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

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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 km^2), 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.

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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 (135 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.

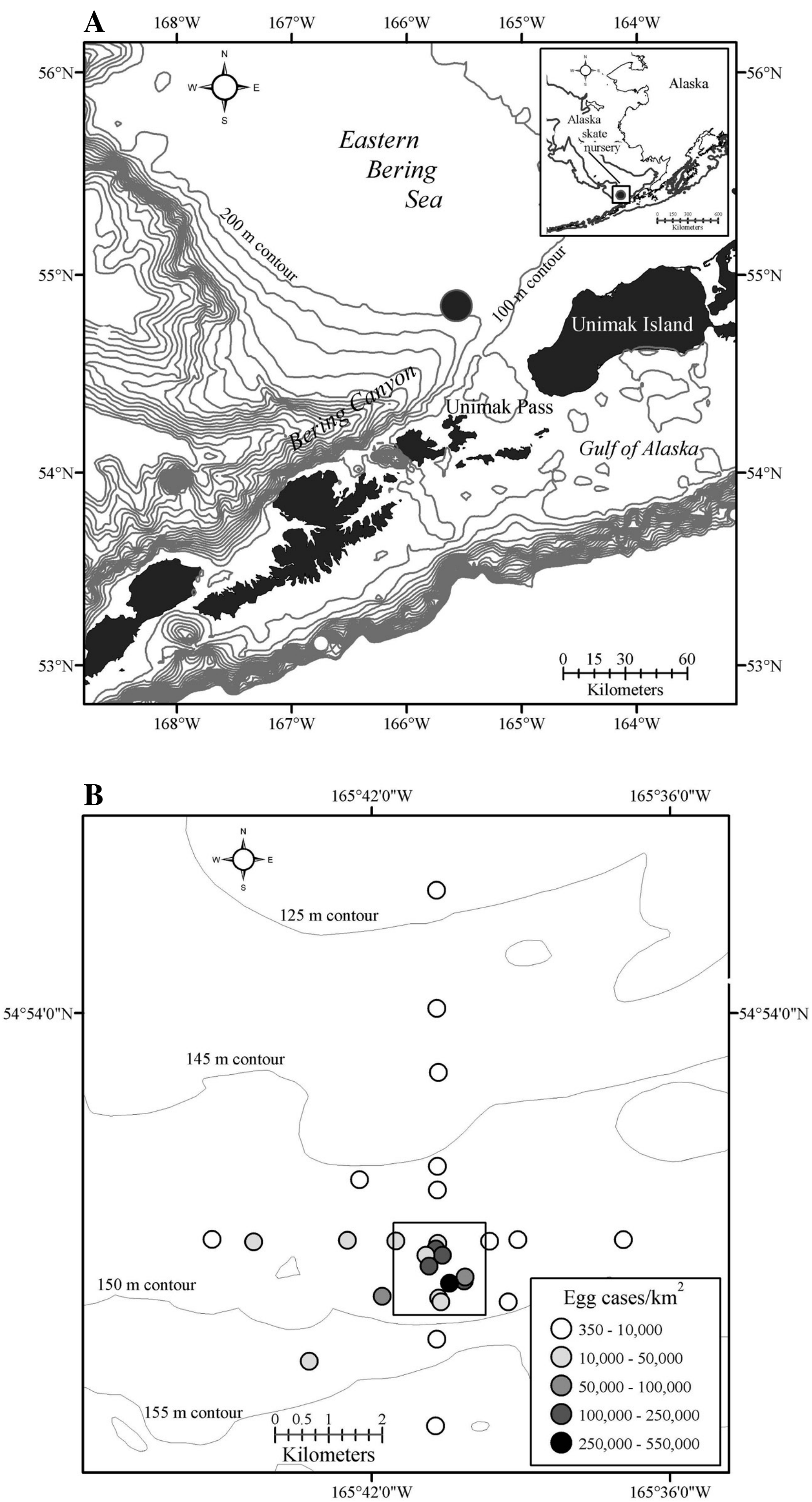

Figure 1

(**A**) Map of the eastern Bering Sea, Alaska, and location of a nursery site (dark circle) for the Alaska skate (*Bathyraja parmifera*) at the head of Bering Canyon. (**B**) Locations at the nursery site for all trawls completed. The area in the box was designated as the index site and targeted for a 14-month seasonal study conducted during 2004–05.

