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Author to whom correspondence should be addressed. Tel.: +1 206-526-4580; email: jerry.hoff@noaa.gov

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The use of more than a single nursery habitat type is examined for oviparous elasmobranchs using data summarized from studies conducted on the Alaska skate *Bathyraja parmifera* and the Aleutian skate *Bathyraja aleutica* in the eastern Bering Sea. The eastern Bering Sea skate species use two discrete areas as nurseries, one for egg deposition and a second for newly emergent juveniles. Egg deposition sites were located along the outer shelf and upper slope near canyons in the eastern Bering Sea. Newly emergent juveniles were found along the outer and middle shelf for *B. parmifera* and deep-slope for *B. aleutica*, suggesting habitat used by newly emergent juvenile skates is distinct from habitat used for egg deposition and embryo development. In reviewing many studies on oviparous elasmobranchs similar patterns emerge of habitat use during their early life history. To distinguish these distinct habitats, appropriate terminology is proposed. Egg case nursery is suggested for areas of egg deposition and juvenile nursery is suggested for areas where juveniles aggregate after emergence. Criteria to describe each habitat type are outlined.

Key words: Alaska skate; Aleutian skate; continental slope; spawning grounds.

-Author Manuscrip

INTRODUCTION

For aquatic animals the nursery concept describes that portion of a species habitat that is specifically identified for the nurturing of early life stages. In general, this term is applied to habitats that promote the well-being (*i.e.* density, growth and survival) of juveniles to reach maturity (Beck et al., 2001), and may be habitats of exceptional quality which produce more recruits than other habitats where juveniles occur (Beck et al., 2001). For the successful management and conservation of any marine species it is necessary to identify all habitats important for successful recruitment (Beck et al., 2001; Dahlgren et al., 2006). It is clear that locations where oviparous elasmobranchs deposit their egg cases is important habitat (Beck et al., 2001; Heupel et al., 2007), and these areas are of critical importance for successful reproduction and recruitment (Hoff, 2008, 2009b, 2010). A demonstration of their recognized importance is the decision by the North Pacific Fishery Management Council (2015) to designate six locations [eight egg deposition sites for three species: the Alaska skate Bathyraja parmifera (Bean 1881), the Aleutian skate *Bathyraja aleutica* (Gilbert 1896) and the Bering skate Bathyraja interrupta (Gill & Townsend 1897)] in the eastern Bering Sea (EBS) as habitat areas of particular concern (HAPC), and consider them for protective measures, the first formal recognition of this habitat type worldwide. The designation of HAPC by definition is the recognition of some part of a species essential fish habitat (EFH) as, having ecological importance, are sensitive to disturbance or development activities, or are rare (Witherell &

Woodby, 2005). In this case the recognition of the ecological importance of areas where skates deposit their egg cases led to the HAPC designation.

The concept of nursery to describe elasmobranch reproductive areas has existed for over 100 years (Heupel et al., 2007), and is commonly applied to viviparous shark habitat where parturition takes place and juveniles remain during their early life period (Heithaus, 2007). Terms used have varied greatly when referring to oviparous elasmobranch (egg laying, *i.e.* skates and sharks) reproductive habitat where eggs are deposited and juveniles spend their early life. To describe the habitat, terms used for egg deposition sites include 'breeding ground' (Orton, 1926), 'beds' (Clark, 1922; Hitz, 1964), 'oviposition areas' (McLaughlin & O'Gower, 1971), 'deposition grounds' (Teshima & Tomonaga, 1986), 'egg deposition sites' (Able & Flescher, 1991; Ellis & Shackley, 1997), 'egg case laying areas' (Mabragana et al., 2002), 'spawning grounds' (Arkhipkin et al., 2008; Henry et al., 2013) and 'egg laying grounds' (Maia et al., 2015). Recently (beginning in c. 2005), however, a number of investigators reported on this habitat referring to it as 'nurseries' (Ellis et al., 2005; Etnoyer & Warrenchuk, 2007; Hoff, 2008,2009b, 2010; Love et al., 2008; Quattrini et al., 2009; Hunt et al., 2011; Treude et al., 2011; Serra-Pereira et al., 2014; Amsler et al., 2015), which has become part of the scientific lexicon when referring to locations where oviparous elasmobranchs deposit their eggs. In addition multiple studies used the term 'nursery' to describe the area juveniles moved to after hatching (McLaughlin & O'Gower, 1971; Able & Flescher, 1991; Skjaeraasen & Bergstad, 2000; Mabragana et al., 2002; Woodland et al., 2011) which was distinguished from areas of egg

