
<td>Hitz and Reid, 1968*</td>
</tr>
<tr>
<td>Spiny rasp skate</td>
<td>Okamejei kenojei</td>
<td>137</td>
<td>14.6</td>
<td>Ishihara et al., 2002</td>
</tr>
<tr>
<td>Thornback skate</td>
<td>Raja clavata</td>
<td>139</td>
<td>14.9</td>
<td>Ellis and Shackley, 1995</td>
</tr>
<tr>
<td>Thornback skate</td>
<td>Raja clavata</td>
<td>137</td>
<td>15.38</td>
<td>Clark, 1922</td>
</tr>
<tr>
<td>Thornback skate</td>
<td>Raja clavata</td>
<td>170</td>
<td>14.31</td>
<td>Clark, 1922</td>
</tr>
<tr>
<td>Small-eyed ray</td>
<td>Raja microcellata</td>
<td>217</td>
<td>14.66</td>
<td>Clark, 1922</td>
</tr>
<tr>
<td>Blonde skate</td>
<td>Raja brachyura</td>
<td>217</td>
<td>14.13</td>
<td>Clark, 1922</td>
</tr>
<tr>
<td>Spotted skate</td>
<td>Raja montagui</td>
<td>155</td>
<td>15.93</td>
<td>Clark, 1922</td>
</tr>
<tr>
<td>Cuckoo skate</td>
<td>Leucoraja naevus</td>
<td>248</td>
<td>13.17</td>
<td>Clark, 1922</td>
</tr>
<tr>
<td>Chain catshark</td>
<td>Scyliorhinus retifer</td>
<td>256</td>
<td>12.25</td>
<td>Castro et al., 1988</td>
</tr>
<tr>
<td>Small spotted catshark</td>
<td>Scyliorhinus canicula</td>
<td>165</td>
<td>13.3</td>
<td>Ellis and Shackley, 1995</td>
</tr>
<tr>
<td>Small spotted catshark</td>
<td>Scyliorhinus canicula</td>
<td>334</td>
<td>10</td>
<td>Thomason et al., 1996</td>
</tr>
<tr>
<td>Small spotted catshark</td>
<td>Scyliorhinus canicula</td>
<td>205</td>
<td>16</td>
<td>Thomason et al., 1996</td>
</tr>
<tr>
<td>Small spotted catshark</td>
<td>Scyliorhinus canicula</td>
<td>160</td>
<td>16</td>
<td>Ballard et al., 1993</td>
</tr>
<tr>
<td>Spotted ratfish</td>
<td>Hydrolagus coliei</td>
<td>300</td>
<td>12.75</td>
<td>Dean, 1906</td>
</tr>
<tr>
<td>Alaska skate</td>
<td>Bathyraja parmifera</td>
<td>1290</td>
<td>4.4</td>
<td>Hoff (this study)</td>
</tr>
</tbody>
</table>

* Indicates an unpublished study for which the author has the original data.

Results

Sampling of nursery site

The nursery site was relatively small in area, covering approximately 2 km² for the highest egg case densities areas. During the initial July–August 2004 nursery investigation, 21 hauls were conducted and egg case densities ranged between 362 and 148,957 eggs/km² (mean=19,470 ±36,030 eggs/km²). A single trawl containing 148,957 eggs/km² possessed >70% viable eggs and was designated as an index site for subsequent seasonal trawl sampling (Fig. 1). The seasonal trawl samples contained between 45,418 and 549,843 eggs/km² (mean =199,683 ±181,467 eggs/km²) from the index site and 53–84% of the eggs per tow were viable. The Alaska skate and the Bering skate (Bathyraja interrupta) were both found during most sampling periods. The Alaska skate predominated in abundance (96%) and in egg case composition (99.6%). Although the Bering skate accounted for about 4% of the skates found at the site, their egg cases contributed only 0.4%, indicating that this was mainly a single species nursery site for the Alaska skate. The most abundant fish species encountered throughout the sampling period included walleye pollock, arrowtooth flounder (Atheresthes stomias), flathead sole (Hippoglossoides elassodon), rex sole (Glyptocephalus zachirus), and Pacific cod. The most abundant invertebrate species (from summer 2004 trawls) were Tanner crab (Chionoecetes bairdi), tentacle-shedding anemone (Liponema brevicornis), and Oregon triton (Fusitriton oregonensis).

