All their eggs in one basket: a rocky reef nursery for the longnose skate (*Raja rhina* Jordan & Gilbert, 1880) in the southern California Bight

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Skates (family Rajidae) are oviparous and lay tough, thick-walled eggs. At least some skate species lay their eggs in spatially restricted nursery grounds where embryos develop and hatch (Hitz, 1964; Hoff, 2007). After hatching, neonates may quickly leave the nursery grounds (Hoff, 2007). Egg densities in these small areas may be quite high. As an example, in the eastern Bering Sea, a site <2 km^2 harbored eggs of Alaska skate (*Bathyraja parmifera*) exceeding 500,000/km^2. All skate nursery grounds have been identified over soft sea floors (Lucifora and García, 2004; Hoff, 2007).

In 2005, while conducting fish surveys using a manned submersible over natural reefs in the Santa Barbara Channel, southern California, we found an area of high skate egg density, located on the edge of Hueneme Submarine Canyon. Until that date, we had rarely observed skate eggs in our southern California surveys. For example, in 362 other submersible dives, in waters between 18 and 365 m deep and encompassing 395 km of transects over a wide range of habitats, we had observed only 44 skate eggs. In 2006, we returned to the Hueneme Submarine Canyon site and examined this nursery ground more closely.

Material and methods

We conducted the study on 24 October 2006 on a feature located on the west side of Hueneme Submarine Canyon (Fig. 1). The study area is a rocky outcrop located at approximately 34°02.3′N, 119°18.1′W. Rocks exposed at the site are likely a submerged extension of the Miocene volcanic rocks that make up Anacapa Island (Vedder et al., 1986). These rocks form gently north-dipping strata of volcanic flows, breccias, conglomerates, or tuffs. Faults and joints observed on the Island, and from the submersible at the site, increase rock resistance against gravitational failure. Bathymetric high spots, such as that of the skate nursery grounds, are north-dipping volcanic-layer outcrops that have not collapsed because of the local strength of the rock substrate in combination with the buttressing structure formed by faulting and jointing. Several diminutive taxa, including squarespot (*Sebastes hopkinsi*), swordspine (*Sebastes ensifer*), and pygmy (*Sebastes wilsoni*) rockfishes, dominate the fish fauna. Among structure-forming invertebrates, the volcanic outcrop also harbors high densities of barrel, flat, foliose, and vase sponges, gorgonian corals, the large anemone *Metridium* sp., basketstars, and the deep-water antipatharian coral *Antipathes dendrochristos*.

This survey was conducted aboard the small (4.8 m in length) research submersible *Delta* (Delta Oceanographics, Ventura, CA). During the dive, we tried to maintain a constant distance within 1 meter of the seafloor and a constant speed between 0.5 and 1.0 knot. The survey was made during daytime hours and we documented the egg density of longnose skates in that area with an externally mounted hi-8 video camera positioned above the middle viewing-porthole on the starboard side of the submersible. The scientific observer conducted a belt-transect survey through this same starboard viewing port, verbally recording onto the videotape all skate eggs observed within 2 m of the submersible.

Navigation fixes (latitude and longitude coordinates) were received from a Thales GeoPacific Winfrog ORE Trackpoint 2 USBL (Fugro-Pelagos, San Diego, CA) system at two-second intervals, and a Winfrog DAT file was generated for the research dive. Distance and duration between fixes were calculated to obtain a point-to-point submersible speed; errant navigation fixes were removed when speed exceeded 2 m/sec. The navigation fixes were then smoothed by using a nine-point moving average, and transect length was

