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Habitat Associations of Catshark Egg Cases (Chondrichthyes: Carcharhiniformes: Pentanchidae) from the U.S. Pacific Coast

Amber N. Reichert

HABITAT ASSOCIATIONS OF CATSHARK EGG CASES (CHONDRICHTHYES: CARCHARHINIFORMES: PENTANCHIDAE) OFF THE U.S. PACIFIC COAST

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ABSTRACT

Habitat Associations of Catshark Egg Cases (Chondrichthyes:
Carcharhiniformes: Pentanchidae) from the U.S. Pacific Coast

by
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Master of Science in Marine Science
California State University Monterey Bay, 2020

Many marine species select sites for reproduction based on habitat suitability, environmental tolerances, and oceanographic conditions, in order to enhance development or survival of their offspring. For many species living in the deep sea, it is unknown which factors influence this aspect of the reproductive process. In this study, the occurrence and influences of oviposition site selection were determined for the brown catshark, *Apristurus brunneus,* and filetail catshark, *Parmaturus xaniurus,* in the greater Monterey Bay region, providing novel insights into specific habitat preferences and depth distributions. Video footage from the Monterey Bay Aquarium Research Institute (MBARI), and the National Oceanographic and Atmospheric Administration's Southwest Fisheries Science Center Fisheries Ecology Division (NOAA-SWFSC-FED) was utilized to predict suitable oviposition habitat using MaxEnt presence-only modeling, identify attachment substrates and faunal associations using qualitative observations, and determine depth and habitat preferences using tests of independence and Manly's selectivity indices. The greater Monterey Bay region was determined as a nursery for both *A. brunneus* and *P. xaniurus* on the basis of meeting all oviparous nursery qualifications: high densities of egg cases deposited in the same region, habitat was benthic, oviposition sites were continually used, and no juvenile sharks were observed in the vicinity of egg cases. Complex geographic and environmental features such as rugosity and depth were shown to influence oviposition sites of *A. brunneus* and *P. xaniurus*. An increase in rugosity indicated higher predictive habitat suitability. The primary depth range of oviposition sites for both species was 150–199 m, with relatively more *A. brunneus* egg cases in the 100–149 m range, and more *P. xaniurus* egg cases observed at deeper depths (200–300 m). Depth ranges for both species are similar and were expanded based on MBARI video observations (*A. brunneus* = 87–550 m, *P. xaniurus* = 99–524 m). Areas of greatest predicted habitat suitability were indicated on the shelf break and upper to mid slope of the Monterey Canyon and in adjacent canyons. MaxEnt model output indicated higher induration (i.e., rockier) habitat was the main driver of oviposition site selection. Structure forming marine invertebrates (SFMI) such as corals and sponges were identified as important faunal attachment structures, with egg cases of both species occurring significantly more often on sponges than other substrates. Nurseries are critically important habitat and this research is necessary for influencing habitat-based management. The vulnerability of these and other species prompts further research concerning the use of SFMI as oviparous nurseries for potential essential fish habitat (EFH) designation.

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INTRODUCTION

The geographical distribution of a species is influenced by physiological tolerances along environmental gradients, as well as by oceanographic processes. Selection of appropriate habitat may be driven by responses to abiotic factors such as temperature or light, but also by ecological factors such as the presence of competitors, or prey availability (Sims 2003). Topographic and habitat complexity play a key role in the population structuring and distribution of marine species. However, there is a paucity of information on the interactions between the combined effect of physical and biological landscape on marine population dynamics (Toews 2012). Habitat requirements for deep sea groundfishes have been previously investigated by focusing on the physical structure and geology of the seafloor (Yoklavich et al. 2000; Greene et al. 2007); however, little is known about the factors that influence their spatial distribution (Navarro et al. 2016). Identifying species-specific habitat associations over varying scales may be a valuable method for identifying areas of essential fish habitat (EFH) (Espinoza et al. 2014), where EFH is defined as ‘‘waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity.’’, by the United States Congress in the 1996 amended Magnuson–Stevens Fishery Conservation and Management Act (Macpherson 2004).

Among the various regions that marine species inhabit, nurseries are critically important habitat and often meet the qualifications for EFH (Heithaus 2007). The physical, environmental, and ecological drivers of nursery selection are variable among marine species. Juvenile rockfish (*Sebastes* spp.) have been found associated with rocky habitat where sponges were the main invertebrates (Hixon et al. 1991). The lemon shark, *Negaprion brevirostris*, select geographically discrete nurseries such as estuaries or reefs which provide nutrient rich waters and protection from predation (Tavares et al. 2016). For the blob sculpin, *Psychrolutes phrictus*, reproductive aggregations are found on small rocky cliffs and slopes with nurseries near cold seeps and hydrothermal vents, which provide prey and increased temperatures for faster development (Drazen et al. 2003).

There are at least 530 extant chondrichthyan species whose distributions include deep sea (> 200 m) habitats (Kyne & Simpfendorfer 2010), accounting for almost half of the world's estimated 1,250 chondrichthyans. A diverse group, the deep sea chondrichthyans are dominated by the dogfishes (Squaliformes), skates (Rajiformes), chimaeras (Chimaeriformes), and the speciose catsharks (Carcharhiniformes: Pentanchidae and Scyliorhinidae). The dogfishes and catsharks alone comprise 84.5% of deep sea shark species (Kyne & Simpfendorfer 2007); with catsharks exhibiting high levels of endemism and representing some of the most geographically and bathymetrically restricted species (Kyne & Simpfendorfer 2010). Complex habitat structures can be used as predictors of species distribution. For example, Espinoza et al. (2014) observed that coastal inshore sites with greater structural complexity (e.g. rocky outcrops, coral reef environments, and habitat dominated by biogenic cover) had more shark species than those with lower structural complexity.

Structure forming marine invertebrates (SFMI) provide some of the most complex biological habitats found on continental slopes and host biologically rich communities (Roberts et al. 2009; Tittensor et al. 2009; Buhl-Mortensen et al. 2010; NOAA 2010; Watling et al. 2011; Baillon et al. 2012). Biodiversity of cold-water coral communities is comparable to those of tropical coral reefs; however; unlike the associations between shallow reefs and fishes, the relationship between deep sea reefs and groundfishes is poorly understood (Auster 2005, 2007). Hixon et al. (1991) found co-occurrence of SFMI and groundfish in rocky regions off the Oregon coast. In deeper waters, corals and sponges modify habitats through their physical presence. Many fishes and macro invertebrates inhabit deep sea coral and sponge communities although their role as autogenic ecosystem engineers is not well understood (Miller et al. 2012).

Structure forming invertebrates such as cold-water coral and sponge communities are predominately considered facultative habitat, important but not essential for species survival (Foley et al. 2010; Kutti et al. 2015). Deep sea corals and sponges provide substrate for attachment, refuge, spawning, and feeding for deep sea fauna (NOAA 2010). Supporting evidence for a functional or obligate role, that would qualify deep sea invertebrate communities as EFH, remains lacking (Baillon et al. 2012; Miller et al. 2012). SFMI may be utilized by sharks for feeding, as nursery grounds, or for social refuges (Etnoyer & Warrenchuk 2007; Morato et al. 2010; Henry et al. 2013; Rossi 2013). Although not well mapped, deep sea sponge ecosystems are often found on similar substrates with deep sea corals (NOAA 2010). Recently, deep sea coral and sponge habitats in the eastern North Pacific (ENP) were identified as possible locations of catshark nurseries, spawning, and refuge, based on the observations of egg cases (Flammang et al. 2007; Stierhoff et al. 2011). Analysis of ROV video footage revealed that two species of deep sea catsharks in the ENP, *Apristurus brunneus* and *Parmaturus xaniurus*, deposit egg cases specifically by wrapping egg case tendrils on sessile invertebrates along rocky outcrops (Flammang 2005).

Oviparous species from the families Pentanchidae and Scyliorhinidae have morphologically distinct egg cases, suggesting that catsharks might differ in life histories, or in habitat utilization (Flammang et al. 2007; Bustamante et al. 2013). Variation in egg case morphology has ecological and biological influences on oviposition. Deep sea sharks preferentially deposit their egg cases at well-ventilated or sheltered locations to increase survivorship (Treude et al. 2011). Catsharks are often known to attach their egg cases to various benthic structures, including gorgonians, octocorals, hydroids, and anthropogenic structures like abandoned fishing gear (Etnoyer & Warrenchuk 2007; Kiel et al. 2013). Many catsharks have some form of tendril or fibrous filament extending from the anterior or posterior ends of the egg case, likely to help secure the egg case to some form of substrate. Recently, catshark egg cases have also been found wrapped in polychaete worm tubes at a deep sea methane cold seep site. These worm tube thickets likely provide protection and ventilation for egg cases that lack tendrils (Treude et al. 2011; Kiel et al. 2013).

Various studies have defined nursery areas for sharks; however, these studies have focused on species with free-swimming neonates and early juveniles (Springer 1967; Clarke 1971; Bass 1978; Heupel et al. 2007). Continuing research is necessary to better understand utilization of these habitats for oviparous species such as catsharks. The following criteria have recently been developed for categorizing oviparous elasmobranch nurseries: 1) geographic locations with large quantities of egg cases, 2) habitat is benthic and egg cases are attached to or contacting benthic or stationary substrate, 3) sites are used over multiple years, and 4) recently hatched juveniles emigrate away from egg deposition sites (Hoff 2016). Catshark nursery habitat may be localized or widespread, as egg cases have only been reported anecdotally and at small scales (e.g. patches of sessile megafauna) (Etnoyer & Warrenchuk 2007; Flammang et al. 2011).

Specific oviposition site features are currently unknown for *A. brunneus* and *P. xaniurus*, but anecdotal information indicates that the Monterey Bay area functions as a nursery. This supposition is based on the recurrence of *A. brunneus* and *P. xaniurus* at oviposition sites in the Monterey Bay (Flammang et al. 2011), however nursery presence and characteristics must be validated by analyzing additional habitat parameters in detail and at different spatial scales.

The purpose of this study is to determine spatial and habitat associations of *A. brunneus* and *P. xaniurus* oviposition sites in the greater Monterey Bay, California region by identifying specific oviposition site features. I will address the following questions:

1) Is there an association between attachment substrate type and egg case occurrence for *A. brunneus* and *P. xaniurus*?
2) Do *A. brunneus* and *P. xaniurus* differentially utilize biogenic habitats (corals or sponges) as oviposition sites?
3) Are there regions where geographic or environmental features are of differential importance for *A. brunneus* and *P. xaniurus* oviposition? If so, what are the influential drivers of oviposition sites?

Addressing these questions will additionally enable a rigorous evaluation of the greater Monterey Bay area as a potential catshark nursery ground.

METHODS

***Study System*:**

The data collected for this research spanned the greater Monterey Bay to Carmel Bay region (36.3–37° N), along the coast of central California (Fig. 1). This study area consists of continental margins that are dynamic, diverse, and are classified by narrow continental shelves and steep slopes, often divided by submarine canyons (Smith & Demopoulos 2003; Miller et al. 2012). Benthic habitat within the Monterey Bay region includes hard substrate (i.e. submarine canyons, rocky reefs, and seamounts) within broad stretches of unconsolidated mud, sand, and gravel. Particles of loose sediment range from silt to boulders (Piacenza et al. 2015; Fildani 2017). Continental shelves are relatively narrow, so the continental slope tends to be close to the coast (Smith & Demopoulos 2003). Submarine canyons play vital roles in sustaining high levels of regional biodiversity (De Leo et al. 2010). The Monterey Submarine Canyon is a major geological feature of the study site, with topographic features on the continental margins that enhance benthic biomass, (Breaker & Broenkow 1989; De Leo et al. 2010) and comprises large areas of granite and sedimentary outcrops that are surrounded by flat, mud-sand seafloor (Yoklavich et al. 1995). Many small tributary canyons lead into the upper Monterey Canyon. Soquel and Cabrillo Canyons, and Carmel Canyon are side canyons that enter Monterey Canyon system from the north and south respectively, such that the Monterey Canyon is the dominant erosional channel (McHugh et al. 1998). The depth range of prominent geological features were characterized by Greene et al. (1995), including: upper continental slope (from the shelf break at 100 m to 500 m), canyon head (10–100 m), upper (100–300 m), middle (300–500 m), and lower canyon (> 500 m).

***Study Species*:**

Deep sea catsharks (Pentanchidae) are the most diverse and largest family of extant sharks, with 11 genera and 109 species (Ebert et al. 2013; Ebert 2016; Weigmann et al. 2018; White et al. 2019; Eschmeyer et al. 2020). Two of the most common shark genera in the deep seas of the ENP are *Apristurus* Garman, 1913 and *Parmaturus* Garman, 1906. To date, approximately 39 species of *Apristurus* (Kawauchi et al. 2014), and 11 species of *Parmaturus* (Soares et al. 2019) have been identified. Two of the most common and widespread ENP species are the brown catshark *A. brunneus* (Gilbert, 1892), and filetail catshark *P. xaniurus* (Gilbert, 1892) (Eschmeyer et al. 1983; Ebert 2003; Ebert et al. 2013; Ebert et al. 2017). Like many deep sea chondrichthyans, there is a paucity of information on the life histories, systematics, and distributions of these species. Past studies of these species have identified areas of occurrence on the outer continental shelf, and upper continental slope regions (Cross 1988; Flammang et al. 2011); however, knowledge of their distribution patterns, habitat associations, and degree of spatial overlap remains ambiguous. *Apristurus brunneus* and *P. xaniurus* are caught over mud or silt bottom, or over rocky areas with high vertical relief. Cross (1988) found *A. brunneus* occurred more frequently on soft substrate but had similar abundance over soft and hard substrates. Conversely, *P. xaniurus* was observed equally frequently on soft and hard substrates but was more abundant on hard substrate (Cross 1988). Sympatric species, such as *A. brunneus* and *P. xaniurus* may limit spatial overlap through differential habitat associations (Cross 1988; Flammang et al. 2011). *Apristurus brunneus* is a poorly studied species that occurs along the outer continental shelf to the upper slope in the eastern Pacific. *Apristurus brunneus* is classified as “data deficient”, whereas *P. xaniurus* is classified as “least concern” by the International Union for Conservation of Nature (IUCN). This species has a known depth range of 33–1,341 m (Weigmann 2016) and a geographical range from the southeastern Gulf of Alaska to central Baja California, Mexico (28–48° N) (Wilson & Hughes 1978; Compagno 1984; Mecklenburg et al. 2002; Ebert 2003; Flammang et al. 2011; Cruz-Acevedo et al. 2018). Additionally, there are isolated records of this or a cryptic species reported off Ecuador, Peru, and Chile (Ebert 2016). At birth, *A. brunneus* are 70–90 mm total length (TL) and grow to approximately 710 mm TL (Stevenson et al. 2007). The egg case of *A. brunneus* is approximately 52–72 mm TL and has long tendrils projecting from anterior and posterior edges (Flammang et al. 2007). Anterior tendrils are threadlike fibers, whereas the posterior tendrils are thicker, tightly coiled, and taper at the ends. The shape is vase-like, with a smooth surface, and coloration ranging from golden-yellow *in utero* to dark brown after > 1 month exposure to seawater (Flammang et al. 2007).