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/km^2 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 predominately in early stages of development (newly deposited) and a large percentage were viable and at high densities (>50,000 eggs/km^2) to allow tracking of embryonic development. The index site constituted an approximate 1-km^2 area where the highest egg case density trawls were located. During each seasonal sampling period, a single 5 to 10 min bottom trawl targeted the index site. The data collected from seasonal samplings 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 numbers 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 km^2 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, reproductive state, and diet composition. During the initial July 2004 sampling, 67 female and 45 male Alaska skates were examined and during all subsequent sampling 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. Reproductive 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 juvenile English sole (*Plueronectes vetulus*) off the Washington 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 regression. 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 by 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 temperatures obtained from this study. Species in this analysis were limited to oviparous elasmobranchs, which encompassed a diverse group of 13 chondrichthyan fishes: a chimera, the spotted ratfish (*Hydrolagus colliei*), two catshark species (*Scyliorhinus* spp.), and ten species of skates in three genera (*Raja*, *Leucoraja*, and *Okamejei*) (Table 1). Species reviewed were found from subtropical to temperate waters spanning a range of temperatures 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 station was estimated as the summed catch per unit of effort (CPUE, number of skates/km^2) obtained at each station for the eight years surveyed. Density estimates were calculated at each trawl station for each life history 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.

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

* 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 km^2 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/km^2 (mean=19,470 ±36,030 eggs/km^2). A single trawl containing 148,957 eggs/km^2 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/km^2 (mean =199,683 ±181,467 eggs/km^2) 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

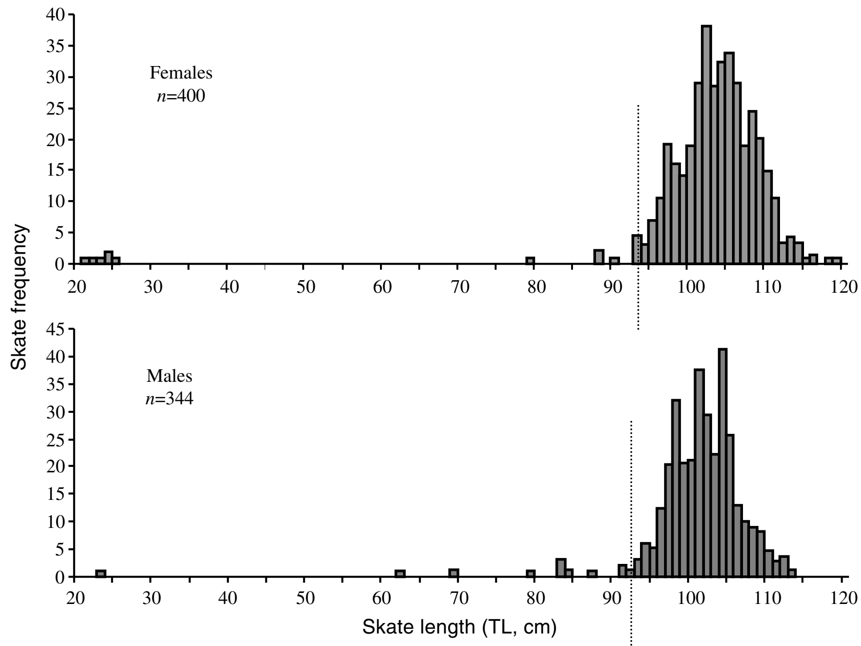

Figure 2

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).

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 walleye pollock to be the predominant prey consumed (81% by weight, n=195), followed by other fish species including 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) nearly always contained full stomachs.

Embryo length-frequency analysis

Embryo length-frequency modal shifts showed a minimum 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 during the November 2004 sampling and persisted during 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 developmental 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 approximately 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 frequencies 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 August: Fig. 6B).