case deposition. Hoff (2008, 2010) found that for many EBS skate species newly hatched juveniles do not occupy the same habitat where eggs are deposited, but move to an adjacent or widely disjunct habitat soon after emerging from the egg case (Hoff, 2010). Clearly the recognition and definition of the entire habitat important for the early life of oviparous elasmobranchs is necessary for conservation and management issues for the *c*. 500 species of oviparous elasmobranchs worldwide.

Bathyraja parmifera and *B. aleutica* are both large (> 1 m, total length, L_T) and abundant skate species that constitute > 92% of the estimated skate biomass in the EBS shelf and slope environments combined (Hoff, 2013; Lauth & Nichol, 2013). *Bathyraja parmifera* is most abundant in the continental shelf environment (20–200 m) and is found at > 91% of the trawling stations completed during the annual U.S. National Marine Fisheries Service (NMFS) shelf bottom trawl survey (Lauth & Nichol, 2013) and only 15% of the slope (200–1200 m) trawl stations (Hoff, 2013). *Bathyraja aleutica* is the most abundant skate species on the slope where it is encountered in > 75% of the bottom trawls and rarely found on the shelf (< 1% of stations; Hoff, 2013; Lauth & Nichol, 2013). Both species are encountered at every life stage on the trawl surveys and a number of locations where skates deposit egg cases have been identified along the outer shelf and upper slope environments (Hoff, 2008,2010) providing information on the complete life cycle and habitat use for both species in the EBS.

To demonstrate how skates use nursery habitats, data were examined from two abundant skate species from the EBS and literature examined from many studies worldwide reporting on a diversity of oviparous elasmobranchs with similar habitat use patterns, with a goal of demonstrating the range of habitats used during their early life history.

MATERIALS AND METHODS

Multispecies surveys to assess the living resources of groundfishes and invertebrates were conducted by the National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC) on both the EBS shelf and upper continental slope. Data from both EBS bottom trawl surveys were used for survey years 2000 to 2013, which included 14 survey years for the shelf and six survey years for the slope (years 2000, 2002, 2004, 2008, 2010 and 2012).

The EBS shelf survey is conducted on an annual basis from 20 to 200 m extending from the Alaska Peninsula in the south to north of St Matthew Island, and from the eastern extent of Bristol Bay to the western edge of the continental margin. The shelf survey was conducted using a standardized 83-112 Eastern otter trawl equipped with a 25.3 m headrope and 34.1 m footrope constructed of a fibre core wire rope wrapped with three strand polypropylene rope and split rubber hose. The net body was constructed of 101 mm stretched-mesh polyethylene netting with an 89 mm stretched-mesh codend equipped with a 31 mm stretched-mesh codend liner. The net was fished using 1.83 x 2.75 m (816 kg) steel doors and the net opening was *c*. 16 m wide

(Stauffer, 2004). The survey is of fixed station design where *c*. 376 stations are sampled at the centre of a 20 nautical mile (37 km) grid. A 30 min bottom trawl is towed at 5.5 km h⁻¹ (3 knots) through the fixed location covering *c*. 2.90 km. For complete survey details see Lauth & Nichol (2013).