The filetail catshark, *P. xaniurus* (Gilbert, 1892), is a poorly known species that appears to be endemic to the eastern Pacific (26–46° N) at depths of 88–1519 m (Compagno 1984; Wilkins et al. 1998; Ebert 2003; Flammang et al. 2011; Love & Passarelli 2020). At birth, *P. xaniurus* are 70–90 mm TL and can grow to a maximum length of 610 mm TL (Cross 1988). The egg case of *P. xaniurus* is approximately 70–110 mm TL and has tendrils on both anterior and posterior ends. Egg case coloration is golden-yellow *in utero* to dark brown after > 1 month exposure to seawater. A thick flange along the lateral edges resembles a “T” in cross-section (Ebert 2003; Flammang et al. 2008). Juveniles have been described as pelagic and are often observed in midwater, whereas adults are more benthic (Ebeling et al. 1970; Cross 1988).

Data Collection

Monterey Bay Aquarium Research Institute Video

Remotely Operated Vehicle (ROV) data provided by the Monterey Bay Aquarium Research Institute (MBARI) were used to examine habitat associations of *A. brunneus* and *P. xaniurus* egg cases. ROV video data were collected opportunistically during routine seafloor surveys that varied greatly in their objectives. These data could not be standardized to produce density estimates for egg cases, and therefore are limited to presence-only information and qualitative evaluation. Catshark egg cases were identified to species using flange morphology, presence or absence of tendrils, coloration, and TL (Gomes & de Carvalho 1995; Flammang et al. 2007; Flammang et al. 2008). Only positive species-level identifications were used in analyses. Individual egg cases and bundles were counted, and the type of attachment substrate was recorded. A bundle of egg cases was classified by having two or more cases attached together by entangled tendrils. The following additional information was extracted from ROV dive video: associated faunal groups (identified to lowest possible taxonomic level), latitude, longitude, age (new or old), condition (hatched, preyed upon, or viable), depth, temperature, and salinity. Invertebrates were classified as associated if in direct contact with an egg case, whereas fishes were considered to be associated if they were no greater than their total body length away. The faunal group sponges were classified by their morphology (i.e., barrel, branching, encrusting, foliose, nipple, shelf (vertical and horizontal), tube, and vase) (Yoklavich et al. 2016). A total of 84 ROV dives were analyzed for egg cases based on positive occurrence annotations in the MBARI database. These dives range from the Gulf of California to Washington (23–48º N) at depths of 66–2228 m, with the majority occurring in the Monterey Bay Submarine Canyon at depths > 400 m.

NOAA-SWFSC-FED Video

Manned submersible data provided by the National Oceanographic and Atmospheric Administration's Southwest Fisheries Science Center Fisheries Ecology Division (NOAA-SWFSC-FED; and will be abbreviated to SWFSC-FED for the remainder of the paper) were used in addition to MBARI video data to examine habitat associations of egg cases. Unlike MBARI dives, during SWFSC-FED surveys the manned submersible was used to conduct quantitative, strip transects that were used to determine egg case densities among a variety of habitat types, based on previously identified habitat categories: 1) Hard (≥ 67% of area swept is rock), 2) Soft (≥ 67% of area swept is soft sediment), and 3) Mixed (< 67% of area swept is rock and < 67% of areas swept is soft sediment). Seafloor habitat was characterized following the protocol of Greene et al. (1999): Cobble, rock, and mud were the three habitat types observed within transects. Cobble is characterized as hard induration substrate, between ≥ 6.5cm & < 25.5 cm diameter. Rock is characterized as hard induration substrate, described as granite and sedimentary outcrops. Mud is characterized as soft induration substrate, < 0.06 mm in diameter. Habitat patches received designated primary and secondary habitats, which were used to further classify the mixed category to hard-mixed and soft-mixed (Laidig & Yoklavich 2016; Yoklavich et al. 2016). When the primary habitat in the patch was hard and the secondary habitat was soft, the habitat was classified as hard-mixed. When the primary habitat in the patch was soft and the secondary habitat was hard, the habitat was classified as soft-mixed.

Surveys were limited to the greater rock habitats within Monterey Bay area (Fig. 1). Transects had a width of 2.5 m and were conducted between 30–365 m, with a cruising speed of ~1.5 kts for 15 min (Yoklavich & O’Connell 2008). Only observations > 100 m in depth were used because occurrence of catsharks on the inner continental shelf of the study region is extremely rare. A total of 89 transects were reviewed for egg case occurrences. As with MBARI data, catshark egg cases were identified to species using flange morphology, presence or absence of tendrils, coloration, and TL (Gomes & de Carvalho 1995; Flammang et al. 2008). Additional data that were extracted with egg case counts were the same as with MBARI ROV data.

Environmental Predictor Variables

Environmental predictor rasters were provided from the Bureau of Ocean Energy Management (BOEM) as part of a deep-sea coral modeling study (Poti et al. 2020). These data included 25 x 25 m resolution grids of environmental predictor variables spanning the U.S. Pacific Coast. Data were projected into GCS WGS 1984 (Geographic Coordinate System, World Geodetic System).

A set of 15 environmental predictor variables (Table 2) characteristic of depth and seafloor topography, seafloor substrate, oceanography, and geography were selected initially for potential use in predicting the distributions of appropriate egg case habitat for each shark species. Environmental features were selected based on relevance to my study species using an ecological understanding of the species to prevent identifying false relationships (Elith & Leathwick 2009; Elith et al. 2011).

Habitat Associations

Due to its quantitative nature, only SWFSC-FED data was used for examination of habitat characteristics, associations between egg cases and habitat type, and associations between egg cases and structure forming invertebrates. A subset of manned submersible dives was randomly selected to further evaluate habitat preferences and associations with the SFMI, corals, and sponges. Egg case observations were pooled across transects to calculate the relative proportions of egg cases per habitat type and depth groups, to examine the relationship between habitat patch type, depth, and egg case occurrence. As a precursor, habitat preferences were analyzed for each species independently, using a contingency table analysis to compare observed and expected proportions of egg case distributions among different habitat patch types (Zar 1999; McDonald 2009). Habitat type had four categories: hard, hard-mixed, soft, and soft-mixed. The G-test goodness of fit formula is represented as $G=2\sum[O\times\ln(O/E)]$, where G = chi-square statistic, O = frequency of observed counts, and E = frequency of expected counts if the null hypothesis is true (Zar 1999; McDonald 2009). Post-hoc chi-squared comparisons were run for habitat groups with more observed egg cases than expected. For a more comprehensive analysis, habitat and depth preferences were analyzed for each species independently, using the same approach looking at proportions of egg case distributions among different habitat patch types at various depth bins. The four habitat type categories remained the same. Depth was grouped into four bins: 100–149 m, 150–199 m, 200–249 m, and 250–300 m. Post-hoc chi-squared comparisons were run for habitat and depth groups with more observed egg cases than expected.

Concurrent with the contingency table analysis, Manly’s selection index was used to evaluate the relative magnitude of habitat associations (Manly et al. 2007; Bizzarro et al. 2014). Manly’s selection index was calculated as $s = (a - b)/(a + b)$, where a = the proportion of egg cases found in a given habitat and b = the habitat patch area as a proportion of the total available habitat area. An electivity value was obtained for each habitat type, ranging from -1.0 (total avoidance) to 1.0 (exclusively used). These selection indices were standardized to ratios that sum to 1.0 for all habitat types by taking s/∑s. Standardized ratios of 1/number of resources, or $B_{i} = 0.25$ for habitat types, and $B_{i} = 0.0625$ for depth and habitat groups, indicated no habitat preference. Values of $B_i < 0.25$ for habitat types, and $B_i < 0.0625$ for depth and habitat groups indicated relative habitat avoidance, and values of $B_i > 0.25$ for habitat types, and $B_i > 0.0625$ for depth and habitat groups indicated relative habitat preference (Krebs 1989; Manly 2007).

The chi-square approach was used to examine the relationship between habitat type and presence of egg cases on corals, sponges, or barren substrate for *P. xaniurus*. A similar analysis could not be conducted for *A. brunneus* due to limited sample size. Habitat types included hard, and hard-mixed substrate. Barren substrate was classified as rock, or any substrate type lacking corals or sponges. The chi-square statistic was used for analysis and was calculated as follows: $X^2 = \sum(O-E)^2/E$, where O and E are the same as in contingency table analysis. Subsequently, Manly's selection index was used to evaluate the relative magnitude of habitat associations. Values of $B_i < 0.17$ for these data indicated relative habitat avoidance, and values above indicated relative habitat preference.

Habitat Suitability Models

MaxEnt

Species-specific habitat associations were examined using manned submersible and ROV data to investigate areas of oviposition importance for *A. brunneus* and *P.*

xaniurus. Although systematic collection methods varied between data sets, both provided useful presence-only data for observing natural conditions and could be incorporated into habitat suitability modeling.

The program, MaxEnt version 3.4.1, (Phillips et al. 2006) was used to predict each species' spatial distribution (observed and potential) using MBARI and SWFSC-FED egg case locations and environmental layers. Maximum entropy modeling, or MaxEnt, is a machine learning technique and is designed to predict distributions from presence-only data (Phillips et al. 2006; Merow et al. 2013). MaxEnt does not require absence data for each species' model. Instead it uses 'background' environmental data (also known as features) for the total study area and compares them to presence points (Baldwin 2009). Background points are pixels where the species has not been detected with certainty. A random sample of 10,000 points was used to derive this background sample (Phillips et al. 2006). MaxEnt distinguishes the features at observed locations to those in the background sample (Phillips et al. 2006; Elith et al. 2011; Merow et al. 2013).

MaxEnt has few assumptions and creates complex response curves from samples drawn from multiple distributions (Tittensor et al. 2009; Merow et al. 2013). Marginal response curves were used to determine how model predictions changed as each environmental variable was varied, while all other variables remained at their average values (Phillips 2006). Collectively, all explanatory variables created the universe of background points (Merow et al. 2013). Presence locations are either correctly classified as suitable habitat ('true positives') or incorrectly classified as unsuitable habitat ('false negatives') for any threshold of habitat suitability index (HSI). Absence locations are similar in that data are either correctly classified as unsuitable habitat (‘true negatives’) or incorrectly classified as being in suitable habitat (‘false positives’) (Gormley et al. 2011). Since false positives cannot be estimated for presence-only data, MaxEnt instead estimates the proportion of cells predicted to have suitable habitat for the species, or the fractional predicted area (Phillips et al. 2006; Gormley et al. 2011).

Model Fitting and Selection

Each model was fit using a maximum entropy modeling structure that measures correlations between presence records and environmental predictor variables (Phillips et al. 2004; Phillips 2006). The subsampling technique was used as the replicate run for randomly selecting test data points. Logistic output, which provides a probability estimate of suitable habitat that ranges between 0 and 1, was used for interpretations (Baldwin 2009; Glover-Kapfer 2015).

Using the random seed option in MaxEnt to select training and validation data helped to produce a more robust estimate of model accuracy by preventing runs from using replicate test and training samples (Madhyastha 2019). 75% of presence data was randomly selected as training data to fit the model and the remaining 25% of sample records were used as validation to evaluate model prediction. The number of background points was set to the maximum of 10,000. Regularization is used as a smoother to avoid fitting too complex a model (i.e., overfitting), and affects the fit of the output distribution. When the regularization multiplier is set < 1.0, the model output is more localized and runs the risk of overfitting. The complexity of the models was decreased by removing the correlated variables so overfitting was less of a concern, and the regularization number was set at 1.0. (Phillips 2006; Elith et al. 2011). Thresholds are used to make binary predictions, with suitable conditions predicted above the threshold and unsuitable below (Phillips 2006; Merow et al. 2013). Escalante et al. (2013) found that using the 10th percentile training presence threshold for the identification of areas of suitable habitat was more consistent than with other thresholds. The 10th percentile training presence logistic threshold was therefore selected for calculating measures of predictive accuracy calculated from a 2 × 2 error matrix. The final MaxEnt models were calculated with the maximum number of iterations set to 5,000, since more iterations produce a more stable model (Young et al. 2011). Variable importance was measured by jackknife resampling and habitat suitability response curves.

Environmental Predictor Variables

To use MaxEnt, species input data and environmental raster layers must be preprocessed to a standard format. The same spatial extent is required for input points and environmental layers. Raster data were exported into ASCII grid format using R. Occurrence data for each species were designated by latitude and longitude.

It is important to remove highly correlated environmental variables before developing a MaxEnt model to eliminate redundancy and create a more parsimonious model. Therefore, environmental predictor variables were analyzed using a multivariate correlation analysis and any highly correlated variables ($|\rho| > 0.7$, $P < 0.05$) were removed. This procedure resulted in a set of eight non-correlated environmental predictors (and units) selected for use in the models: rugosity, depth (meters), latitude (degrees), percent mud, percent gravel, annual Northern bottom current velocity (m/s), annual vertical bottom current velocity (m/s), and annual Eastern bottom current velocity (m/s). All measures of bottom current velocity have magnitude and are directional.

After a model run, MaxEnt creates a table with each environmental variable's contribution, and the stability, or permutation importance of the variable. Values are normalized so that the data can be represented as percentages for both the percent contribution and the permutation importance (Phillips 2006). The amount of increase or decrease of the model fit determines variable percent importance, which indicates how much the MaxEnt model used each variable to create the final output. Higher percentages indicate greater weight (i.e., relative contribution) of those variables when creating the distribution model. Permutation importance is determined by randomly permuting the values of that variable among the presence and background training points and measuring the resulting decrease in training area under the curve (AUC). The lower the permutation importance, the more stable a variable's contribution is to the model (Phillips et al. 2006; 2008).

Model Evaluation

The receiver operator characteristic (ROC) curve plots true-positive rate (TPR) on the y-axis against false-positive rate (FPR) on the x-axis and serves to further evaluate model performance (Allouche et al. 2006). When the same data are used for training and for testing, the ROC curves will be identical (Phillips 2006). AUC, area under the (ROC) curve, is the probability (0–1.0) that a location chosen at random will be correctly ranked above a randomly chosen absence location (Phillips & Dudik 2008). AUC measures the model's performance by plotting test data ROC against a random prediction of AUC = 0.5. Test AUC (AUC_{test}) measures the capability of model predictions to differentiate observed presence and absence for a test dataset (West et al. 2016).

During a model run, MaxEnt improves model fit with each iteration, referred to as the gain (Philips et al. 2006). Gain is related to a likelihood (deviance) statistic, a measure of goodness of fit that MaxEnt minimizes (Elith et al. 2011). It begins at the value 0 and increases to an asymptote during each run. MaxEnt generates a probability distribution during this process, starting from the uniform distribution and repeatedly improving the fit to the data. Training gain is derived from points used to train the model, and test gain is derived from presence points used to test the predictive ability of the model. Gain indicates how closely the model is concentrated around the presence samples at the end of each model run (Elith et al. 2011). Regularized training gain describes how much better the model distribution fits the presence data compared to a uniform distribution. The exponential of the test gain measures how many times greater the sample likelihood is compared to random (Yost et al. 2008; Young et al. 2011).