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

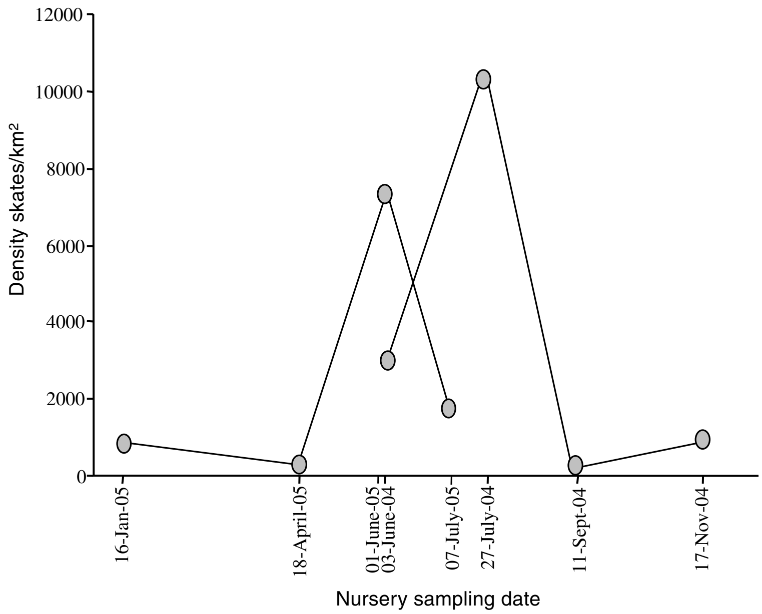

Figure 3

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.

Sampling period	Cohort 1 mean length (mm)	*n*	Cohort 2 mean length (mm)	*n*	Cohort 3 mean length (mm)	*n*
3 June 2004	41.6 ±8.09	20	91.5 ±15.12	10	187.89 ±7.88	9
27 July 2004	46.96 ±10.43	23	118.13 ±16.76	8	199.53 ±8.86	15
11 September 2004	57.44 ±8.13	73	131.89 ±12.97	46	207.82 ±9.57	11
17 November 2004	65.24 ±10.33	53	141 ±1.41	2	217 ±12.28	8
16 January 2005	84.17 ±6.19	18	156.38 ±13.31	21	233 ±11.31	2
18 April 2005	97.11 ±7.25	28	171.85 ±18.75	13	Hatching	
1 June 2005	113.83 ±10.25	24	193.27 ±7.92	27		
7 July 2005	116.07 ±11.45	57	200.5 ±0.71	7		
Linear equation	$y=0.1819x+13.40$		$y=0.2214x+68.17$		$y=0.1899x+158.80$	
Growth rate of cohort	0.18 mm/day		0.22 mm/day		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.