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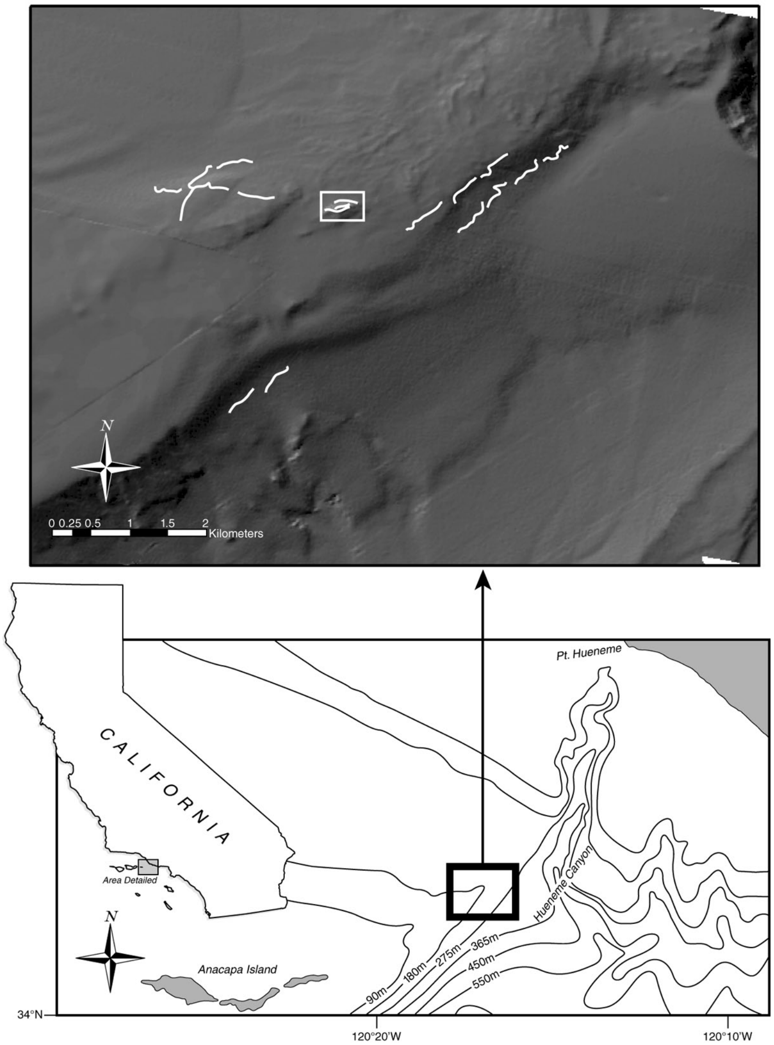

Figure 1

(Lower map) The general location (black box) of the longnose skate (*Raja rhina*) nursery ground on the edge of Hueneme Submarine Canyon, southern California Bight. (Upper map) The area within the black box in the lower map has been enlarged and the white box represents the nursery ground within that area; the other white lines in the upper map denote transects followed by the *Delta* submersible. Transects outside the box did not contain skate eggs.

estimated from the total distance between the smoothed points. Transect length was divided by transect duration to obtain an average transect speed. The length of individual habitat patches was estimated from average speed of the submersible during each transect.

During the survey, the observer verbally noted each egg or egg aggregation, estimated the number of eggs in the aggregation, and whether the eggs were living or dead. We assumed that yellow or green, shiny and full eggs still contained embryos and that those that were dark, deflated, and heavily biofouled were empty. It should be noted that in other studies dark egg cases have been found to still hold living embryos and thus our estimates of viability may be low. At that time, the observer also described whether the egg(s) had been laid on rock, cobble, sand, or on such structure-forming animals as sponges and gorgonians. Lastly, in order to identify the species using this nursery ground, five eggs were collected.

In the laboratory, the abiotic habitats of the nursery ground were also characterized from the survey videotape. We defined these habitats using the different categories of substrata and standard geological definitions defined by Yoklavich et al. (2000). In order

Table 1

Expected and actual (observed) longnose skate (*Raja rhina*) egg numbers by habitat type. Observations were made from the *Delta* submersible, eastern Santa Barbara Channel, October 2006. Habitat types were rock ridge (R), boulder (B), cobble (C), and sand (S). A two-character code was assigned each time a distinct change in substratum type was noted. The first character of the code represents the substratum that accounted for at least 50% of the survey patch, and the second character represents the substratum accounting for at least 20% of the patch. Expected numbers were calculated by assuming that the density of skate eggs was not different across habitat types. Expected numbers were rounded to the nearest integer. Habitats are ordered from most to least area surveyed (m^2).

Habitat	Area surveyed (m^2)	Expected egg numbers	Actual egg numbers
RR	2219.0	1513	1721
RC	208.6	142	13
RB	76.1	52	2
RS	37.6	26	4
CR	10.4	7	0

of decreasing particle size, these substrata were the following: rock ridge (R), boulder (B), cobble (C), and sand (S). A two-character code was assigned each time a distinct change in substratum type was noted. The first character of the code represented the substratum that accounted for at least 50% of the survey patch, and the second character represented the substratum accounting for at least 20% of the patch. Thus, RB represented a patch composed of at least 50% rock ridge and at least 20% boulders.

Results

In the nursery area, we surveyed 2551.8 m^2 of sea floor in waters between 125 and 151 m depth (average depth 139 m) and with bottom temperatures ranging from 9.1° to 10.1°C (Fig. 1). The study site was primarily composed of high-relief rocky ridge (RR), along with lesser amounts of rock-cobble (RC), rock-boulder (RB), rock-sand (RS), and cobble-rock (CR) (Table 1).