There are limitations to using AUC to evaluate performance for presence-only models because AUC is rank-based. High AUC values indicate that the model can distinguish between sample presences and potentially unsampled background locations; however, this is not necessarily a pertinent distinction as the background sample contains both sample presence and absence (Lobo et al. 2008; Elith et al. 2011). Jackknife analyses were therefore used to better evaluate model performance of each variable, and of the overall best model (Elith et al. 2011; Gearman 2018). Jackknifing is a resampling technique that can be used to evaluate the relative strengths of each predictor variable. Maxent runs three models and generates diagnostic plots for comparison (Phillips 2006; Yost et al. 2008; Young et al. 2011): one with a single feature, one with all but one feature, and one with all environmental features. The relative importance of each environmental variable can be assessed by examining at how they affect training gain, test gain, and AUC_{test}.

Sensitivity is the probability that the model will correctly classify a presence, whereas specificity is the probability that the model will correctly classify an absence. Sensitivity and specificity are derived from a 2x2 confusion matrix and are used to evaluate the predictive accuracy of models; true positive rate, true negative rate, false positive rate, and false negative rate (Allouche et al. 2006). Sensitivity, calculated by $a/(a+c)$, is the proportion of presence that was predicted correctly, where a is the number of cells with true presence and c is the number of cells with false absences. Specificity, calculated by, $d/(b+d)$, is the proportion of observed absences that are accurately predicted, where b is the number of cells with false presence, and d is the number of cells with true absences (Allouche et al. 2006).

The true skill statistic (TSS) is an independent measure of model validity that accounts for omission (false negative), and commission (false positive) error rates. It is calculated using the sensitivity and specificity of the model, as TSS = $ad - bc/(a + c)(b + d)$ or Sensitivity + Specificity – 1. The result of this equation is a value ranging from 1, a perfect model, to values < 0, indicating no better performance than a random model (Allouche et al. 2006). The 10th percentile training presence logistic threshold for *A. brunneus* egg cases (0.112), and for *P. xaniurus* egg cases (0.182) were used as the presence/absence cutoff. These values indicated when the model included 90% of the training data. For the model of *A. brunneus* oviposition site suitability, a is represented by the number of test points above the threshold value ($n = 85$), b the number of background points above the threshold value ($n = 290$), c the number of test points below the threshold value (n = 8), and *d* the number of background points below the threshold value (n = 9710). For the model of *P. xaniurus* oviposition site suitability, *a* = 94, *b* = 148, *c* = 10, and *d* = 9852.

Cohen's Kappa, or kappa, defines the accuracy of the model prediction in relation to the accuracy that may have resulted by chance alone. Specifically, kappa corrects the total accuracy of the model fit by adjusting it by the model fit expected by chance, as follows: $(P_o – P_e) / (1 – P_e)$, where P_o = the relative observed accuracy, and P_e = the hypothetical accuracy expected to occur by chance (Allouche et al. 2006; Mainali et al. 2015). Kappa is a less biased measure of predictability than jackknifing as it considers both omission and commission (areas of absence predicted present) errors (Baldwin 2009). It ranges from -1 to 1, where values ≤ 0 are indicative of model performance that is no better than random classification and a value of 1 indicates a perfectly accurate fit between predictions and observations (Cohen 1960; Tsoar et al. 2007). For a more detailed classification, 0.01–0.20 = slight agreement, 0.21– 0.40 = fair agreement 0.41–0.60 = moderate agreement, 0.61–0.80 = substantial agreement, and 0.81–0.99 = almost perfect agreement (Cohen 1960; Viera & Garret 2005).

Models for both *A. brunneus* and *P. xaniurus* oviposition site distributions were initially run using all 15 selected environmental variables. After each model run, the variable with the highest possible AUC_{test} when removed was then left out of the next model until gain could no longer improve. This process resulted in removing vertical and Northern current bottom velocity from *A. brunneus* catshark egg case models and removing latitude from *P. xaniurus* egg case models. Kappa and TSS were calculated during each model run and used in final model selection.

RESULTS

Attachment Substrate

The majority of observed *A. brunneus* egg cases were obtained from SWFSC-FED video (n = 4,816), whereas only 209 were observed from MBARI video. *Apristurus brunneus* oviposition site depth ranged from 87–550 m (MBARI), and 105–321 m (SWFSC-FED). SWFSC-FED showed *A. brunneus* egg cases were observed more often at or above the shelf break > 200 m (% = 79), while MBARI data showed *A. brunneus* egg cases were observed more often below the shelf break < 200 m (% = 97). *A. brunneus* oviposition site temperature ranged from 5.5–8.8 °C, and salinity ranged 33.9–34.4 ppt (Table 3). In total, 602 *A. brunneus* egg cases occurring individually or in a bundle had associated substrate information (Fig. 2). *Apristurus brunneus* had egg case counts up to 150 per oviposition site. The majority of bundles had 2–20 with a mean of 9 egg cases per bundle. There was a single occurrence of 300 old *A. brunneus* egg cases that were in a pile on soft sediment.

Attachment substrate included amphipod tubes, catshark egg cases (CEC), corals, crinoids, fishing line, rock, soft sediment, sponges (barrel, branching, encrusting, foliose, nipple, shelf [vertical and horizontal], tube, unidentified, and vase), and other (anemone = 1, basket star = 1, urchin = 1, detrital accumulation = 5). The most common attachment substrate were sponges (n = 237, % = 39.5), followed by rock (n = 138, % = 22.9). CEC (n = 70 , % = 11.6), soft sediment (n = 60, % = 10.0), and corals (n = 43, % = 7.14) had similar quantities of *A. brunneus* egg cases. Unidentified sponges were observed most often, (n = 115, % = 48.52), however the counts of foliose (n = 28, % = 11.81), shelf (n = 43, % = 18.14), and vase (n = 39, % = 16.46) combined comprised the majority of sponges (% = 46.41) with identifiable morphology that served for oviposition sites.

Although observations of egg cases attached to corals were relatively low in comparison to other substrate types, they were the second most frequent among invertebrates. The combined remaining attachment substrata were of relatively trivial importance (n = 53, % = 8.8) (Fig. 2).

The majority of observed *P. xaniurus* egg cases were obtained from SWFSC-FED video (n = 15,553), with only 1,419 observed from MBARI video. *Parmaturus xaniurus* oviposition site depth ranged from 99–524 m (MBARI), and 100–326 m (SWFSC-FED). *Parmaturus xaniurus* egg cases were observed more often below the shelf break < 200 m for both SWFSC-FED (% = 63) and MBARI (% = 97) data sources. Overall, for *P. xaniurus* egg case locations, temperature ranged from 5.6–11.3 °C and salinity ranged 33.9–34.4 ppt (Table 3). There were 1,189 *P. xaniurus* egg cases occurring individually or in a bundle where attachment substrate was noted (Fig. 2). *Parmaturus xaniurus* had egg case counts of ≤ 450 per oviposition site. The majority of oviposition sites had 1–20 egg cases, with a mean of 15. Several oviposition sites had > 100 *P. xaniurus* egg cases in piles on soft sediment.

Attachment substrate included amphipod tubes, catshark egg cases (CEC), corals, crinoids, fishing line, rock, soft sediment, sponges (of various morphologies), and other (brachiopod = 1, detrital accumulation = 1). The most common attachment substrate was sponges (n = 445, % = 37.5), followed by rock (n = 299, % = 25.2). CEC (n = 141 , % = 11.9), soft sediment (n = 127, % = 10.7), and corals (n = 91, % = 7.6). Unidentified sponges were observed most often (n = 234, % = 52.4), however the counts of shelf sponges (n = 129, % = 28.9) comprised the majority of sponges with identifiable morphology. The combined remaining attachment substrata were rarely used (n = 85, % = 7.2) (Fig. 2).

Faunal Associations

A total of 426 *A. brunneus* egg cases were observed in association with a specific faunal group. Some egg cases had multiple associations (e.g. an egg case bundle attached to a sponge that includes a seastar). Identified associated faunal groups included: amphipod tubes, corals (*Lophelia* sp., *Desmophyllum* sp., *Heteropolypus ritteri*, Octocorallia, and *Corallimorphus* spp.), crinoids, fishes (*Sebastes* spp., and *Sebastolobus* spp.), sea stars (*Luidia foliata*, *Stylasterias forreri*, *Mediaster aequalis*, *Rathbunaster californicus,* and Ophiuroidea), sponges, and other: anemones, Anthozoa (n = 3), and *Metridium* spp. (n = 1); crab (n = 1); gastropod, *Boreotrophon tripherus* (n = 1); urchin, *Strongylocentrotus fragilis* (n = 4); and salp egg (n = 1). Most *A. brunneus* egg case associations were with sponges (n = 244, % = 57.3), with unidentified sponges observed most often, (n = 101, % = 41.4), however the counts of foliose (n =28, % = 11.5), shelf (n = 56, % = 23.0), and vase (n = 39, % = 16.4) combined, comprised the majority of sponges (% = 50.8) with identifiable morphology. Seastars (n = 64, % = 15.0), and corals (n = 55, % = 12.9) were the next most associated fauna with similar egg case counts. Fishes (n = 21, % = 4.9), crinoids (n = 16, % = 3.8), and amphipod tubes (n = 15, % = 3.5), were less commonly associated but had similar egg case counts. Other taxa were rarely observed with *A. brunneus* egg cases (n = 11, % = 2.58) (Fig. 3).

A total of 876 *P. xaniurus* egg cases were observed in association with a similar faunal assemblage as *A. brunneus*. Identified associated faunal groups included:

amphipod tubes, corals (*Lophelia* sp., *Desmophyllum* sp., *H. ritteri*, *Clavularia* sp., Scleractinia, Octocorallia, and *Corallimorphus* spp.), crinoids, fishes (*Sebastes* spp., *Sebastolobus* spp., and *Ophidon elongatus*), sea stars (*L. foliata, S. forreri, M. aequalis, R. californicus,* and Ophiuroidea), sponges of various morphologies (i.e., barrel, branching, encrusting, foliose, nipple, shelf [vertical and horizontal], tube, and vase), and other: anemones, Anthozoa (n = 1), and *Actinostola* spp. (n = 1), brachiopod (n = 1); spot prawn, *Pandalus platyceros* (n = 1); giant Pacific octopus, *Enteroctopus dofleini* (n = 1); and unidentified gastropod (n = 1). The most observed faunal associations were with sponges of various morphologies (n = 460, % = 52.5). Of the sponges, unidentified sponges were observed most often, (n = 251, % = 56.2), while the counts of shelf sponges (n = 111, % = 24.8) comprised the majority of sponges with identifiable morphology. Seastars (n = 166, % = 19.0) were the next most frequently observed associated fauna with *P. xaniurus* eggs, followed by corals (n = 108, % = 12.3), and fishes (n = 72, % = 8.2). Amphipod tubes (n = 21, % = 2.4), and crinoids (n = 28, % = 3.2) were less commonly associated. Other taxa were rarely observed with *P. xaniurus* egg cases (n = 21, % = 2.4) (Fig. 3).

Due to video resolution and the small size of *A. brunneus* and *P. xaniurus* egg cases, it was difficult to tell if egg cases were damaged due to predation. Boreholes were, however, observed from MBARI still frames of older egg cases of *A. brunneus* and *P. xaniurus*. *Stylasterias forreri* was observed on an older, damaged *P. xaniurus* egg case. Based on observations from this study it is likely that predation on these catshark egg cases is a relatively common phenomena, but one that requires further detailed quantification.

Habitat Associations

For all subsampled transects, rocks were the dominant attachment substrate for *A. brunneus* (n = 30, % = 46.9), followed by catshark egg cases (CEC) (n = 19, % = 29.7). Sponges had the next highest frequency of substrate use and the greatest frequency among biogenic habitats (n = 7, % = 11.0), followed by corals (n = 3, % = 4.7). Soft sediment (n = 11, % = 5.5) and fishing line (n = 1, % = 0.5) were the least commonly utilized attachment substrates (Fig. 4). Rocks were the dominant attachment substrate for *P*. *xaniurus* (n = 95, % = 47.3), followed by catshark egg cases (CEC) (n = 52, % = 25.9). Sponges had the next highest frequency of substrate use and the greatest frequency among biogenic habitats (n = 30, % = 14.9), with shelf sponges comprising the majority (n = 14, % 46.6). Soft sediment (n = 11, % = 5.5), and corals (n = 10, % = 5.0) were utilized at similar frequencies. Crinoids (n = 2, % = 1.0), and fishing line (n = 1, % = 0.5) were rarely utilized (Fig. 4).

High induration habitats, hard (14691.6 m^2) and hard-mixed (7925.8 m^2), comprised the majority of available habitat area for egg case attachment at all depth bins. The lower induration habitats, soft (11098.1 m^2), and soft-mixed (5967.3 m^2) comprised the least available habitat for egg case attachment at all depth bin ranges (Fig. 5) The primary available habitat per transects was hard (% = 50.6) substrate followed by soft (% = 23.4) substrate. Hard-mixed (% = 14.2) and soft-mixed (% = 11.8) substrate had near equal availability among sampled transects. The highest counts of *A. brunneus* egg cases were seen on hard (n = 225) and hard-mixed habitat (n = 115), while soft (n = 17) and soft-mixed habitat (n = 6) recorded the fewest egg cases. The highest counts of *P. xaniurus* egg cases were found on hard-mixed (n = 1164) and hard habitat (n = 762), while soft-mixed (n = 312) and soft habitat (n = 14) recorded the fewest egg cases. Hard and hard-mixed habitat was the most utilized and had majority of egg cases for both species. *Apristurus brunneus* egg cases were observed most frequently on hard habitat (150–199 m, n = 195), while *P. xaniurus* egg cases were observed most frequently on hard-mixed habitat (150–199 m, n = 776) (Table 4).

Significant habitat associations were found for *A. brunneus* ($X^2{}_{(3)} = 91$, $P < 0.0001$) and for *P. xaniurus* ($X^2{}_{(3)} = 1047$, $P < 0.0001$). Manly's habitat selection identified hard and hard-mixed habitats with a selectivity index greater than random ($B_i > 0.25$) for *A. brunneus* and identified hard-mixed and soft-mixed habitats with a selectivity index greater than random ($B_i > 0.25$) for *P. xaniurus*. All habitat groups recorded significantly more observed egg cases than expected: *A. brunneus* hard ($X^2{}_{(1)} = 18.65$, $P < 0.0001$), *A. brunneus* hard-mixed ($X^2{}_{(1)} = 9.68$, $P < 0.001$), *P. xaniurus* hard-mixed ($X^2{}_{(1)} = 96.94$, $P < 0.0001$), and *P. xaniurus* soft-mixed ($X^2{}_{(1)} = 25.93$, $P < 0.0001$). These results identified hard-mixed as the primary oviposition habitat type used by both species, while *A. brunneus* used hard as secondary oviposition habitat and *P. xaniurus* used soft-mixed as secondary oviposition habitat (Fig. 6).