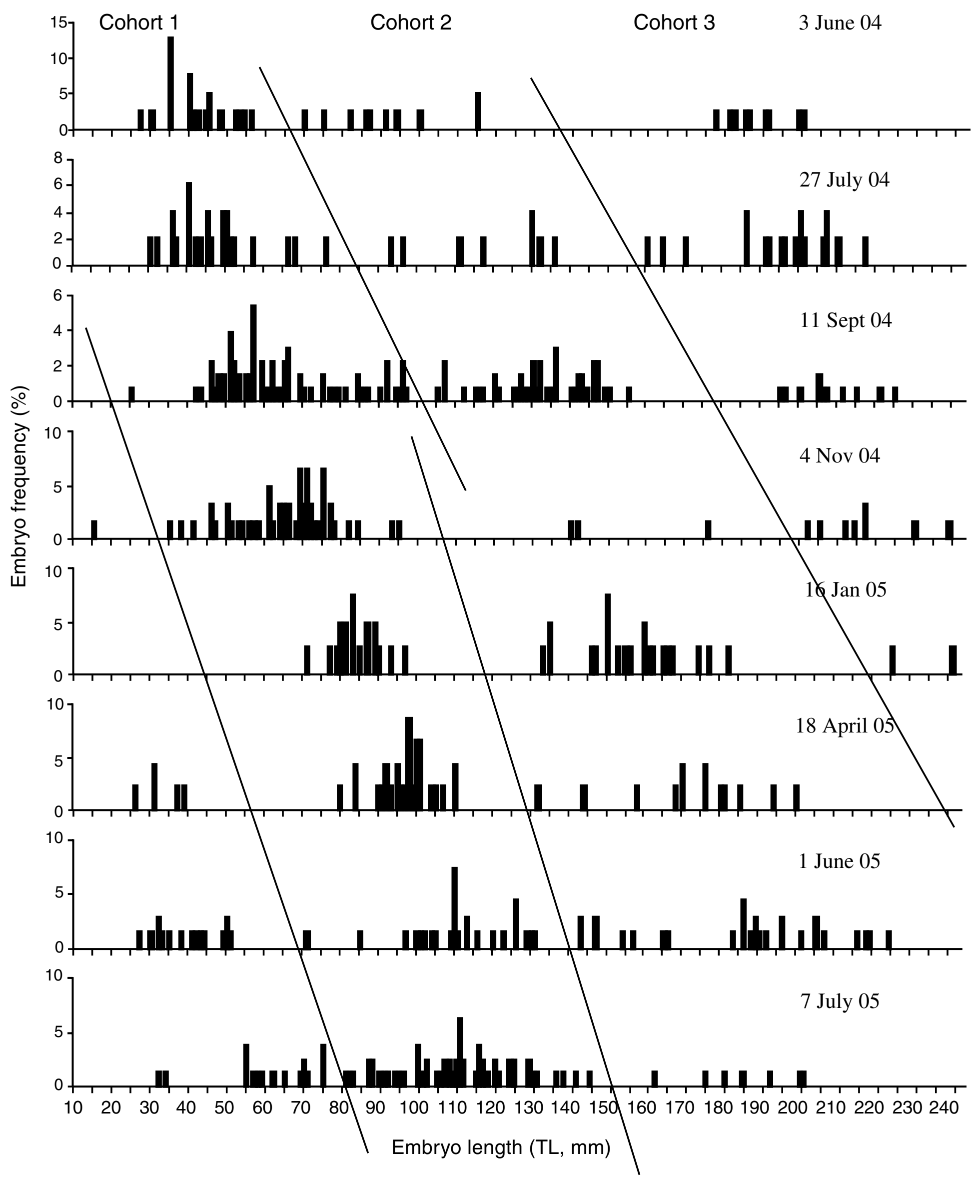

Figure 4

Length frequency for embryos of the Alaska skate (*Bathyraja parmifera*) collected during each sampling date at the nursery index site in the eastern Bering Sea. Embryos were assigned to cohorts 1, 2, or 3 (separated by diagonal lines) following mode frequencies. A fourth cohort was evident that was detected in the November 2004 sampling and persisted through July 2005 (graph left) but was not used for growth-rate estimates.

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).

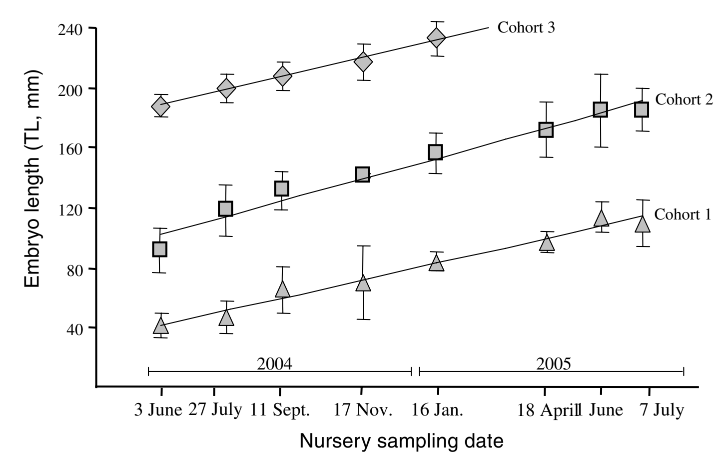

Figure 5

Mean embryo total length (±1 standard deviation) at each sampling date for each cohort from the length-frequency data for the Alaska skate (*Bathyraja parmifera*). Growth rates were estimated from the slope of the linear relationships for each cohort.