We observed 1740 eggs, of which 238 were characterized as intact. As far as we could ascertain, all of the eggs observed were those of the longnose skate (*Raja rhina* Jordan & Gilbert, 1880) (Fig. 2). We observed a range of egg states, from those that appeared to be newly deposited to ones that had almost disintegrated. The eggs did not appear to have been randomly laid over the substrata because significantly more eggs were observed over the highest relief areas (habitat RR) than over the other habitats (chi-square=13.1, df=4, P=0.01) (Table 1). Eggs also appeared to be clumped in their distributions. Although many of the eggs were deposited singly, we

Table 2

Number of observations (from the *Delta* submersible) of each size of longnose skate (*Raja rhina*) egg cluster (no. of eggs in cluster) in the nursery ground on the edge of Hueneme Submarine Canyon, October 2006, categorized by habitat type. Habitat types were rock ridge (R), boulder (B), cobble (C), and sand (S). A two-character code was assigned each time a distinct change in substratum type was noted. The first character of the code represents the substratum that accounted for at least 50% of the patch, and the second character represents the substratum accounting for at least 20% of the patch.

Number of eggs in cluster	Number of observations RB	RC	RR	RS
1	0	13	145	4
2	1	1	38	0
3	0	0	23	0
4	0	0	9	0
5	0	0	6	0
6	0	0	4	0
8	0	0	1	0
10	0	0	6	0
12	0	0	1	0
20	0	0	3	0
24	0	0	1	0
25	0	0	1	0
30	0	0	4	0
40	0	0	2	0
≥50	0	0	8	0
Total	1	14	1722	4

observed several aggregations with 300 or more eggs (Table 2). Most of the eggs were laid on rocks and relatively few on such invertebrates as sponges, deep-water corals, and sea anemones (Table 3). However, the eggs that were laid on invertebrates were significantly more likely to be intact than were those on rocks (intact on invertebrates=95%, 95% confidence interval, 83–99%; intact on rock=12%, 95% confidence intervals 10–13%; chi-square=225, df=1, P<0.0001).

We estimated the total number both of all eggs and only those that were intact. We assumed that our survey transect path demarcated the outer perimeter of the nursery grounds because we noted eggs all along the transect path. Using densities of both all eggs (0.68183/m^2) and only intact ones (0.093 eggs/m^2) and the area bounded by our transects (27,878 m^2), we estimated that there were 19,008 eggs in the nursery grounds, of which 2593 were intact.

Discussion

According to our many years of visual observations, skate nursery grounds are uncommon in southern