Significant depth and habitat associations were found for *A. brunneus* egg cases ($X^2{}_{(3)} = 1171.91$, $P < 0.0001$). Manly's habitat selection identified three of the 16 habitat and depth groups with a selectivity index greater than random ($B_i > 0.0625$): hard (150–199 m, $B_i = 0.42$), hard-mixed (100–149 m, $B_i = 0.23$), and hard-mixed (150–199 m, $B_i = 0.19$), suggesting positive selection for egg case deposition in these habitat areas. All of these depth-habitat groups recorded significantly more observed egg cases than expected: hard (150–199 m, $X^2{}_{(1)} = 67.28$, $P < 0.0001$), hard-mixed (100–149 m, $X^2{}_{(1)} = 10.81$, $P <$

0.01, and hard-mixed (150–199 m, $X^2_{(1)} = 8.58$, $P < 0.01$). These results suggest differential usage of high induration habitat between 100–199 m for egg case deposition by *A. brunneus* (Fig. 7).

Significant depth and habitat associations were determined for *P. xaniurus* egg cases ($X^2_{(9)} = 2426.77$, $P < 0.0001$). Manly's habitat selection identified five of the 16 habitat and depth groups with a selectivity index greater than random ($B_i = 0.0625$): hard (150–199 m, $B_i = 0.07$), hard (200–249 m, $B_i = 0.09$), hard-mixed (150–199 m, $B_i = 0.36$), hard-mixed (200–249 m, $B_i = 0.13$), and soft-mixed (200–249 m, $B_i = 0.21$). All of these depth-habitat groups with the exception hard (150–199 m, $X^2_{(1)} = 2.17$, $P = 0.140$), recorded significantly more observed than expected egg cases: hard (200–249 m, $X^2_{(1)} = 13.30$, $P < 0.01$), hard-mixed (150–199 m, $X^2_{(1)} = 271.83$, $P < 0.0001$), hard-mixed (200–249 m, $X^2_{(1)} = 23.83$, $P < 0.0001$), and soft-mixed (200–249 m, $X^2_{(1)} = 70.60$, $P < 0.0001$). These results suggest differential usage of high induration habitat between 150–249 m for egg case deposition by *P. xaniurus* (Fig. 8).

Hard substrate comprised more available habitat for attachment than hard-mixed for the subsampled transects examining egg case associations with corals or sponges: barren-hard (% = 63.2), coral-hard (% = 21.1), sponge-hard (% = 8.7), barren-hard-mixed (100–149 m, % = 5.1), coral-hard-mixed (% = 0.0), sponge-hard-mixed (% = 1.8). Significant associations were detected between *P. xaniurus* egg cases and their attachment substrate ($X^2_{(2)} = 1295.50$, $P < 0.0001$). The relationship between presence of *P. xaniurus* egg cases on corals, sponges, or barren substrate, and habitat type revealed barren substrate had the most associated egg cases, and corals had the least: barren-hard (n = 337, % = 75.9), barren-hard-mixed (n = 39, % = 6.1), coral-hard (n = 26, % = 4.1), coral-hard-mixed (n = 0, % = 0.0), sponge-hard (n = 67, % = 10.5), and sponge-hard-mixed (n = 21, % = 3.3). Manly's habitat selection identified hard ($B_i = 0.21$), hard-mixed ($B_i = 0.21$), sponge-hard ($B_i = 0.21$), and sponge-hard-mixed ($B_i = 0.33$) habitats with a selectivity index greater than random ($B_i = 0.17$). The relationships hard ($X^2_{(1)} = 6.25$, $P = 0.01$), and hard-mixed ($X^2_{(1)} = 87.69$, $P > 0.0001$) had significant associations, while sponge-hard ($X^2_{(1)} = 0.19$, $P = 0.66$), and sponge-hard-mixed ($X^2_{(1)} = 1.27$, $P = 0.26$) did not have significant associations. These results suggest that *P. xaniurus* was utilizing barren rocky substrate more than sponges, however; although not statistically significant, sponges still proved important as the sponge-hard-mixed group had the highest selectivity index.

Habitat Suitability Models

Potential Distribution

The final *A. brunneus* egg case model was found to be robust, with realistic occurrence probabilities compared with the presence data (Fig. 9A) and the currently described distribution of *A. brunneus* oviposition sites. There was a dense amount of oviposition sites at the shelf break to mid Monterey canyon (≥ 200 m), with sparse oviposition sites at the Monterey canyon head and on the continental shelf (< 200 m) (Fig. 9B). There was a high probability of oviposition site occurrence on the upper continental slopes and shelf break of Monterey Bay and Carmel Bay, and towards the head of the Carmel and Soquel Canyons, a moderate probability of finding egg cases on the shelf break of Cabrillo Canyon, and low probability of occurrence on the continental shelf (Fig. 9A).

The final *P. xaniurus* egg case model was also robust, with realistic occurrence probabilities compared with the presence data (Fig. 10A) and the currently described distribution of *P. xaniurus* oviposition sites. The majority of oviposition sites were observed at the shelf break to mid Monterey canyon (≥ 200 m), with sparse oviposition sites at the Carmel and Monterey canyon heads, and on the continental shelf (Fig. 10B). There was high probability of oviposition site occurrence on the upper shelf break of Monterey and Soquel Canyons (≤ 100 m and ≥ 300 m), and a moderate probability of finding egg cases on the shelf break (≥ 200 m) of Cabrillo Canyon, and in Carmel Bay, and a low probability of *P. xaniurus* egg cases being found near the head of Carmel and Monterey canyons or on the continental shelf (Fig. 10A).

At the 10% training presence the fractional predicted area (FPA) was 2.7% for *A. brunneus*, and 1.6% for *P. xaniurus*. For both species, test points were predicted better than by a random prediction with the same fractional predicted area ($P < 0.0001$). *Apristurus brunneus* had a larger predicted suitable habitat range for oviposition sites than *P. xaniurus*. Areas of high occurrence probability for both species were predicted more often on the upper shelf and continental slope, with low to 0 probability for oviposition sites on the continental shelf, or at deeper regions of the canyons.

Environmental Factors Influencing Egg Case Habitat Distribution

The variable with the highest percent importance in predicting suitable habitat for the final *A. brunneus* egg case MaxEnt model was rugosity (% = 54.7), which also had the second highest permutation importance (% = 18.6) (Table 5). Jackknife training, test, and AUC plots (Fig. 11) indicated that rugosity had the highest gain when used in isolation and was the most effective single variable for predicting the distribution of the occurrence test data when predictive performance is measured using AUC (AUC > 0.96). Depth had the second highest percent importance (% = 24.0) in predicting suitable habitat, and the highest permutation importance at (% = 71.9) (Table 5). Jackknife training, test, and AUC plots (Fig. 11) indicated depth had the next highest gain when used in isolation and was the second most effective variable for predicting the distribution of the occurrence data (AUC > 0.90).

The remaining four variables contributed little to the final *A. brunneus* egg case model (% = 21.6) combined and had little permutation importance (% = 9.5) (Table 5). The range of latitude degrees was restricted to the Monterey Bay area and had a small percent contribution to the final MaxEnt model; however, latitude permutation importance and jackknife plots indicated that aside from rugosity and depth, the model depended on latitude. Furthermore, when used as the only environmental variable in the model, model performance was good (AUC > 0.85). Percent mud achieved almost no training or test gain and was not useful by itself in estimating suitable egg case habitat (Fig. 11A, 11B). Although it is possible that variable importance may change when using test data compared to training data, the same trend was observed in the test gain plot (Fig. 11B). The remaining three variables had poor performance when used in isolation (AUC < 0.85) (Fig. 11C).

The response curve output here is presented in order of variable importance. The probability of suitable habitat increased for *A. brunneus* oviposition sites as substrate became more rugose. This response curve exhibited a maximum likelihood > 0.90 (Fig. 12A). Bottom depth (Fig. 12B) between 150–400 m contained the highest probability of suitable habitat, with a maximum suitability of 0.80 at 300 m. Percent gravel (Fig. 12C) indicated a peak of predicted egg case presence at 10% gravel, with probability of suitable habitat of 0.80. The probability of suitable habitat rapidly decreased as percent gravel increased above 10%. The probability of suitable habitat for egg case deposition increased as the percent mud increased (Fig. 12D) with maximum predictive probability of 0.80–0.85. It was observed that mud (% = 60) had the same predictive probability as gravel (% = 10) at 0.80 probability of suitable habitat. Latitude (Fig. 12E) had a maximum probability of suitable habitat of 0.80 at a range of 0.45 degrees (36.45 to 36.00° N), located in the middle of the Monterey Bay. Eastern bottom current velocity (Fig. 12F) had maximum predictive probability of suitable habitat of ~0.80 at 0.012 m/s to the east. Suitable habitat for oviposition rapidly declined as velocity increased and had a steep decline as current velocity was directed west.

The variable with the highest percent importance in predicting suitable habitat for the final *P. xaniurus* egg case MaxEnt model was rugosity (% = 66.1), which also had the highest permutation importance (% = 55.7) (Table 6). Jackknife training, test, and AUC (Fig. 13) plots indicated rugosity had the highest gain when used in isolation and was the most effective variable for predicting the distribution of the occurrence test data when predictive performance is measured using AUC (AUC > 0.95). Depth had the second highest percent contribution (% = 21.9) and second highest permutation importance (% = 35.9) (Table 6). Jackknife training (Fig. 13A), test (Fig. 13B), and AUC (Fig. 13C) plots indicated depth had the second highest gain when used in isolation and was the second most effective variable for predicting the distribution of the occurrence test data when predictive performance is measured using AUC (AUC > 0.90).

The remaining five variables contributed little to the final model combined (% = 12.1) and had little permutation importance (% = 8.4) (Table 6). The test gain plot (Fig. 13B) differed slightly from the training gain plot (Fig. 13A), as percent gravel exceeded test gain demonstrating how predictive performance improved when this variable was omitted. Percent gravel dropped to the second least useful variable when used in isolation, with percent mud remaining the least useful variable. With the exception of latitude which was slightly greater than AUC = 0.85, all other variables had AUC < 0.85 when used in isolation (Fig. 13C).

The response curve output here is presented in order of variable importance. The probability of suitable habitat increased for *P. xaniurus* oviposition sites as substrate became more rugose, with a maximum suitable habitat probability > 0.9 (Fig. 14A). Bottom depths (Fig. 14B) between 175–400 m had the highest probability of suitable habitat, with a maximum of > 0.75 at 300 m. Percent gravel (Fig. 14C) indicated a peak of oviposition at 9% gravel, with a probability of suitable habitat of 0.75. Probability of suitable habitat rapidly decreased as percent gravel increased. Habitat suitability of annual Northern bottom current velocity (Fig. 14D) exhibited a steep incline to 3 m/s, with probability of suitable habitat of 0.75. Percent mud (Fig. 14E) ranged between 20–80%, with maximum suitable habitat probability of 0.70. Annual vertical bottom current velocity (Fig. 14F) had peak predictive probability of 0.87 in the downward direction at 5.25 m/s, while there was a 0.75 probability of suitable habitat at 2.0 m/s in the vertical direction. Eastern bottom current velocity (Fig. 14G) exhibited maximum probability of suitable habitat of 0.89 at 0.02 m/s. The probability of finding suitable habitat steeply declined as current velocity was directed west.

Model Evaluation

The high AUC value of the final *A. brunneus* model indicates that MaxEnt did significantly better than random (AUC = 0.5) to represent catshark egg case occurrence locations. The AUC_{Test} and AUC_{Train} for the final *A. brunneus* egg case model (0.989, 0.987) indicated the model can derive robust predictions of the locations of potential suitable habitat (Fig. 15A). Sensitivity and specificity results were high for *A. brunneus*, (0.91, 0.99). The kappa value for *A. brunneus* was 0.50. The TSS for *A. brunneus* was 0.89. These values indicated that both models performed statistically better than random (Table 7).

The high AUC value of the final *P. xaniurus* egg case model demonstrates that MaxEnt did significantly better than random (AUC = 0.5) model to represent catshark egg case occurrence locations. The AUC_{Test} and AUC_{Train} for the *P. xaniurus* egg case model (0.991, 0.991) indicated the model can derive robust predictions of the locations of potential suitable habitat (Fig. 15B). Sensitivity and specificity results were high for *P. xaniurus* (0.90, 0.99). The kappa value for *P. xaniurus* egg cases was 0.58. These values are in moderate agreement with each model's performance. The TSS *P. xaniurus* egg case model was 0.89. These values indicate that both models performed statistically better than random (Table 7).

DISCUSSION

Nursery Ground Documentation

The current study is the first to verify specific nursery habitats for *A. brunneus* and *P. xaniurus* oviposition. The criteria to qualify as oviparous elasmobranch nurseries

(Hoff 2016) were all met in this study, supporting the determination of EFH for *A. brunneus* and *P. xaniurus* in the Monterey Bay area. 1) Large quantities of egg cases of *A. brunneus* and *P. xaniurus* were observed in various geographic locations within the study region. 2) All egg cases were attached to or contacting benthic or stationary substrate, from rocky outcrops to fishing line, and were also observed in direct contact with the seafloor. 3) It was evident that oviposition sites were used over multiple years based on observations of egg cases at different stages of development. Furthermore, the observation of new egg cases bound to bundles of older eggs was indicative that oviposition sites are used over multiple years. 4) No free-swimming sharks were observed near *A. brunneus* and *P. xaniurus* egg case locations, suggesting that juvenile sharks emigrate from deposition sites, and that juvenile nurseries exist elsewhere. Shark habitat use patterns are most commonly studied in nursery areas (Heithaus 2007; Simpfendorfer & Heupel 2012). This emphasis on early life stages indicates the importance of identifying such habitats for population maintenance and for the determination of EFH for habitat-based management via Fishery Management Plans (Heithaus 2007; USDOC 2007). I propose that the shelf break, upper slope, and upper canyon regions within the Monterey-Ascension canyon system should be classified EFH, specifically the Monterey Canyon due to its size.

Attachment Substrate

Oviposition sites may be obligate for some oviparous species but appeared to be facultative for *A. brunneus* and *P. xaniurus*. Egg cases were observed on anthropogenic material such as fishing line and on naturally occurring structures, indicating that morphology, induration, and stability of these structures has an influence on oviposition (Henry et al. 2013). Overall, sponges, rock, and CEC were the primary attachment substrates for all qualitative oviposition site observations as well as the subsampled oviposition site proportions. Newly deposited *A. brunneus* and *P. xaniurus* egg cases were attached to older egg cases at greater frequencies than egg cases of all developmental stages were attached to corals, potentially due to substrate availability, while also exhibiting facultative selection of oviposition sites.