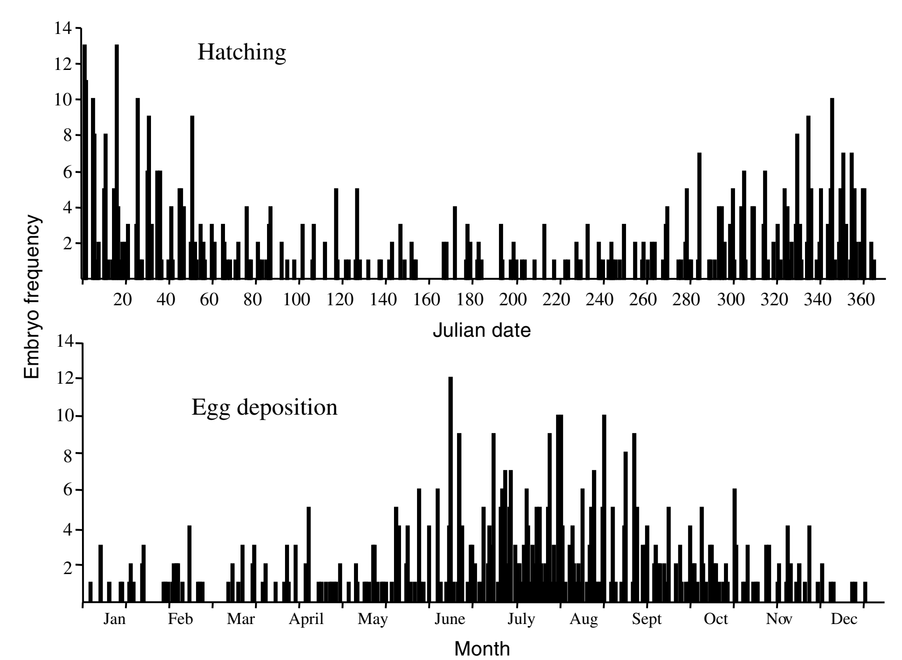

Figure 6

Estimated time of hatching (top) and egg deposition (bottom) frequency for all embryos measured from the Alaska skate (*Bathyraja parmifera*) nursery site. Hatching and egg deposition dates were determined from the average growth rate of 0.2 mm/day and an estimated hatching size of 224 mm total length. The *x*-axis indicates the Julian date (top) and the corresponding month (bottom).

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

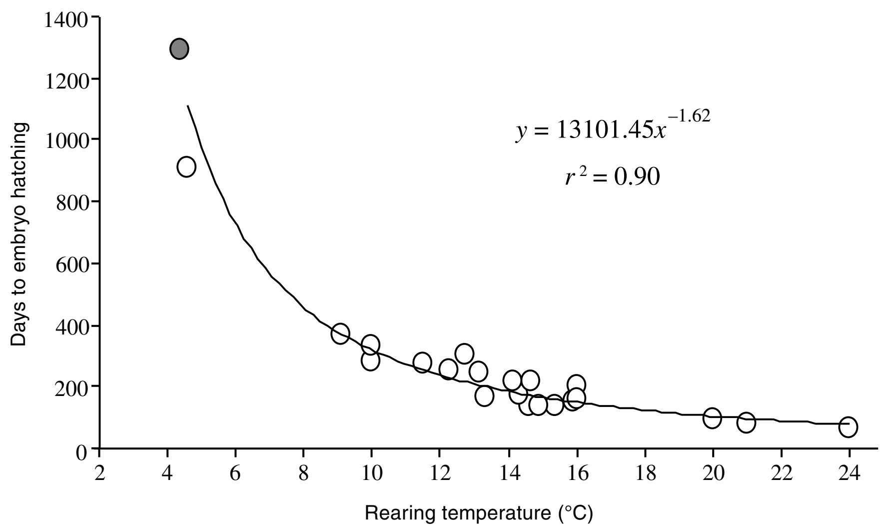

Figure 7

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.