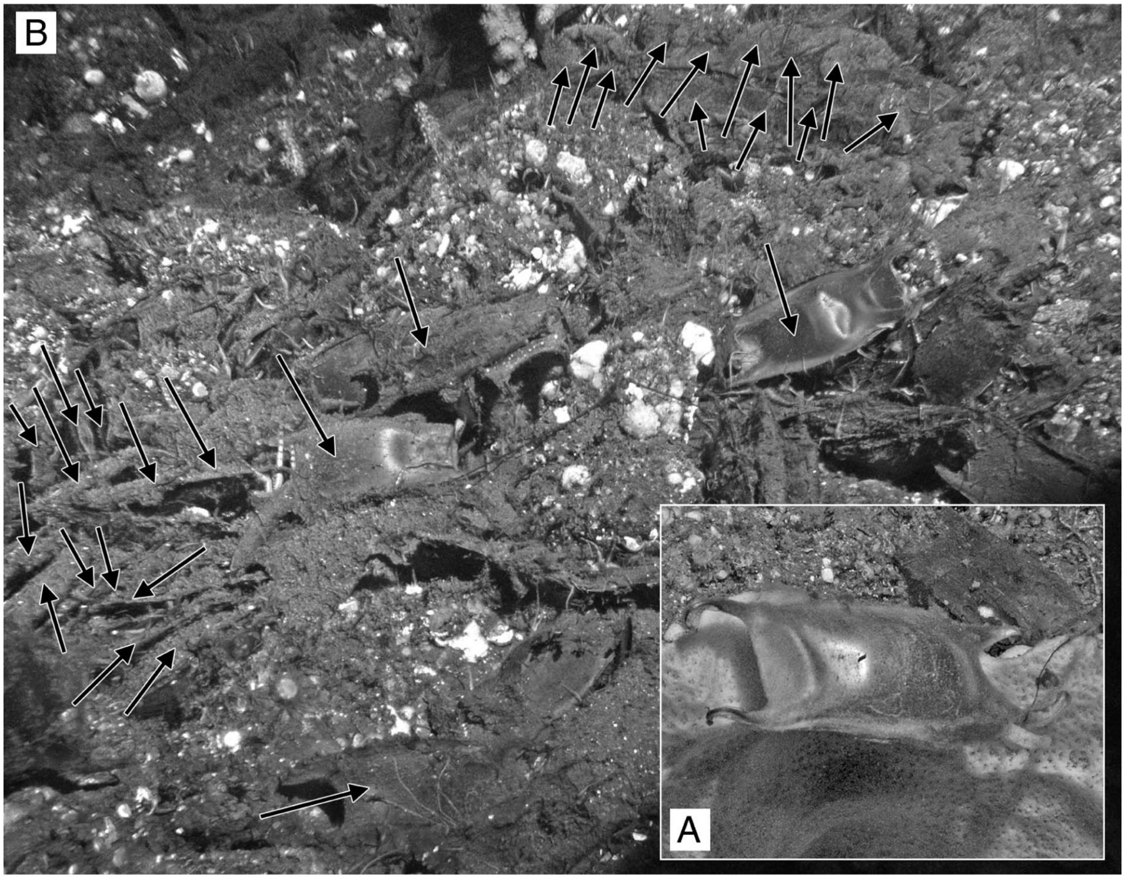

Figure 2

(**A**) An intact longnose skate (*Raja rhina*) egg, (**B**) an aggregation of eggs (see arrows), many of which are covered in fine sediment.

Table 3

Numbers of intact and empty longnose skate (*Raja rhina*) eggs on abiotic (rocks and fishing line) and biotic substrata, observed from the *Delta* submersible, eastern Santa Barbara Channel, October 2006.

Substrata	Number of eggs intact	Number of eggs empty
Abiotic		
Rocks	197	1500
Fishing line	1	0
Total abiotic	198	1500
Biotic		
Sponges	35	1
Gorgonians	3	1
Corals	1	0
Sea anemones	1	0
Total biotic	40	2

California waters (at least at depths <360 m), and like that observed by Hoff (2007) the nursery site that we observed was relatively small in area because visual transects conducted within 1 km over similar habitats yielded no eggs (Fig. 1). However, whereas previously described skate nursery grounds lay on soft sea floors, the study site was a rocky outcrop sitting on the edge of a submarine canyon. This reef appears to be a relatively high-energy area (little sediment was found on the substrata) with high densities of structure-forming invertebrates. Because so few visual surveys have been conducted on the Pacific Coast, we do not know if the nursery ground that we observed was atypical or if there are other such grounds in Pacific Coast waters.

Longnose skates do not randomly lay their eggs over the sea floor. Among the various habitat types in the nursery area, rock ridges contained statistically more eggs and these eggs were often found in clumps. It would be expected that eggs laid on the highest relief would be most exposed to currents and arguably less available to at least some predators than eggs lying on low substrata.

Skate reproduction, with its emphasis on highly spatially restricted nursery grounds, appears to be an example of "predator swamping" (Van Montfrans et al., 1995). In addition, the observation that intact skate eggs are more likely to be found on sponges than on bare rocks may reflect an antipredator **strategy** by adult skates. Boring snails, including those in the families Muricidae, Naticidae, and likely Ranellidae, are major predators on skate eggs and predation rates in nursery grounds can reach 40% or more (Lucifora and García, 2004; Hoff, 2007). Snails of all of these families are found in southern California waters (McLean and Gosliner, 1993). Although they could not identify them in their trawl-based study, Lucifora and Garcia (2004) speculate that microhabitat differences in egg placement could lead to variable protection from predators. It is possible that sponges, with their spicule-rich skeletons and potent chemical defenses, may deter snails or other egg predators.

The Bering Sea skate nursery ground that Hoff (2007) investigated was notable for having 1) high currents and productivity and 2) the presence of only mature fish. The nursery site of our study was composed of high-relief rocks situated on the edge of a submarine canyon. Because of the relative absence of fine particulates on the substrata and the presence of unusually high densities of sponges, gorgonians, and other structure-forming invertebrates, we surmised that this nursery ground is bathed by high currents and is likely quite productive. In addition, we observed no juvenile or adult skates, providing additional evidence for Hoff's (2007) hypothesis that newly hatched skates quickly leave their nursery grounds.

In the context of this nursery ground much about longnose skate reproduction remains unknown. For instance, we do not know when the eggs are laid, their incubation period, nor the fate of the juveniles. We do not know how many skates use this habitat and how they migrate. Lastly we note that the extent to which female skates seek out sponges is unknown. However, if skate eggs deposited on sponges are at a competitive advantage, damage to these invertebrate communities (i.e., through destructive fishing practices) and the subsequent increase in egg predation, would have a detrimental effect on skate reproductive success.

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