Catshark nurseries occur on various colonies of sessile megafauna, often corals or sponges (Etnoyer & Warrenchuk 2007; Flammang 2011; Cau et al. 2017). Sponges are important SFMI, forming complex and delicate ecosystems throughout the world's oceans (NOAA 2010). *Apristurus brunneus* and *P. xaniurus* were most commonly attached to shelf sponges such as *Poecillastra* spp., which were often observed growing perpendicular to rock walls. Surprisingly, egg cases of both species were found attached to white encrusting sponges. Encrusting sponges are relatively small, with variable amounts of relief per species, and are predominately found on rocks (Lee et al. 2007). The underlying rock morphology was likely influential for oviposition on these sponges.

Habitats with increased structural complexity like rock outcrops influence the distribution of species as complex habitats offer more attachment surface area (Auster 2005). Hard habitat was the primary available habitat within all surveyed regions. Catshark nurseries of different species have been identified in association with rocky vertical relief. For example, horn sharks, *Heterodontus* spp., wedge their egg cases into rock crevices in steeply sloping regions for protection from getting displaced in the currents (Powter & Gladstone 2008), similar to how *A. brunneus* and *P. xaniurus* demonstrated utilization of hard habitat by wrapping egg cases into crevices of or around rock structures to anchor them.

Rocky outcrops had an abundance of egg case bundles that fell outside the transect or had too poor of resolution to enumerate, though some of these large bundles were observed along transects as well. These dense bundles, some of which appeared to contain hundreds of egg cases, extended meters in length, and filled the entire surface space on some rock overhangs. Only *P. xaniurus* egg cases were observed occurring in these large strings. Newly deposited egg cases were found on a variety of substrates but were often attached to these large strings. It therefore appears that *P. xaniurus* uses recurring oviposition sites.

Much of the benthos consists of mud and other fine sediment, especially as the Monterey Canyon serves as a conduit of sediment transport (Wolf 1970; Edwards 2002; Callow et al. 2014). Soft sediment was the second most available habitat type out of all surveyed transects. Egg cases in various stages of development were seen on soft sediment either singularly or in piles at same proportions they were observed attached to CEC. When a large pile of egg cases was seen on soft sediment it is plausible the weight of the egg cases was too heavy for the structure they were originally attached to and broke off. These piles were largely dead and decaying, suggesting that soft sediment is not selected oviposition habitat.

Structure Forming Marine Invertebrate Associations

Corals and sponges are complex, 3-dimensional structures which make them ideal habitat for other species, including fishes and invertebrates (Brancato et al. 2007). SFMI have an ecological role as biotic components of habitat within invertebrate and fish communities (Hourigan et al. 2017). The coral and sponge colonies associated with *A. brunneus* and *P. xaniurus* egg cases are part of a diverse assemblage of invertebrates and fishes as SFMI have increased habitat complexity that contributes to community structure (Hourigan et al. 2017). *Apristurus brunneus* and *P. xaniurus* oviposition sites were found to occur on SFMI throughout the Monterey Bay nursery area with many bundles (2–20 egg cases per bundle) identified. This finding is similar to that of Etnoyer and Warrenchuck (2007) who observed a field of coral colonies > 1 km in the Gulf of Mexico where the majority of coral colonies had 1–3 attached eggs. SFMI provide a variety of ecosystem services, including foraging, allowing access to stronger currents, refuge from predators, and by acting as nurseries (Brancato et al. 2007). This study demonstrated the importance of SFMI for oviposition of *A. brunneus* and *P. xaniurus* egg cases.

SWFSC-FED did not annotate sponges < 10 cm so many of the egg cases attached to these sponges were not included in analyses. The low amount of *P. xaniurus* egg cases found on sponges or corals in comparison to barren substrate is likely an artifact of overlooking egg cases amongst the dense biologically rich community (Henry & Roberts 2017). Significantly more barren rock was available than sponges or corals, an explanation for majority of egg cases found on this habitat. Despite this observation, corals and sponges were identified as important SFMI for catshark egg case nurseries.

Geographic and Environmental Influence

The shelf break of Monterey Bay Canyon and several adjacent canyons in the region were the most geographically important locations for *A. brunneus* and *P. xaniurus* oviposition. Submarine canyon systems exhibit locally elevated oxygen and nutrient concentrations which are important for maintaining benthic communities (Callow et al. 2014). Canyon slopes are often characterized by distinct faunal assemblages with higher diversity than surrounding continental slopes (Treude et al. 2011; Callow et al. 2014) and were important geographic features for oviposition sites. Able and Flescher (1991) described locations of high vertical relief and stronger currents as important features of reproductive aggregation sites for the chain catshark, *Scyliorhinus rotifer*. Similarly, areas with high vertical relief were verified as important for both *A. brunneus* and *P. xaniurus* oviposition attachment substrate.

The physical structure of the seafloor is a key component in understanding benthic associations and was important for identifying preferred oviposition site features (Wilson et al. 2007; Dunn & Halpin 2009). Rugosity had the greatest environmental influence on oviposition sites for *A. brunneus* and *P. xaniurus*. Areas of high rugosity are predominately hard structures (Wilson et al. 2007; Dunn & Halpin 2009). As seen in previous catshark nursery site studies (Etnoyer & Warrenchuk 2007; Kiel et al. 2013), areas of highly rugose seafloor were preferentially used as egg case deposition sites. This was also observed at *A. brunneus* and *P. xaniurus* oviposition sites. The majority of oviposition sites for both species were observed on high induration habitat.

Depth is a strong predictor of diversity for North Pacific groundfish assemblages (Piacenza et al. 2015) and was the second greatest environmental influence on oviposition sites for *A. brunneus* and *P. xaniurus*. At increasing depths, benthic organisms are frequently strongly associated with certain substrates, such as sand, mud, and rock, which can influence distributional patterns (Piacenza et al. 2015). *Apristurus* *brunneus* and *P. xaniurus* egg cases were previously recorded as occurring between 300–500 m (Flammang et al. 2011). Due to a more comprehensive analysis of oviposition sites a depth range expansion to 87–550 m for *A. brunneus* egg cases, and 99–524 m for *P. xaniurus* egg cases has been confirmed. Flammang et al. (2011) found gravid females of *A. brunneus* and *P. xaniurus* between 300–500 m depths. A better understanding of the depth distributions of these species provides further insight to the range adult sharks utilize for oviposition. Although there were similar depth ranges for both species' oviposition sites, subsampled SWFSC-FED data indicated that *A. brunneus* egg cases occurred more often at shallower depths (100–199 m), and *P. xaniurus* egg cases occurred deeper (150–250 m). This result is substantiated by the observations of *P. xaniurus* egg cases occurring more often > 200 m from both MBARI and SWFSC video, while majority of *A. brunneus* egg cases occurred < 200 m from SWFSC video which comprised the majority of all *A. brunneus* egg case observations.

The ranges of temperature and salinity at oviposition sites for *A. brunneus* and *P. xaniurus* were similar. Flammang et al. (2011) reported temperature at a mean of 5 ℃ for catshark nurseries based on the reported mean depth range (300–500 m) in Central California. MBARI and SWFSC-FED data yielded *A. brunneus* egg cases at mean temperatures of 7.20 ℃ ± 0.82, and 8.88 ℃ ± 0.51, respectively, and *P. xaniurus* egg cases at mean temperature 7.47 ± 0.60, and 8.81 ℃ ± 0.55, respectively. The slight difference in temperature and salinity ranges between MBARI and SWFSC-FED observations can be attributed to the variation in survey depth.

Although outside the study region of our presence-only modelling, MBARI data indicated latitude ranges of 33.9–39.6° N for *A. brunneus* egg cases. Archived Northwest

Fisheries Science Center (NWFSC), Fishery Resource Analysis and Monitoring Division (FRAM) trawl data from 2003–2019 reported egg cases of *A. brunneus* between southern California and Washington (32.3–48.3° N). The FRAM database contains no records of *P. xaniurus* egg case occurrence (WCGBTS 2020). However, given the similarities in egg case morphology between species, and inexperience of volunteers and observers in identifying catshark egg cases, there is a possibility that *P. xaniurus* egg cases have a larger geographic distribution than was reported.

An overlap in geographic and environmental features between *A. brunneus* and *P. xaniurus* oviposition sites supports a general conclusion that egg cases of different species and genera can and do co-occur. *Apristurus brunneus* and *P. xaniurus* egg cases were at times observed centimeters away from each other but were never contained in the same bundle or attached to each other. The similarities in CTD values further supports that both species are occupying oviposition sites in close proximity. A likely reason that both species egg cases were commonly found on similar attachment substrate is their morphology, specifically having filamentous tendrils on anterior and posterior ends of the egg cases (Flammang et al. 2008), which facilitate their adhesion to structures. The third and final deep sea catshark species that occurs within the study region, *A. kampae*, has egg cases that lack attachment tendrils, and none were observed despite the existence of juveniles and adults in the region.

Species in highly diverse deep sea communities often coexist in specific partitioned ecological niches with various habitat requirements (McClain & Schlacher 2015); however, *A. brunneus* and *P. xaniurus* oviposition sites overlapped with no discernable evidence of interspecific competition within the sampled benthic communities. More concentrated locations of *P. xaniurus* egg cases were observed compared to those of *A. brunneus*. This difference is likely attributed to the higher frequency of *P. xaniurus* egg cases observed throughout the study region, suggesting there are more *P. xaniurus* oviposition sites within the Monterey Bay nursery region than those of *A. brunneus*. While reviewing MBARI video for this project, adult and juvenile *Parmaturus xaniurus* were observed 907 times with a total count of 1,576 sharks, while *Apristurus brunneus* were observed 193 times with a total count of 193 sharks. Thus, the higher frequency of occurrence of *P. xaniurus* egg cases is likely due to the adults being more abundant in the study region.

CONCLUSIONS

Nurseries are of critical importance for chondrichthyan reproductive success, especially for deep sea species that typically are among the least productive and are therefore highly susceptible to exploitation. Although *A. brunneus* and *P. xaniurus* populations appear to be stable, both species have low fecundity and protracted incubation periods. This potential vulnerability during embryo development necessitates the identification of catshark nurseries for EFH designation and habitat-based management. In this study, nursery grounds for *A. brunneus* and *P. xaniurus* were documented in the Monterey-Ascension Canyon system, especially in association with rugose rock habitats and SFMI (especially sponges) at the shelf break (150–199 m). Nursery ground characteristics were similar between species, though *A. brunneus* utilized a slightly shallower depth range including the headward part of submarine canyon. In addition, *P. xaniurus* egg cases were far more abundant than those of *A. brunneus*. These newly discovered nursery locations can be compared with future observations to monitor potential changes in utilization due to environmental or anthropogenic factors, such as climate change or commercial fishing.

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TABLES

Table 1: Environmental predictors used for modelling oviposition site habitat suitability for *A. brunneus* and *P. xaniurus*.

Environmental Feature	Description	Units
Bottom Current Velocity Eastness	Annual current velocity	m/s
Bottom Current Velocity Northness	Annual current velocity	m/s
Bottom Current Velocity Vertical	Annual current velocity	m/s
Bottom Salinity	Annual mean salinity	ppt
Bottom Temperature	Annual mean temperature	℃
Depth	Distance below sea level	m
Hard/Soft	Seafloor induration	-
Latitude	Geographic coordinates (N–S)	(0–90°)
Mean Grain Size	Mean grain diameter	mm
Gravel	Amount of gravel	% (0–100)
Mud	Amount of mud	% (0–100)
Sand	Amount of sand	% (0–100)
Rugosity	Topographic roughness	-
Slope	Mean slope (steepness)	(0–90°)
Slope of Slope	Direction of slope	(0–360°)

Table 2: Descriptive statistics for *A. brunneus* and *P. xaniurus* egg case occurrences, including depth range and CTD averages.

Species	n	Source	Depth range	Mean depth (m)	Mean salinity (ppt)	Mean temperature (℃)
A. brunneus	209	MBARI	87-550 m	352 ± 81	34.14 ± 0.08	7.18 ± 0.82
A. brunneus	4,816	SWFSC	105-322 m	216 ± 49	34.05 ± 0.10	8.88 ± 0.51
P. xaniurus	1,419	MBARI	99-524 m	328 ± 68	34.14 ± 0.06	7.47 ± 0.60
P. xaniurus	15,553	SWFSC	99-326 m	225 ± 50	34.06 ± 0.09	8.81 ± 0.55

Table 3: Counts of *A. brunneus* and *P. xaniurus* egg cases with proportions of habitat categories in each depth bin.

Species	Depth bin (m)	Hard	Hard-mixed	Soft	Soft-mixed
A. brunneus	100-149	16 (0.14)	57 (0.05)	0 (0.10)	0 (0.06)
	150-199	195 (0.09)	55 (0.05)	17 (0.06)	0 (0.03)
	200-249	10 (0.09)	0 (0.05)	0 (0.06)	6 (0.04)
	250-300	4 (0.05)	3 (0.05)	0 (0.06)	0 (0.02)
P. xaniurus	100-149	138 (0.14)	96 (0.05)	0 (0.10)	0 (0.06)
	150-199	245 (0.09)	776 (0.05)	12 (0.06)	0 (0.03)
	200-249	334 (0.09)	229 (0.05)	3 (0.06)	312 (0.04)
	250-300	45 (0.05)	63 (0.05)	0 (0.06)	0 (0.02)

Table 4: Final MaxEnt model environmental feature percent contribution and permutation importance for *A. brunneus* egg case habitat suitability probability.

Variable	Percent contribution	Permutation importance
Rugosity	54.7	18.6
Depth (m)	24.0	71.9
% Gravel	14.0	1.5
% Mud	3.6	1.1
Latitude (degrees)	3.4	6.3
Eastern bottom current velocity (m/s)	0.4	0.6

Table 5: Final MaxEnt model environmental feature percent contribution and permutation importance for *P. xaniurus* egg case habitat suitability probability.

Variable	Percent contribution	Permutation importance
Rugosity	66.1	55.7
Depth (m)	21.9	35.9
% Gravel	8.5	5.6
Northern bottom current velocity (m/s)	2.2	1.5
% Mud	1.0	0.7
Vertical bottom current velocity (m/s)	0.3	0.2
Eastern bottom current velocity (m/s)	0.1	0.4

Table 6: MaxEnt output metrics for model evaluation.