Biological sampling

The size composition of Alaska skate, for all samples combined, indicated that males and females of mature sizes and reproductive state used the nursery nearly exclusively of other posthatching stages; immature and newly hatched juvenile skates were rarely found (Fig. 2). Gonad examination revealed developed ovaries and egg cases in the uterus of female Alaska skates, and fully developed claspers and testes in males during all seasons examined, indicating sexual maturity and that skates were in actively reproducing states. Recent studies have provided evidence that the eastern Bering sea populations of Alaska skate reach a mature state around 93 cm TL for both sexes (Matta and Gunderson, 2007); thus nearly all individuals found within the nursery site of the present study were of reproductive size.

Seasonal nursery use was evident from trawl samples collected at the index site. The Alaska skate showed
Hoff: A nursery site of *Bathyraja parmifera* in the eastern Bering Sea
trends of increased abundance (skate density) in the nursery area during 
summer months of June and July in 2004 and 2005 respectively, and few skates 
were found during the nonsummer months of January, April, September, and 
November (Fig. 3).

Stomach analysis of the Alaska skate revealed wall-
eye pollock to be the predominant prey consumed (81% 
by weight, *n*=195), followed by other fish species includ-
ing flatfish, salmon, and unidentified fishes (14.6%), 
and invertebrate species (snow crabs [*Chionoecetes* spp.]
and shrimp that represented the third most important 
component by weight [4.4%]). Seasonal diet analyses 
revealed that feeding occurred throughout the year and 
that skates in advanced reproductive states (gravid) 
early always contained full stomachs.

**Embryo length-frequency analysis**

Embryo length-frequency modal shifts showed a mini-
mum of three cohorts developing simultaneously during 
all sampling periods. The mean length of each cohort 
increased slightly at each subsequent sampling and 
showed a natural progression of development over time, 
and individual cohorts appeared and disappeared as 
time progressed (Fig. 4).

The length data showed that a cohort appeared dur-
ing the November 2004 sampling and persisted dur-
ging the April, June, and July 2005 sampling periods.

The approximate developmental period was 180 days 
from egg deposition (June) until the length samples 
revealed the presence of the cohort (November). The 
long period of early development was similar to that 
of the small spotted catshark (*Scyliorhinus canicula*) 
(Ballard et al., 1993) and the clearnose skate (*Raja 
eglanteria*) (Luer et al., 2007); for these two species, it 
takes approximately 15–16% of the early development-
period before an embryo is visible at 8 to 10 mm. 
This finding was similar to that for the Alaska skate; 
the smallest embryo visible at 15 mm had taken ap-
proximately 14% of the development period to reach 
this size.

Cohorts 1, 2, and 3 showed no difference in linear 
growth rates throughout their size ranges (test of 
slopes *F*=32.11, *P*=0.129; Fig. 5). The estimated daily 
growth rates (slopes) obtained for the cohort length data 
ranged from 0.18 to 0.22 mm/day (mean: 0.20 mm/day 
[Table 2]). The distribution of expected birthdates and 
egg deposition dates from the embryo length frequen-
cies revealed that although there is continuous hatching 
and egg case deposition throughout the year, the peak 
hatching event occurs during fall and winter months 
(October to February: Fig. 6A) and egg case deposition 
peaks during spring and summer months (June to Au-
gust: Fig. 6B).

From average growth rates of 0.20 mm/day, an embry-
onic development period of 3.5 years to reach 224 mm

**Figure 2**

Length frequency for all Alaska skates (*Bathyraja parmifera*) for all trawl samples 
combined from the nursery site in the southeastern Bering Sea. The vertical 
dashed line on each graph indicates the skate length at 50% maturity (male, 
91.75 cm; female, 93.28 cm) for the eastern Bering Sea Alaska skate population 
as determined by Matta and Gunderson (2007).
Figure 3
Density estimates of posthatching Alaska skates (*Bathyraja parmifera*) from the eastern Bering Sea nursery site at each seasonal sampling period. Each density estimate was determined from a single tow conducted near the center of the nursery at the index site.