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 Gunderson, 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

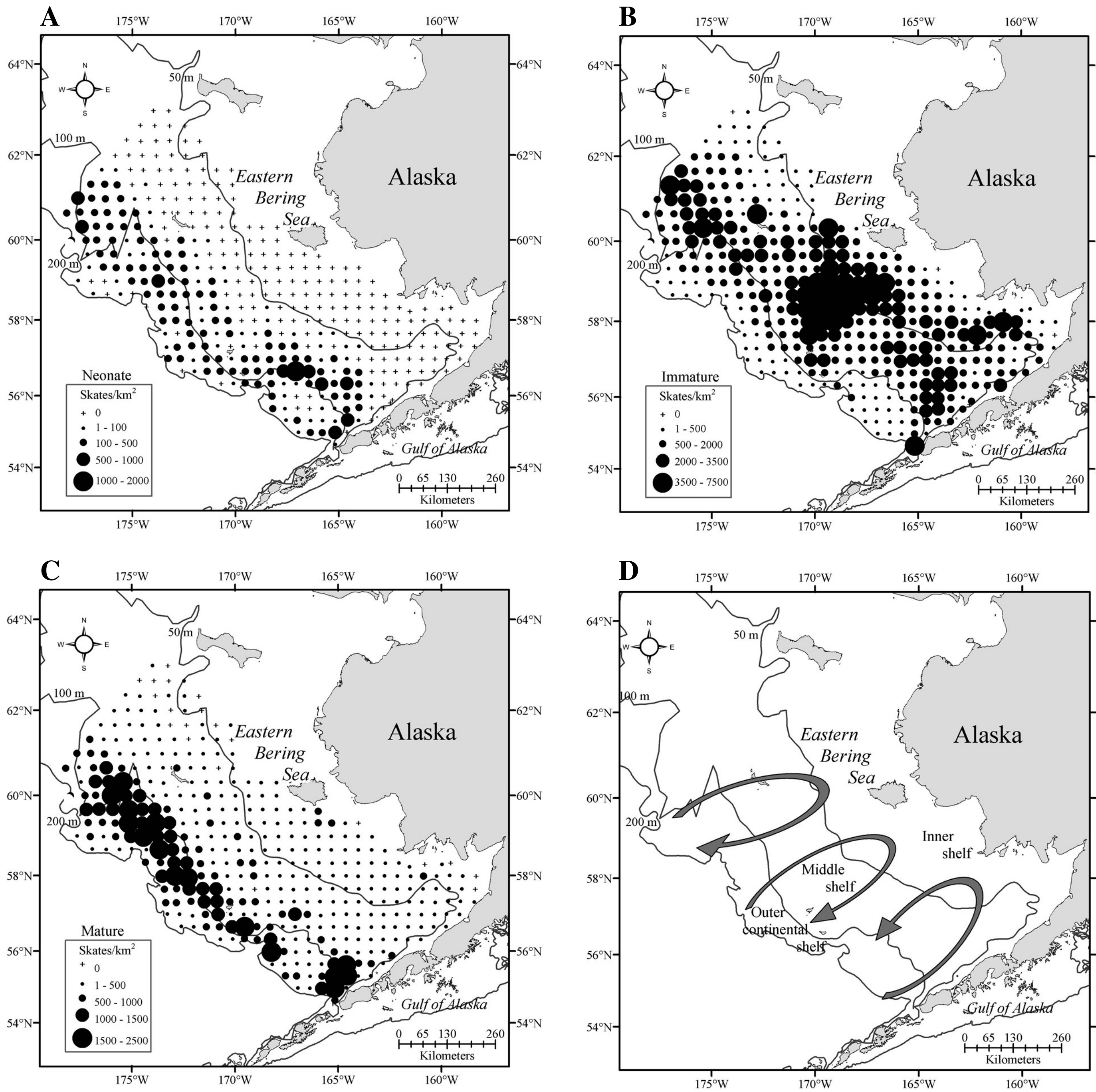

Figure 8

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/km^2) 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 elasmobranch fishing mortality increases, recognition and protection of nursery habitats may be one approach to ensure healthy populations. Likewise, 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.

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Literature cited

Ballard, W. W., J. Mellinger, and H. Lechenault.
1993. A series of normal stages for development of *Scyliorhinus canicula*, the lesser spotted dogfish (Chondrichthyes: Scyliorhinidae). J. Exp. Zool. 267:318–336.