Species	Test gain	AUC_{test}	Kappa	TSS	Sensitivity	Specificity
A. brunneus	3.43	0.99	0.50	0.90	0.91	0.99
P. xaniurus	3.55	0.99	0.58	0.89	0.90	0.99

FIGURES

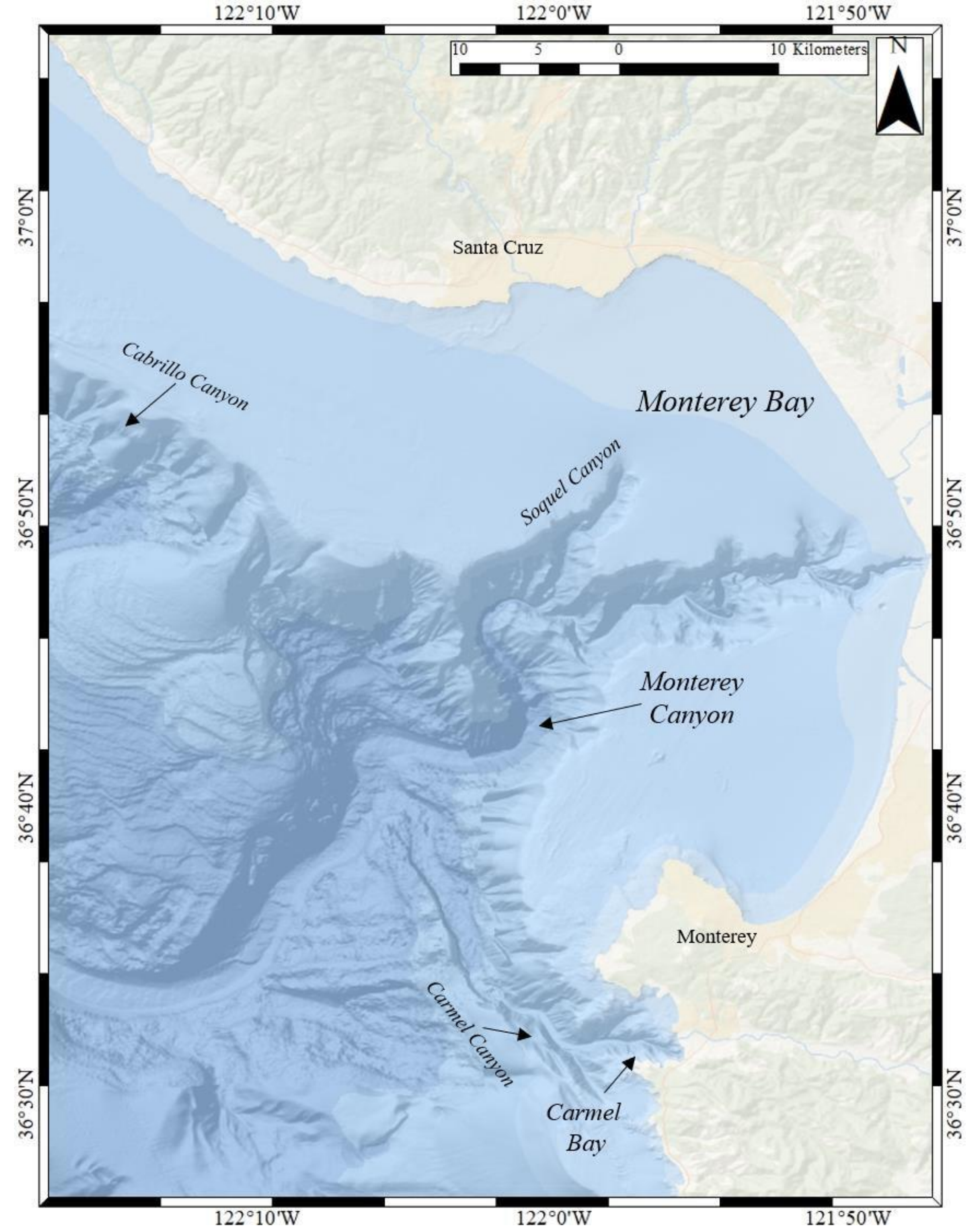

Figure 1: Study location in the greater Monterey Bay (36.3–37°N) region, showing the locations of major submarine canyons.

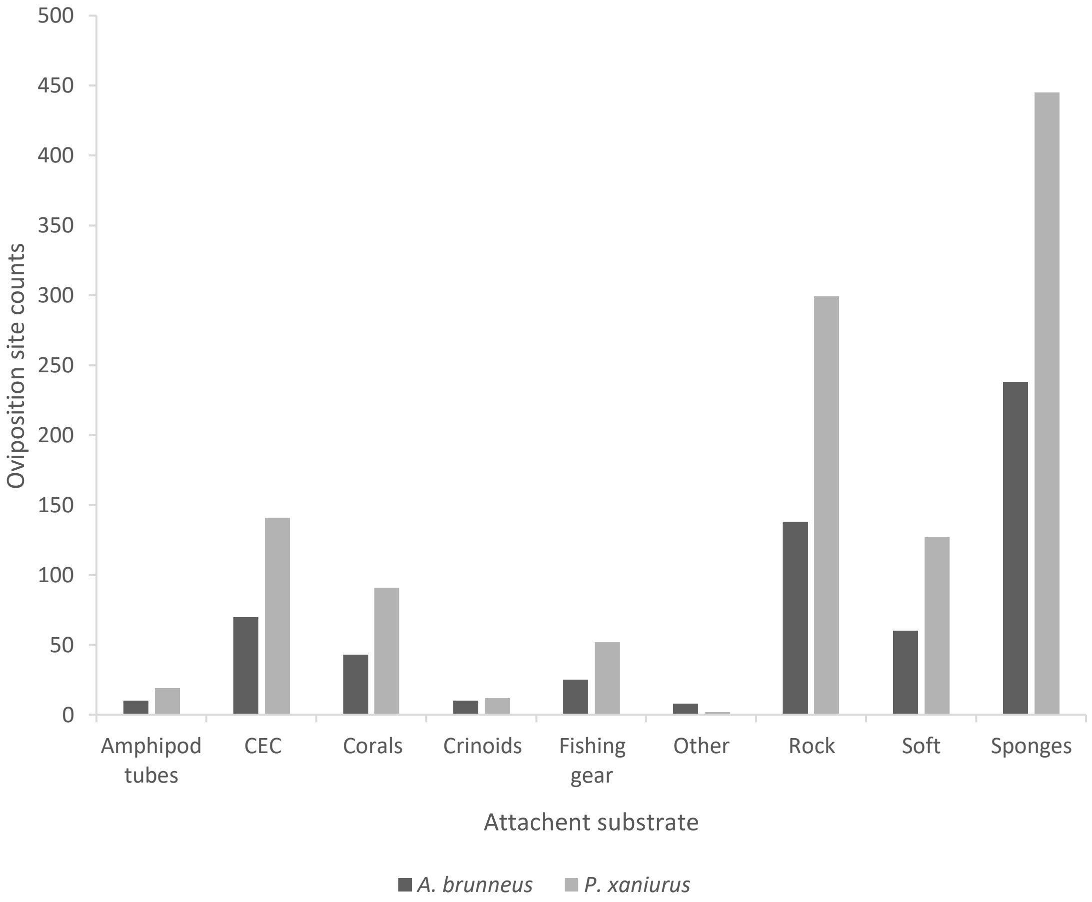

Figure 2: Oviposition site counts among attached substrate types. CEC (catshark egg case), Soft (mud or silt).

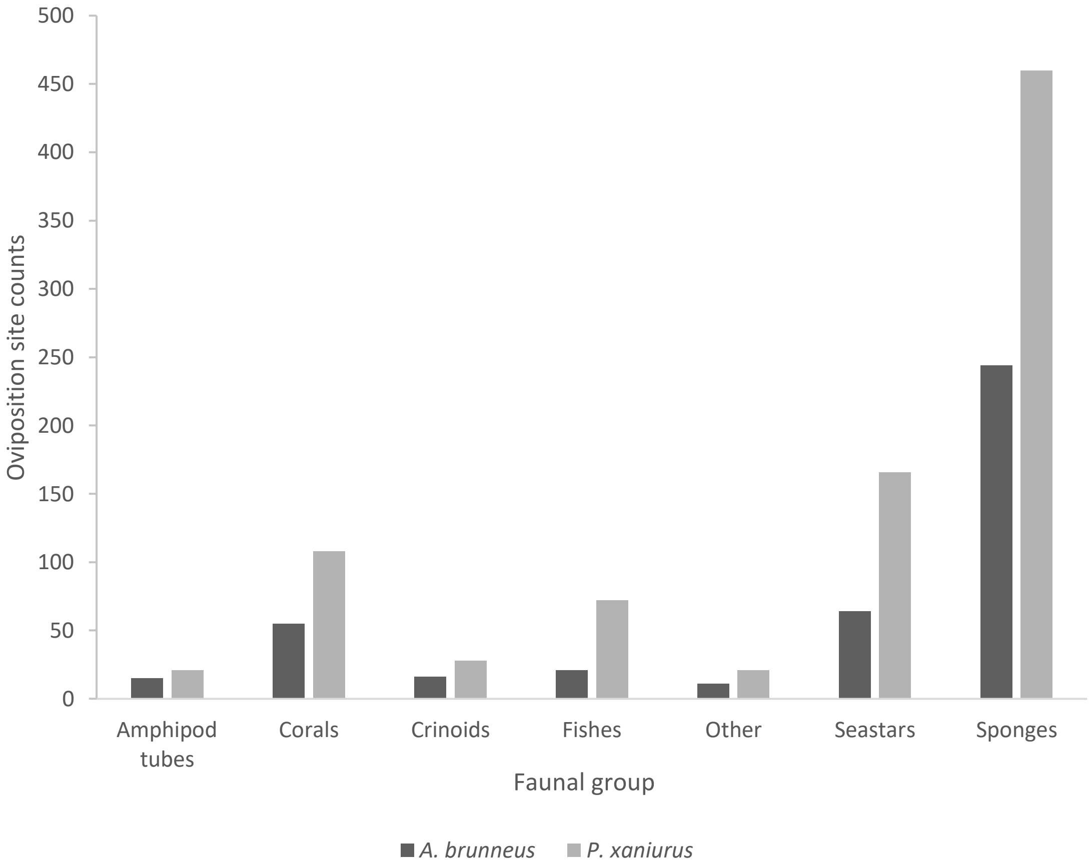

Figure 3: Oviposition site counts of *A. brunneus* and *P. xaniurus* among associated faunal groups.

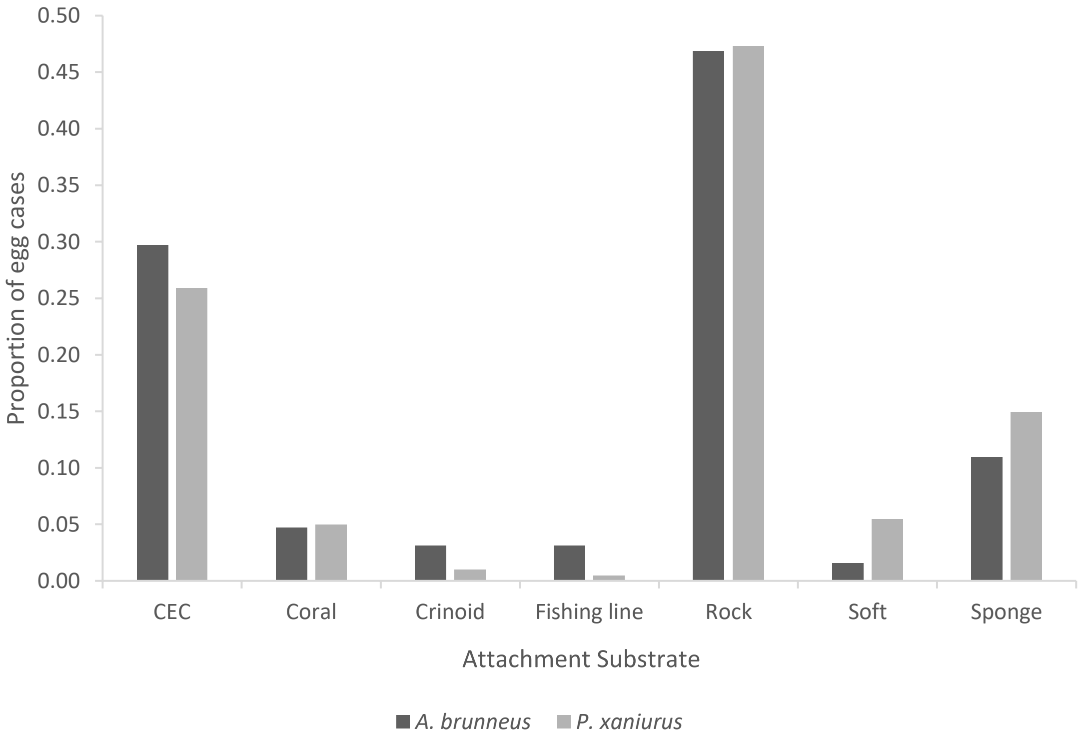

Figure 4: Proportions of egg cases among attached substrate for *A. brunneus* and *P. xaniurus* from the SWFSC-FED subsampled transects.

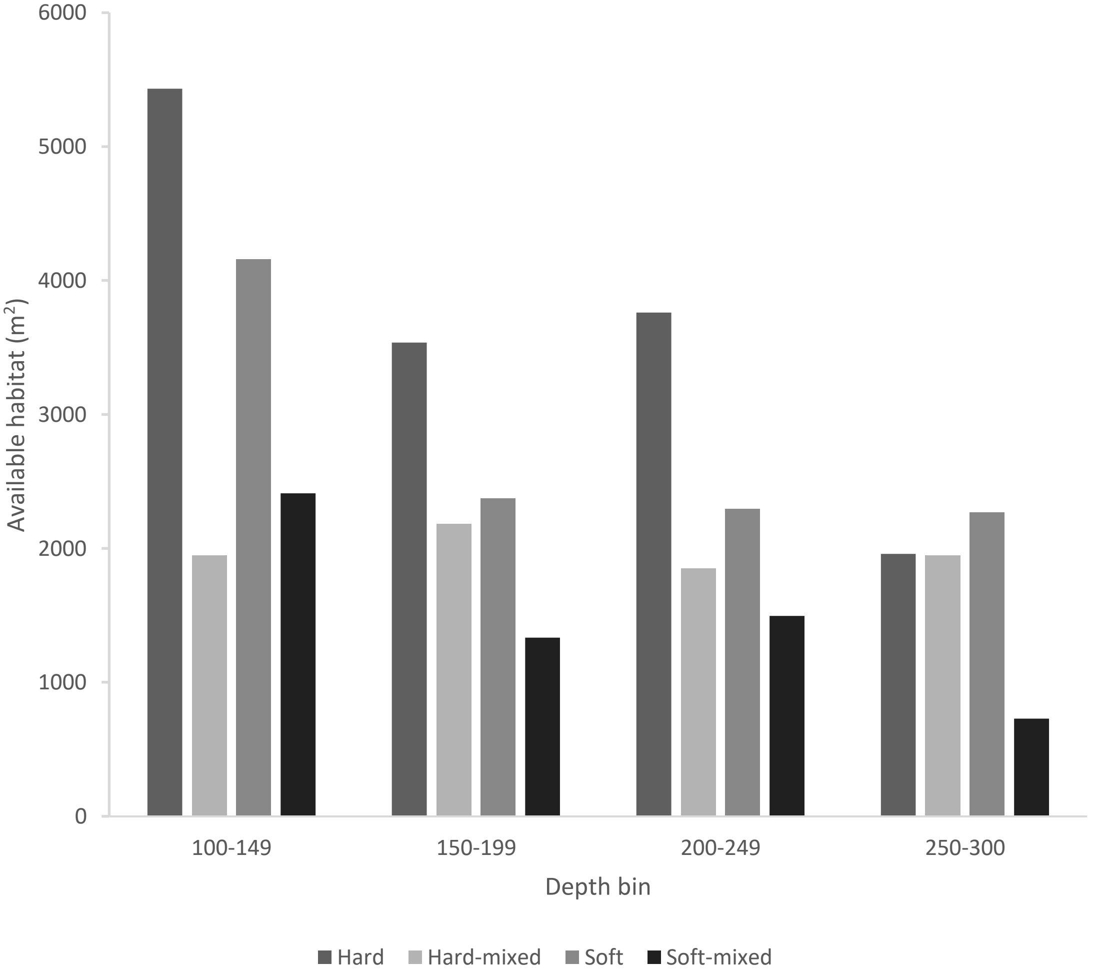

Figure 5: Area available (m^2) of habitat categories as a function of depth from SWFSC subsampled transects.