Table 2
Mean length and standard deviation for each cohort of embryos during each sampling period for the Alaska skate (*Bathyraja parmifera*) at the eastern Bering Sea nursery site. A linear regression equation and growth rate for each cohort was estimated from mean embryo lengths. Number of embryos included in each mean length (±1 standard deviation) is denoted by *n*. The time lag between cohorts is the estimated interval between the cohorts—a period determined from mean cohort lengths and growth rates at each sampling period. Cohort 3 had hatched by 18 April 2005 sampling.

<table>
<thead>
<tr>
<th>Sampling period</th>
<th>Cohort 1 mean length (mm)</th>
<th>n</th>
<th>Cohort 2 mean length (mm)</th>
<th>n</th>
<th>Cohort 3 mean length (mm)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 June 2004</td>
<td>41.6 ±8.09</td>
<td>20</td>
<td>91.5 ±15.12</td>
<td>10</td>
<td>187.89 ±7.88</td>
<td>9</td>
</tr>
<tr>
<td>27 July 2004</td>
<td>46.96 ±10.43</td>
<td>23</td>
<td>118.13 ±16.76</td>
<td>8</td>
<td>199.53 ±8.86</td>
<td>15</td>
</tr>
<tr>
<td>11 September 2004</td>
<td>57.44 ±8.13</td>
<td>73</td>
<td>131.89 ±12.97</td>
<td>46</td>
<td>207.82 ±9.57</td>
<td>11</td>
</tr>
<tr>
<td>17 November 2004</td>
<td>65.24 ±10.33</td>
<td>53</td>
<td>141 ±1.41</td>
<td>2</td>
<td>217 ±12.28</td>
<td>8</td>
</tr>
<tr>
<td>16 January 2005</td>
<td>84.17 ±6.19</td>
<td>18</td>
<td>156.38 ±13.31</td>
<td>21</td>
<td>233 ±11.31</td>
<td>2</td>
</tr>
<tr>
<td>18 April 2005</td>
<td>97.11 ±7.25</td>
<td>28</td>
<td>171.85 ±18.75</td>
<td>13</td>
<td>Hatching</td>
<td></td>
</tr>
<tr>
<td>1 June 2005</td>
<td>113.83 ±10.25</td>
<td>24</td>
<td>193.27 ±7.92</td>
<td>27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 July 2005</td>
<td>116.07 ±11.45</td>
<td>57</td>
<td>200.5 ±0.71</td>
<td>7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Linear equation
- Cohort 1: *y* = 0.1819*x* + 13.40
- Cohort 2: *y* = 0.2214*x* + 68.17
- Cohort 3: *y* = 0.1899*x* + 158.80

Growth rate of cohort
- Cohort 1: 0.18 mm/day
- Cohort 2: 0.22 mm/day
- Cohort 3: 0.19 mm/day

Average growth rate
- 0.20 ±0.02 mm/day

Time lag between cohort 1 and 2
- 348.79 ±41.27 days

Time lag between cohort 2 and 3
- 411.07 ±44.28 days

TL was estimated. The time lag between cohorts 1 and 2 was mean=348 ±41 days and between cohorts 2 and 3 mean=411 ±44 days and an overall mean=371 ±50 days between egg deposition events of cohorts one, two, and three combined (Table 2). These data indicate an annual egg deposition cycle, and each cohort represents the result of a single reproductive event that occurs during the summer months.
Analysis of published developmental periods

Developmental period for the Alaska skate was the longest period yet observed for any oviparous elasmobranch species. Embryonic developmental periods were highly correlated with the rearing temperatures for the other oviparous elasmobranchs included in this review (Fig. 7). Most studies were conducted in >8°C water temperatures and developmental periods were one year or less. However, a single study conducted on the thorny skates (*Raja radiata*) (Berestovskii, 1994) in water temperatures near those found for the Alaska skate revealed that the developmental periods of these two species to be comparable (thorny skate, 4.6°C, 912 days; Alaska skate, 4.4°C, 1290 days).
Habitat use

Analysis of trawl catch data and depth soundings showed that the nursery site had little benthic structure or habitat diversity and the bottom was generally flat, and composed of sandy mud. The trawl samples within the nursery did not contain any attached benthic invertebrates that would have constituted a unique habitat. Bottom depths varied by only several meters throughout the nursery site (145 to 150 m) and the average bottom depth was 149 m, weighted by egg case density. Bottom temperatures at the nursery index site varied little throughout the year, ranging between a low of 4.1°C in June 2004 and April 2005, to a high of 5.0°C in July of 2004. The mean bottom temperature for the 14-month study period was 4.40°C ±0.327°C.