The EBS upper continental slope survey is conducted on a biennial basis of the EBS upper continental slope region of 200–1200 m depth and extends from Unimak Pass in the south to the Russian Federation and U.S. international border, running through Navarin Canyon in the north. The slope survey was conducted using a standardized Poly Nor'eastern bottom trawl equipped with mud-sweep roller gear, a 27.2 m headrope and 24.9 m footrope constructed of 203 mm solid rubber dises. The net body was constructed of 127 mm stretched-mesh polyethylene netting with an 89 mm stretched-mesh codend equipped with a 32 mm stretched-mesh codend liner. The net was fished using 1.83 x 2.75 m (1000 kg) steel doors and the net opening was *c*. 15 m wide (Stauffer, 2004). The survey is of a stratified random design in which sampling effort is distributed across the survey based on area with a target of *c*. 200 stations completed in each survey year. A pre-selected station is sampled by trawl for 30 min at a tow speed of 4.6 km h⁻¹ (2.5 knots) covering *c*. 2.3 km. For complete survey details see Hoff (2013).

Surveys were conducted during daylight hours (*c*. 0700 to 2100 hours) from late May to early August. The entire contents of each haul were sorted, weighed and enumerated (if appropriate),

and recorded or a sub-sample was taken for large contents and data extrapolated to represent the entire haul. Skates were identified to species, and L_T and sex were recorded for each specimen.

The location of sites where skate deposit eggs came from two sources: random encounters during the aforementioned bottom trawl surveys in both the EBS shelf and slope, and directed studies in which bottom trawls were used to sample and identify egg deposition sites (Hoff, 2008, 2010). Sites for each species were identified by the predominant egg case encountered and by high densities of skate egg cases in a small spatial area [> 15 egg cases per trawl or > 1000 egg cases km⁻² (Hoff, 2010)].

A caveat of the 'nursery' habitat definition is use during the early life history of an organism and generally within the first year of life. Following this determination the data examined were limited to the estimated young-of-the-year (YOY) for skate juveniles. Both *B. parmifera* and B. *aleutica* hatch at *c*. 22–25 cm L_T (Teshima & Tomonaga, 1986; Hoff, 2009*a*) and both are estimated to be 1 year post hatching at 35 cm L_T based on previous studies (Matta & Gunderson, 2007; Haas, 2011). Therefore data from both species that were considered to be YOY juveniles (< 36 cm L_T) were used. Adults are considered to be sexually mature at > 95 cm L_T for *B. parmifera* and > 109 cm L_T for *B. aleutica* (Matta & Gunderson, 2007; Haas, 2011). Data presented here were restricted to only those believed to be sexually mature based on L_T for both species and sexes. Catch per unit effort (CPUE), defined here as the number of fish divided by the area sampled (net width × distance fished) was calculated at each station for each species and L_T category and included all trawls successfully completed even where no skates of the appropriate juvenile or adult designation were encountered. Estimated CPUE from survey data of both juvenile and adult *B. parmifera* and *B. aleutica* were plotted to determine the depth distribution of the first year post-hatching and sexually mature adults (Fig. 1). Distribution plots of the YOY *B. parmifera* (Fig. 2) and *B. aleutica* [Fig. 3(a),(b)] were made using the relative CPUE for that species from each station.

RESULTS

Juvenile *B. parmifera* occurred shallower than the eight egg deposition sites identified for the species (145–316 m) along the upper continental slope and outer shelf of the EBS (Hoff, 2010) (Figs 1 and 2). Juveniles were widely scattered over the deeper part of the middle shelf (50–100 m) and shallow regions of the outer shelf and slope (100–250 m). Juveniles > 62% of the YOY were found at < 145 m with > 84% of the juveniles found at depths < 200 m (Figs 1 and 2). Mature *B. parmifera* were found primarily from 60 to 220 m and habitat overlapped considerably with the juvenile and egg deposition sites.