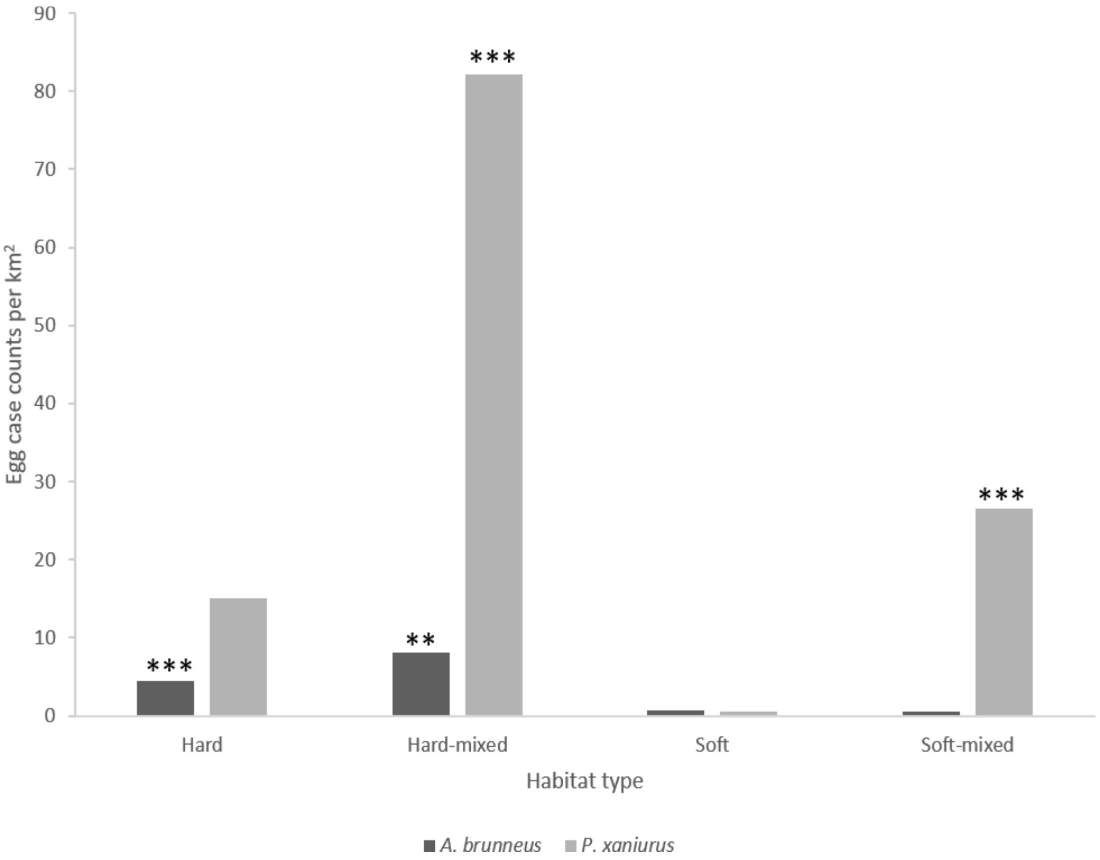

Figure 6: Egg case counts per available habitat type (km^2) for *A. brunneus* and *P. xaniurus*. * = P < 0.01, ** = P < 0.001, *** = P < 0.0001 for the Chi-square test.

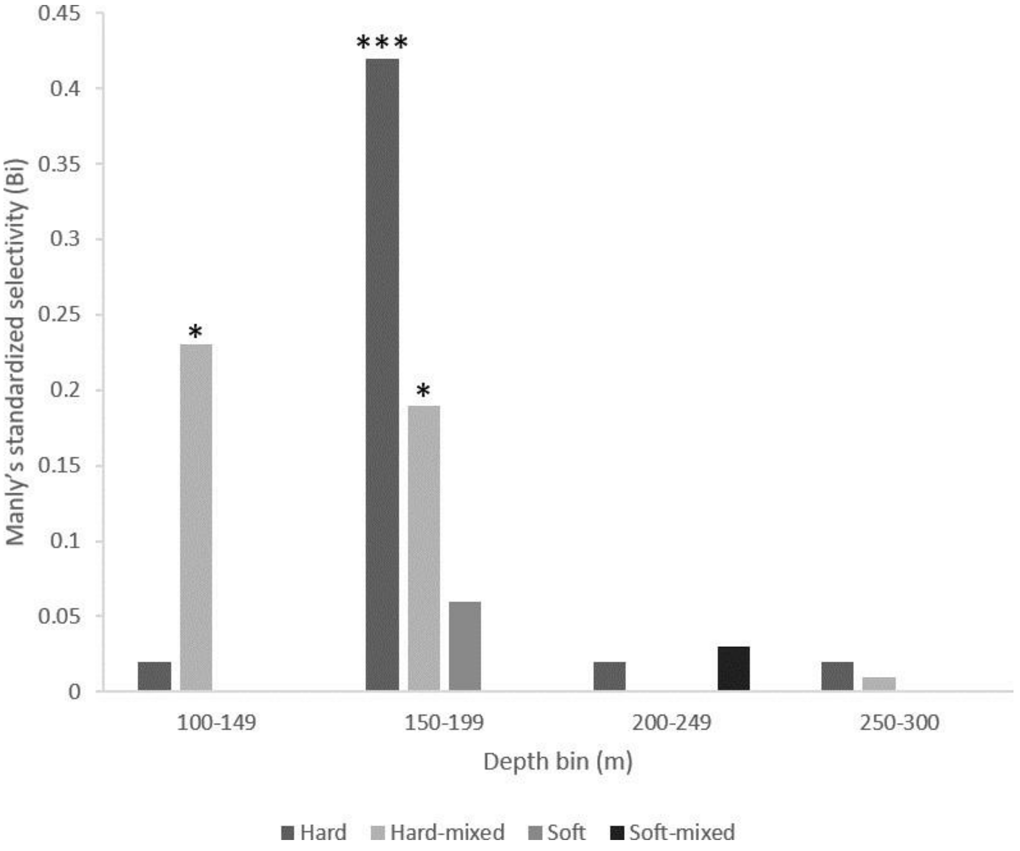

Figure 7: Manly's selection index for *A. brunneus* egg case habitat suitability preferences as a function of depth. * = P < 0.01, ** = P < 0.001, *** = P < 0.0001 for the Chi-square test.

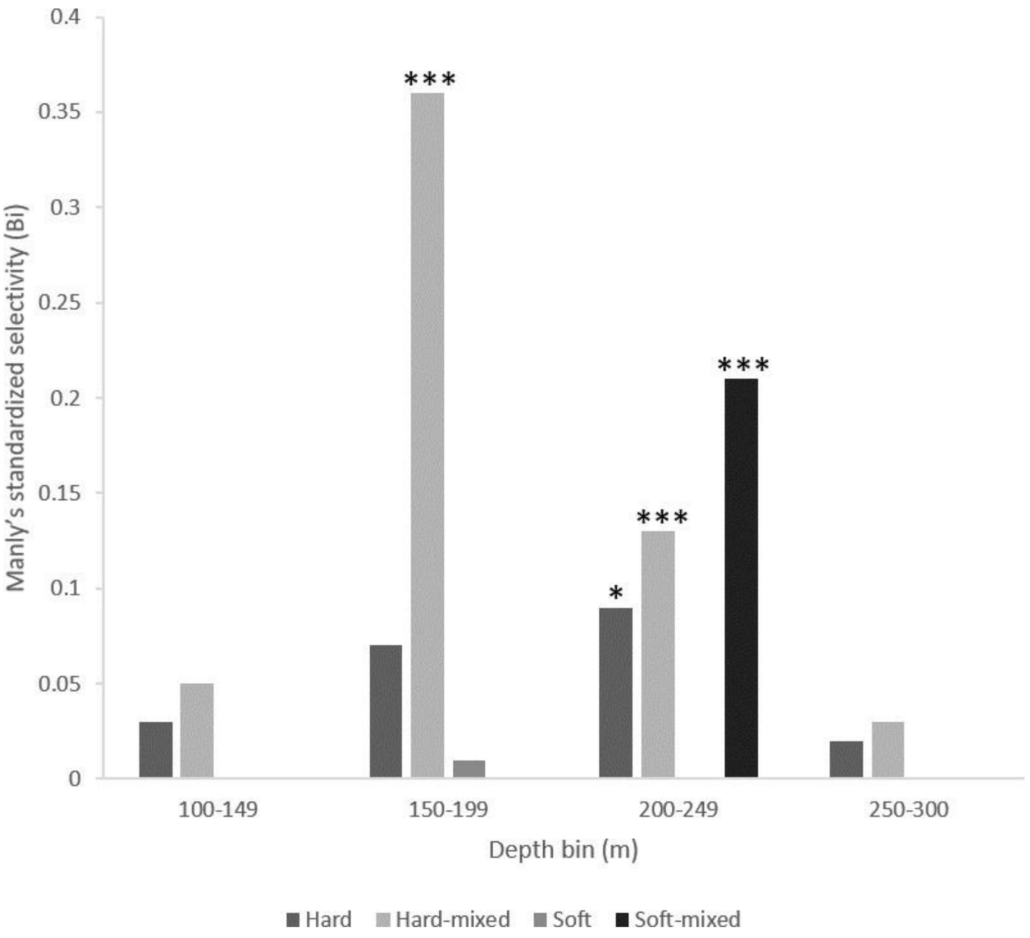

Figure 8: Manly's selection index for *P. xaniurus* egg case habitat suitability preferences as a function of depth. * = P < 0.01, ** = P < 0.001, *** = P < 0.0001 for the Chi-square test.

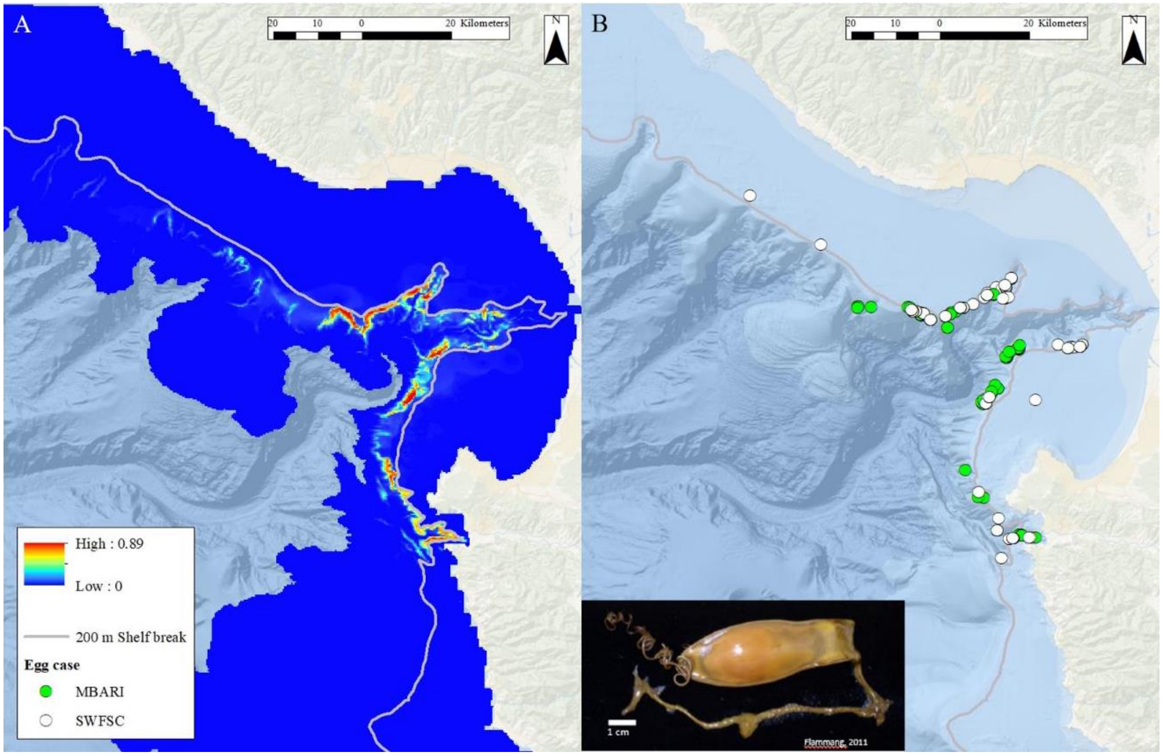

Figure 9. *Apristurus brunneus* egg case habitat suitability map. A) Map of probability of suitable habitat for *A. brunneus* egg cases. B) Locations of *A. brunneus* from both Monterey Bay Aquarium Research Institute (MBARI) and Southwest Fisheries Science Center – Fisheries Ecology Division (SWFSC-FED) data with an inset photo of *A. brunneus* egg case (Flammang 2005). Legend: Blue to red gradient indicates increasing probability of suitable habitat; Green (MBARI) and white (SWFSC) circles indicate observed locations of *A. brunneus* egg cases.