The Alaska skate was widely distributed across the eastern Bering Sea shelf and the immature stages used a different portion of the habitat than that used by newly hatched juveniles and mature adults. Juvenile skates were distributed along the outer continental shelf (100−200 m) and overlapped in distribution with mature adults (Fig. 8). Immature Alaska skates were distributed mainly in the middle and inner shelf regions and were found less on the outer shelf. A model lifetime movement pattern for the Alaska skate indicates an ontogenetic shift in habitat use in which there is a cyclical movement across the shelf after hatching to the shallow inner shelf, followed by a return to the outer shelf as maturity is reached (Fig. 8).

Discussion

Recent advances in elasmobranch biology have stressed the importance of identification and conservation of nursery sites for oviparous elasmobranchs (Ellis et al., 2004). Understanding habitat requirements for skate reproduction may be critical for successful management plans for these vulnerable species. The results presented here are the first reported dynamics of a skate nursery with regard to reproductive patterns and habitat use.

Because of their inherent low fecundity and slow growth rates, skates may reproduce with distinct seasonal pulses, over protracted periods, or in some cases continuously throughout the year (Templeman, 1982; Sulikowski et al., 2005). Results from previous
studies have shown that the Alaska skate is reproductively active year-round and that peak egg production occurs during summer months (Matta, 2006; Matta and Gundersen, 2007). A distinct summertime pulse of egg deposition was evident from the nursery site seasonal skate abundance data, and distinct cohorts of embryos were present in the nursery throughout the year.

Embryonic development of the Alaska skate was estimated to take over 3.5 years from egg deposition until hatching, and as a consequence multiple cohorts were developing simultaneously at the nursery site. Embryonic developmental rates are most likely coupled with environmental temperatures and produce a Q_{10} effect where there is an exponential change in metabolic processes as temperature changes (Schmidt-Nielsen, 1997; Charnov and Gillooly, 2003). The sensitivity of the developmental period to temperature increases is significant; if one uses the regression equation parameters, a mean increase of 0.5°C in environmental temperatures could decrease the developmental period of the Alaska skate by nearly 16% (~6 months) and there would be stronger effects as greater temperature changes occurred. This has dramatic implications on what influence climate change may have on the shelf-slope environment, and skate reproduction and recruitment. The dramatic increase or decrease in recruitment success due to environmental changes may become an important model parameter for stock assessments and management plans for elasmobranch species.

For the estimate of growth rate for the Alaska skate in this study, linear growth was assumed during the developmental period and an effect of environmental temperature on growth rate was not considered because environmental temperatures varied little during this study. These variables recognizably may influence daily growth estimates and therefore the length of developmental period, however averaging across three years of cohorts may provide an accurate estimate of the relatively long developmental period for the Alaska skate, as well as for other oviparous species in cold waters. Linear growth during embryonic development for the size range reported here for the Alaska skate was similar to that for the clearnose skate from approximately 18 mm through hatching (Luer et al., 2007).

Site selection criteria for skate nurseries are as of yet unknown, however areas of high biological productivity may be a requirement for nursery sites because of the protracted reproductive activity and energy requirements of adults. The Alaska skate nursery site is in a region of high slope-shelf water transport and is one of the most productive regions in the eastern Bering Sea (Stabeno et al., 1999); it has supported walleye pollock and Pacific cod bottom trawl fisheries for more than 25 years. Walleye pollock, the main food source of adult Alaska skates (Lang et al., 2005), co-exist in the outer-shelf region during summertime (Kotwicki et al., 2005). Results from the nursery seasonal diet analysis indicated that reproductively active skates feed throughout the year, almost exclusively on walleye pollock. A ready supply of food may allow skates to remain near the nursery site and minimize foraging excursions during protracted reproductive cycles.