Juvenile *B. aleutica* were distributed at much greater depths along the slope (Figs 1 and 3) than known egg deposition sites and were rarely encountered at or around these locations and depths.

Bathyraja aleutica egg deposition sites (four) are known from 315 to 372 m depth (Figs 1 and 3), but 99% of the juveniles were found at > 400 m with > 75% found at > 800 m (Fig. 1). The greatest concentrations occurred at depths from 800 to 1200 m. Mature *B. aleutica* occurred primarily from 200 to 500 m, which overlapped with egg deposition site depths, but very little with juveniles.

Like *B. parmifera*, the juveniles of *B. aleutica* are distant from egg deposition sites and each life stage (embryo, juvenile and adult) utilizes different slope or shelf habitats. Distribution of *B. parmifera* juveniles and egg deposition sites showed overlap in the depth distribution of the juvenile, egg deposition sites and the adult habitat (Fig. 1), but the habitats were distinct spatially (Figs 1, 2 and 4) with little overlap. *Bathyraja aleutica* juveniles used habitats disjunct from that of the egg deposition sites and adult habitat (Figs 1, 3 and 4) where they did not overlap, but occurred much deeper along the slope.

To distinguish the two habitat types the terms egg case nursery for sites where oviparous elasmobranchs deposit their eggs in mass and juvenile nursery for habitats where skates move to soon after emergence from the egg are suggested. To distinguish the two habitat types a set of criteria to guide identification of each type are proposed.

EGG CASE NURSERY

(1) Identify geographic location where eggs are deposited at high densities; (2) the habitat is benthic and eggs are contacting benthic or stationary materials (*i.e.* non-mobile on a large scale); (3) sites are used over multiple years as egg case nurseries; (4) post-hatching juveniles identify with habitats other than egg case nursery habitat.

JUVENILE NURSERY

(1)YOY juveniles consistently occur in high abundance; (2) the habitat is distinct from the egg case nursery (*i.e.* little to no overlapping habitats); (3)the habitat has attributes as to contribute significantly to population recruitment success.

DISCUSSION

Locations identified as egg case nursery sites are likely to have oceanographic qualities or particular habitat features conducive for successful embryo development and hatching (Ellis *et al.*, 2005; Etnoyer & Warrenchuk, 2007; Hoff, 2008, 2009*b*, 2010; Love *et al.*, 2008; Quattrini *et al.*, 2009; Hunt *et al.*, 2011; Treude *et al.*, 2011; Serra-Pereira *et al.*, 2014; Amsler *et al.*, 2015) that have yet to be defined. Reported sites are identifiable, however, as discrete habitats with extremely high densities of egg cases when compared to surrounding similar habitats. Hoff (2008, 2010) found egg case nurseries for *B. parmifera* had concentrations of > 800 000 eggs km⁻² with > 86% of the eggs containing embryos of multiple stages of development. Love *et al.* (2008) reported on a site for the longnose skate *Raja rhina* Jordan & Gilbert 1880 from Hueneme Submarine Canyon (California) in which egg cases were estimated at 19 008 eggs in the small

area. Likewise Hunt et al. (2011) discovered an area on the Shiribeshi Seamount (Japan) where egg cases of the golden skate Bathyraja smirnovi (Soldatov & Pavlenko 1915) were deposited in mass over a relatively small area (2000 m^2) with discrete edges to the distribution and egg cases not widely scattered around the site. Two sites found associated with cold seeps in the Mediterranean Sea and south-eastern Pacific Ocean showed similar characteristics to those mentioned for an unidentified deep water skate (Bathyraja sp.) and a deep-water catshark Galeus melastomus Rafinesque 1810, where eggs were highly concentrated over small areas (Treude et al., 2011). Those reported for skates off California, Japan and the south-eastern Pacific Ocean (Love et al., 2008; Hunt et al., 2011; Treude et al., 2011) occurred over rocky reefs where they used the rock structure to deposit their eggs in crevices and structure attached to the rock. The Port Jackson shark Heterodontus portusjacksoni (Meyer 1793) was reported to use rocky habitat similar to some skates to deposit its eggs within the crevices between rocks (Mclaughlin & O'Gower, 1971). For oviparous catsharks benthic structure appears important as species are reported to use corals (DeLacy & Chapman, 1935; Etnoyer & Warrenchuck, 2007; Henry et al., 2013), sponges, bryozoans and hydroids (Able & Flescher, 1991; Ellis et al., 2005), tubeworms (Treude et al., 2011) or seagrass (Orton, 1926) to deposit eggs, keeping them fastened in place above the bottom substrata.