Berestovskii, E. G.
1994. Reproductive biology of the family Rajidae in the seas of the far north. J. Ichthyol. 34(6):26–37.

Castro, J. I., P. M. Bubucis, and N. A. Overstrom.
1988. The reproductive biology of the chain dogfish, *Scyliorhinus retifer*. Copeia 1988:740–746.

Charnov, E. L., and J. F. Gillooly.
2003. Thermal time: body size, food quality and the 10°C rule. Evol. Ecol. Res. 5:43–51.

Clark, R. S.
1922. Rays and skates (Rajidae). No 1. Egg-capsules and young. J. Mar. Biol. Assoc. U.K. 12(4):577–643.

Dean, B.
1906. Chimaeroid fishes and their development. Carnegie Institution of Washington 32:1–194.

Dulvy, N. K., J. D. Metcalfe, J. Glanville, M. G. Pawson, and J. D. Reynolds.
1999. Fishery stability, local extinctions, and shifts in community structure in skates. Conserv. Biol. 14(1):283–293.

Ellis, J. R., A. Cruz-Martinez, B. D. Rackham, and S. I. Rogers.
2004. The distribution of chondrichthyan fishes around the British Isles and implications for conservation. J. Northw. Atl. Fish. Sci. 35(5):195–213.

Ellis, J. R., and S. E. Shackley.
1995. Observations on egg-laying in the thornback ray. J. Fish Biol. 46:903–904.

Frisk, M. G., T. J. Miller, and N. K. Dulvy.
2004. Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. J. Northw. Atl. Fish. Sci. 35(4):27–45.

Frisk, M. G., T. J. Miller, and M. J. Fogarty.
2002. The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analysis. ICES J. Mar. Sci. 59:576–586.

Hamlett, W. C., and T. J. Koob.
1999. Female reproductive system. *In* sharks, skates and rays; the biology of elasmobranch fish (W. C. Hamlett, ed.), p. 398–443. Johns Hopkins Univ. Press, Baltimore, MD.

Hitz, C. R.
1964. Observations on egg cases of the big skate (*Raja binoculata* Girard) found in Oregon coastal waters. J. Fish. Res. Board Can. 21(4):851–854.

Hoff, G. R.
2006. Biodiversity as an index of regime shift in the eastern Bering Sea. Fish. Bull. 104:226–237.
2007. Reproductive biology of the Alaska skate *Bathyraja parmifera*, with regard to nursery sites, embryo development and predation. Ph. D. diss., 161 p. Univ. Washington, Seattle, WA.

Hoff, G. R., and L. L. Britt.
2003. The 2002 eastern Bering Sea upper continental slope survey of groundfish and invertebrate resources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-141, 261 p.
2005. Results of the 2004 eastern Bering Sea upper continental slope survey of groundfish and invertebrate resources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-156, 276 p.

Ishihara, H., T. Mochizuki, K. Homa, and T. Taniuchi.
2002. Reproductive strategy of the Japanese common

skate (spiny rasp skate) *Okamejei kenojei*. *In* Elasmobranch biodiversity, conservation and management, p. 236–240. Occasional Paper of the IUCN Species Survival Commission 25.

Knight, D. P., D. Feng, and M. Stewart.
1996. Structure and function of the Salachian egg case. Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci. 71:81–111.

Kotwicki, S., and K. L. Weinberg.
2005. Estimating capture probability of a survey bottom trawl for Bering Sea skates (*Bathyraja* spp.) and other fish. Alaska Fish. Res. Bull. 11(2):135–145.

Kotwicki, S., T. W. Buckley, T. Honkalehto, and G. Walters.
2005. Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration. Fish. Bull. 103:574–587.

Lang, G. M., P. A. Livingston, and K. A. Dodd.
2005. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1997 through 2001. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-158, 230 p.

Lauth, R. R., and E. Acuna.
2007. Results of the 2006 eastern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrates resources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-176, 175 p.

Libby, E. L., and P. W. Gilbert.
1960. Reproduction in the clear-nosed skate, *Raja eglanteria*. Anat. Rec. 138(3):365.