Adequate current flows and stable temperatures such as those encountered in the upper slope area of the eastern Bering Sea may be critical for successful hatching and embryo development. From early stages of development, the embryo is dependent on a constant current of fresh seawater to supply tissues with oxygen, remove metabolic waste (Hamlett and Koob, 1999), and prevent the egg case from being buried in sediment. Although strong currents pose a hazard to egg cases by transporting them out of the nursery site, this does not appear to happen frequently because egg cases are rarely found widely scattered outside the nursery, and within nurseries egg cases often cover a small area and are highly concentrated. The upper slope environment provides a nearly constant bottom temperature through upwelled waters that inundate the outer shelf.

![Figure 7](image-url)

**Figure 7**

Relationship between rearing temperature and days to hatching determined from 21 published studies and 13 oviparous chondrichthyan species. Open circles represent values from the literature and the shaded circle is estimated embryonic developmental period for the Alaska skate (*Bathyraja parmifera*) in the present study. The hatching time of the Alaska skate was not used to determine the equation parameters. See Table 1 for data sources.
Figure 8

Distribution in the eastern Bering Sea of the Alaska skate (*Bathyraja parmifera*) at three life stages: (A) neonate, (B) immature, and (C) mature. Data are from a summertime (June–July) bottom trawl survey conducted on the eastern Bering Sea shelf from 20–200 m by the Alaska Fisheries Science Center. Dots represent a summation of catch per unit of effort (number skates/km²) at each survey station for the eight survey years 2000–07. Life stages are defined as the following: neonate < 310 mm total length; immature = 310–920 mm total length; and adult > 920 mm total length. (D) Diagram of life-time movement patterns for the Alaska skate in the eastern Bering Sea based on summertime survey data. Young skates are distributed along the outer continental shelf edge where nursery sites occurred. The newly hatched skates move to the middle and inner shelf where they remain until returning to the outer continental shelf at maturity.

(Pavlov and Pavlov, 1996; Luchin et al., 1999) and the nursery experiences relatively stable year-round water temperatures from 4.1° to 5.0°C. By comparison, middle shelf bottom waters are extremely cold throughout the year and may reach <0°C (Luchin et al., 1999; Lauth and Acuna, 2007). Annually the upper slope water may provide the most stable and relatively warm environment for embryo development.
Habitat requirements of newly hatched juvenile skates may not be the criteria for nursery-site selection because very few newly hatched skates were found at the site. The most likely explanation is that neonate skates move out of the nursery area shortly after emergence, possibly to reduce intraspecific competition along the slope edge or to avoid large predators that prey on juvenile skates (Hoff, 2007). In trawl studies with the same designs and methods as those of the present study and conducted across the outer continental shelf region, newly hatched juvenile Alaska skates were found to be common (Kotwicki and Weinberg, 2005; Lauth and Acuna, 2007). Many individuals encountered on the outer shelf still possessed tail filaments, providing evidence of recent emergence from the egg case (Hoff, 2007). The reason why juvenile skate move to inner and outer shelf waters remains unclear; however, a pattern in their movements from inner to outer shelf regions in the eastern Bering Sea and in their use of different habitats at different life stages is evident.

These patterns indicate that skate nurseries may be occupied by skates at two of most critical life stages (embryos and adults), and conservation efforts targeting these stages may have the greatest impact on population protection (Frisk et al., 2002, 2004). Skate nurseries in general may be located in areas of high biological productivity and therefore are susceptible to disturbances caused by increased fishing activities. As oviparous elasmobranchs, fishery mortality and fishery stability of these nursery sites may become important locations to be monitored for the health and recruitment potential of skate species. Long-term monitoring of these important habitats can provide a wealth of information with minimal effort because of the permanence or long-term stability of these nursery sites.

Acknowledgments

I thank the skippers and crew of the FVs Ocean Explorer, Sea Storm, Nordic Fury, Arcturus, Aldebaran, and Great Pacific. I especially thank D. Stevenson, S. Kotwicki, S. Gaichas, R. Reuter, E. Iwamoto, E. Acuna, E. Jorgenson, C. Gredzens, B. Voss, B. Lauth, R. Nelson, G. Stauffer, and G. Walters for their support. I also thank T. Essington, D. Gunderson, D. Kimura, T. Pietsch, and C. Rooper for their review and helpful suggestions to improve this manuscript. This project was supported by North Pacific Research Board (NPRB grant no. 415), Essential Fish Habitat (EFH), and the Alaska Fisheries Science Center.

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