Reports of older post-hatched eggs mixed with newly deposited ones for egg-case nursery sites and various concurrent embryo development stages in the mid-Atlantic Ocean (Able & Flescher, 1991), California (Love *et al.*, 2008) and Japan (Hunt *et al.*, 2011) anecdotally suggest multiple

spawning events at a single site and therefore habitat use over multiple years. Hoff (2008, 2010) examined the same egg case nursery sites over several years and found not only distinct seasonality to deposition, but multiple cohorts coexisting at sites with *B. parmifera* and *B.* aleutica, ranging from undeveloped eggs to completely developed juveniles near emergence. Coupled with evidence of a much protracted development time of 3 to 4 years (Hoff, 2008) this indicates a site is occupied and serves as an egg case nursery site constantly for many years. A egg case nursery site for *B. parmifera* in Bering Canyon has been reported by fisheries observers (AFSC's North Pacific Fisheries Groundfish Observer Programme, unpubl. data) indicating high incident of skate egg cases present for at least 25 years (Hoff, 2008, 2010). Likewise, an eggcase nursery for B. parmifera in Pribilof Canyon was first encountered more than 30 years earlier during a standard bottom trawl survey and was successfully revisited in 2009 based on the 1979 location records (Hoff, 2010). Egg case nursery sites are important habitat for many elasmobranch species and undoubtedly most oviparous elasmobranchs use habitat in similar ways. Although the challenge is to identify sites for every species, the lack of known locations should not hinder the recognition of their existence and importance as nursery habitat.

Criteria for juvenile habitat is similar for many species of teleosts and viviparous sharks where the YOY congregate after hatching or settlement providing an environment that promotes exceptional growth and species recruitment. Data available suggest similar patterns of habitat use for most EBS skate species (Hoff, 2010) based on juvenile and adult distribution, as well as other oviparous elasmobranch species worldwide (Etnoyer & Warrenchuck, 2007; Love *et al.*, 2008;

Hunt *et al.*, 2011; Treude, *et al.*, 2011). The reason for rapid movement from egg-case nursery sites by skates is unknown, however, it may be linked to predation and avoidance of large predators such as Pacific cod *Gadus macrocephalus* Tilesius 1810 and Pacific halibut *Hippoglossus stenolepis* Schmidt 1904, which have been shown to consume newly hatched skates in the EBS (Hoff, 2010).

Criteria set forth for juvenile nursery habitat, that of exceptional habitat quality to produce higher recruitment, or the 'effective juvenile habitat' concept of Dahlgreen *et al.* (2006), has yet to be shown for most species and is not easily demonstrated for skates (Beck *et al.*, 2001; Kraus & Secor, 2005; Heupel *et al.*, 2007). Acknowledging this limitation, however, the lack of complete understanding of the structure, function and contribution of a nursery habitat should not limit the recognition of them nor hinder conservation measures given the best available data (Layman *et al.*, 2006). The aim here was not specifically to identify nursery habitat for oviparous elasmobranehs, but to bring to light the recognition that they utilize more than a single nursery habitat during their early life and the roles these habitats may serve in the species successful recruitment. Identification of all critical early-life habitats is a necessary step in conservation and management planning for these vulnerable species.

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Author