Luchin, V. A., V. A. Menovshchikov, V. M. Lavrentiev, and R. K. Reed.
1999. Thermohaline structure and water masses in the Bering Sea. *In* Dynamics of the Bering Sea (T. R. Loughlin, and K. Ohtani, eds.), p. 61–91. Univ. Alaska Sea Grant Rep. AK-SG-99-03, Fairbanks, AK.

Luer, C. A., and P. W. Gilbert.
1985. Mating behavior, egg deposition, incubation period, and hatching in the clearnose skate, *Raja eglanteria*. Environ. Biol. Fish. 13:161–171.

Luer, C. A., C. J. Walsh, A. B. Bodine, and J. T. Wyffels.
2007. Normal embryonic development in the clearnose skate, *Raja eglanteria*, with experimental observations on artificial insemination. Environ. Biol. Fish. 80:239–255.

Matta, M. E.
2006. Aspects of the life history of the Alaska skate, *Bathyraja parmifera*, in the eastern Bering Sea. M.S. thesis, 86 p. Univ. Washington, Seattle, WA.

Matta, M. E., and D. R. Gunderson.
2007. Age, growth, maturity, and mortality of the Alaska skate, *Bathyraja parmifera*, in the eastern Bering Sea. Environ. Biol. Fish. 80:309–323.

Musick, J. A., G. Burgess, G. Cailliet, M. Camhi, and S. Fordham.
2000. Management of sharks and their relatives (Elasmobranchii). Fisheries 25(3):9–13.

Pavlov, V. K., and P. V. Pavlov.
1996. Oceanographic description of the Bering Sea. *In* Ecology of the Bering Sea: A review of Russian Literature (O. A. Mathisen, and K. O. Coyle, eds.), p. 1–96. Univ. of Alaska Sea Grant Rep. AK-SG-96-01, Fairbanks, AK.

Perkins, F. E.
1965. Incubation of fall-spawned eggs of the little skate, *Raja erinacea* (Mitchill). Copeia 1965:114–115.

Schmidt-Nielsen, K.
1997. Animal physiology: adaptation and environment, 5^{th} ed., 612 p. Cambridge Univ. Press, Cambridge, U.K.

Shi, Y., D. R. Gunderson, and P. J. Sullivan.
1996. Growth and survival of 0+ English sole, *Pleuronectes vetulus*, in estuaries and adjacentnearshore waters off Washington. Fish. Bull. 95:161–173.

Stabeno, P. J., J. D. Schumacher, and K. Ohtani.
1999. The physical oceanography of the Bering Sea. *In* Dynamics of the Bering Sea (T. R Loughlin, and K. Ohtani, eds.), p.1–28. Univ. Alaska Sea Grant Rep. AK-SG-99-03, Fairbanks, AK.

Steele, S. L., P. H. Yancey, and P. A. Wright.
2004. Dogmas and controversies in the handling of nitrogenous wastes: osmoregulation during early embryonic development in the marine little skate *Raja erinacea*; response to changes in external salinity. J. Exp. Biol. 207:2021–2031.

Stevens, J. D., R. Bonfil, N. K. Dulvy, and P. A. Walker.
2000. The effects of fishing on sharks, rays, and chimaeras (chondricthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. 57:476–494.

Stevenson, D. E., J. W. Orr, G. R. Hoff, and J. D. McEachran.
2007. Emerging patterns of species richness, diversity, population density, and distribution in the skates (Rajidae) of Alaska. Fish. Bull. 106:24–39.

Sulikowski, J. A., J. Kneebone, S. Elzey, J. Jurek, P. D. Danley, W. H. Howell, and P. C. W. Tsang.
2005. The reproduction cycle of the thorny skate (*Amblyraja radiata*) in the western Gulf of Maine. Fish. Bull. 103:536–543.

Templeman, W.
1982. Development, occurrence and characteristics of egg capsules of the thorny skate, *Raja radiata*, in the Northwest Atlantic. J. Northw. Atl. Fish. Sci. 3:47–56.

Thomason, J. C., W. Conn, E. L. Comte, and J. Davenport.
1996. Effect of temperature and photoperiod on the growth of the embryonic dogfish, *Scyliorhinus canicula*. J. Fish Biol. 49:739–742.