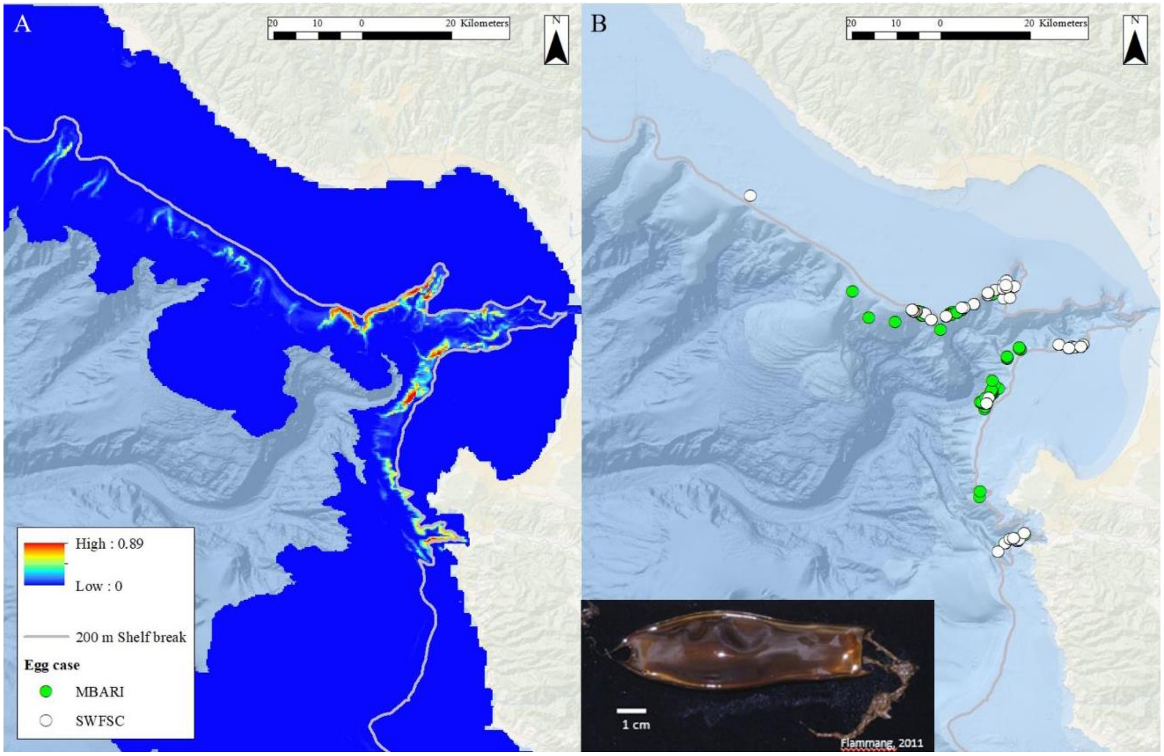

Figure 10. *Parmaturus xaniurus* egg case habitat suitability and presence maps. A) Map of probability of suitable habitat for *P. xaniurus* egg cases. B) Locations of *P. xaniurus* from both Monterey Bay Aquarium Research Institute (MBARI) and Southwest Fisheries Science Center – Fisheries Ecology Division (SWFSC-FED) data with an inset photo of *P. xaniurus* egg case (Flammang 2005). Legend: Blue to red gradient indicates increasing probability of suitable habitat; Green (MBARI) and white (SWFSC) circles circles indicate locations of *P. xaniurus* egg cases.

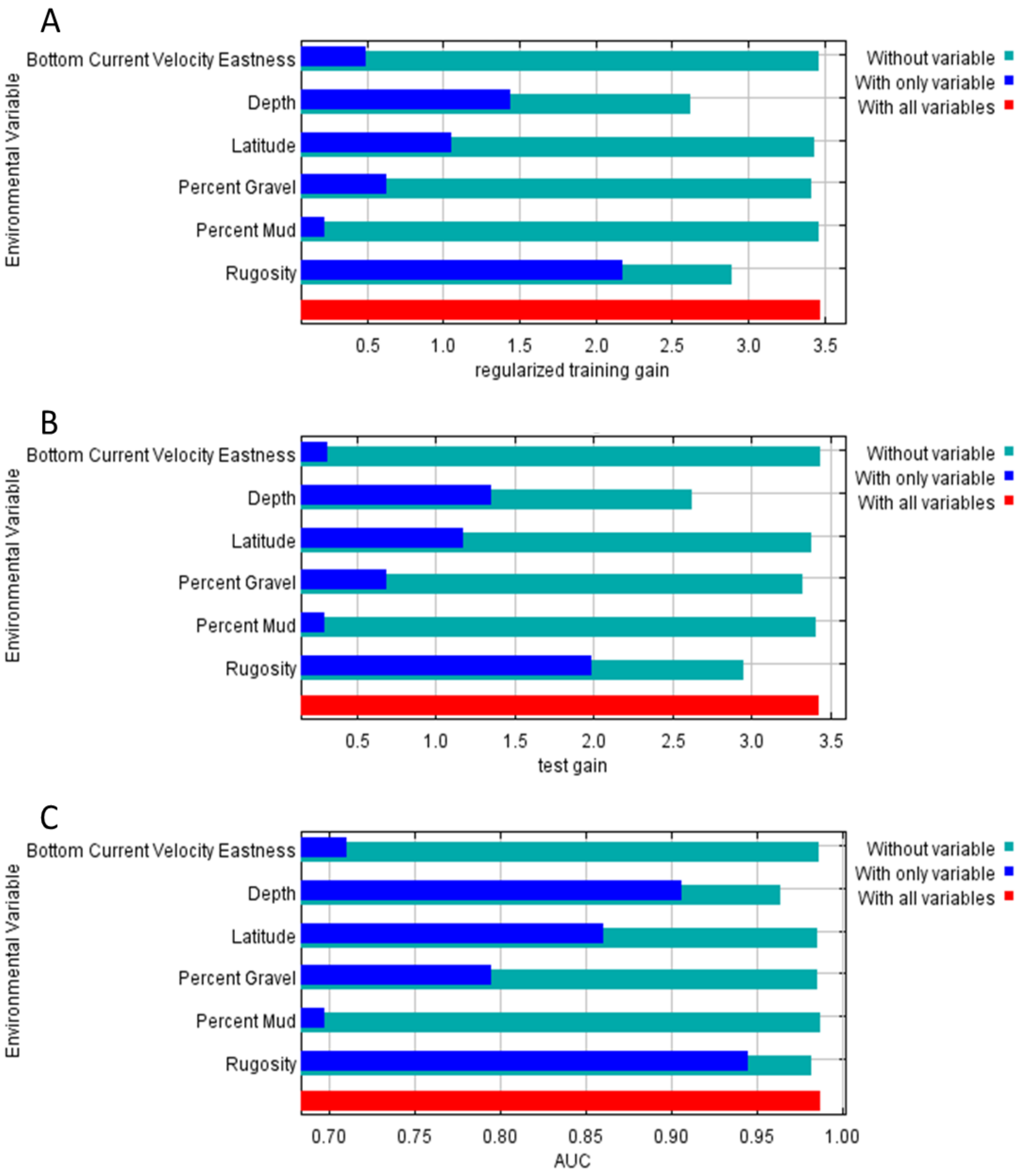

Figure 11. Jackknife test for evaluating the relative importance of environmental variables for *A. brunneus* egg cases. AUC = Area under the curve; A) Regularized training gain variable importance; B) Test gain variable importance; C) AUC variable importance. On each plot, the teal bars indicate how the model performs without that variable, the blue bars indicate how useful the information within each variable is for model creation, and the red bar indicates model gain using all variables (Phillips 2006; Young et al. 2011).

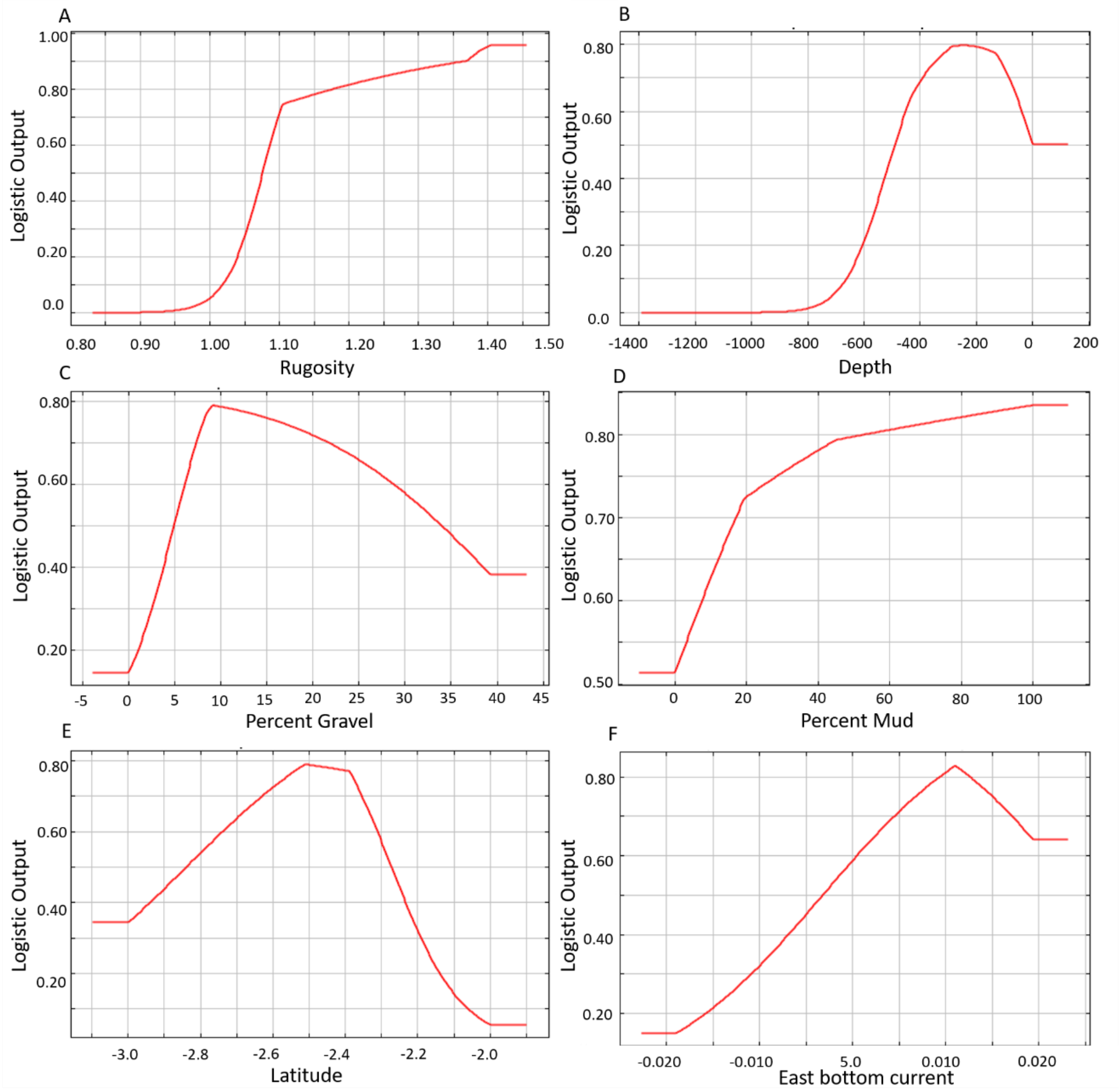

Figure 12. Response curves of environmental variables that were included in the final MaxEnt model of habitat suitability probability for *A. brunneus* egg cases. Higher values indicate higher predicted presence of egg cases as a function of the environmental variables. A) = rugosity, B) = depth, C) = % gravel, D) = % mud, E) = latitude, and F) = Eastern bottom current velocity.

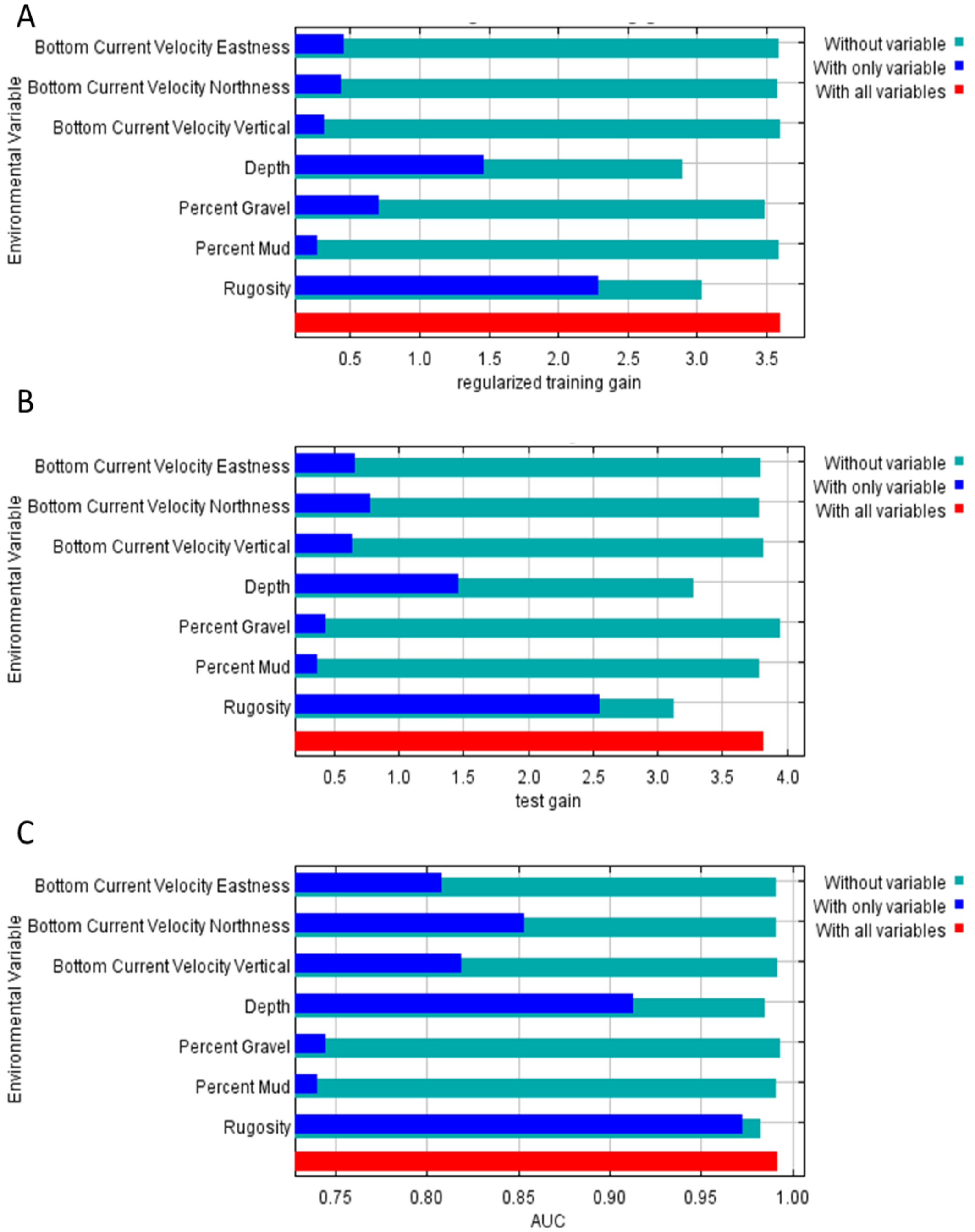

Figure 13. Jackknife test for evaluating the relative importance of environmental variables for *P. xaniurus* egg cases. AUC = Area under the curve; A) Regularized training gain variable importance; B) Test gain variable importance; C) AUC variable importance. On each plot, the teal bars indicate how the model performs without that variable, the blue bars indicate how useful the information within each variable is for model creation, and the red bar indicates model gain using all variables (Phillips 2006; Young et al. 2011).

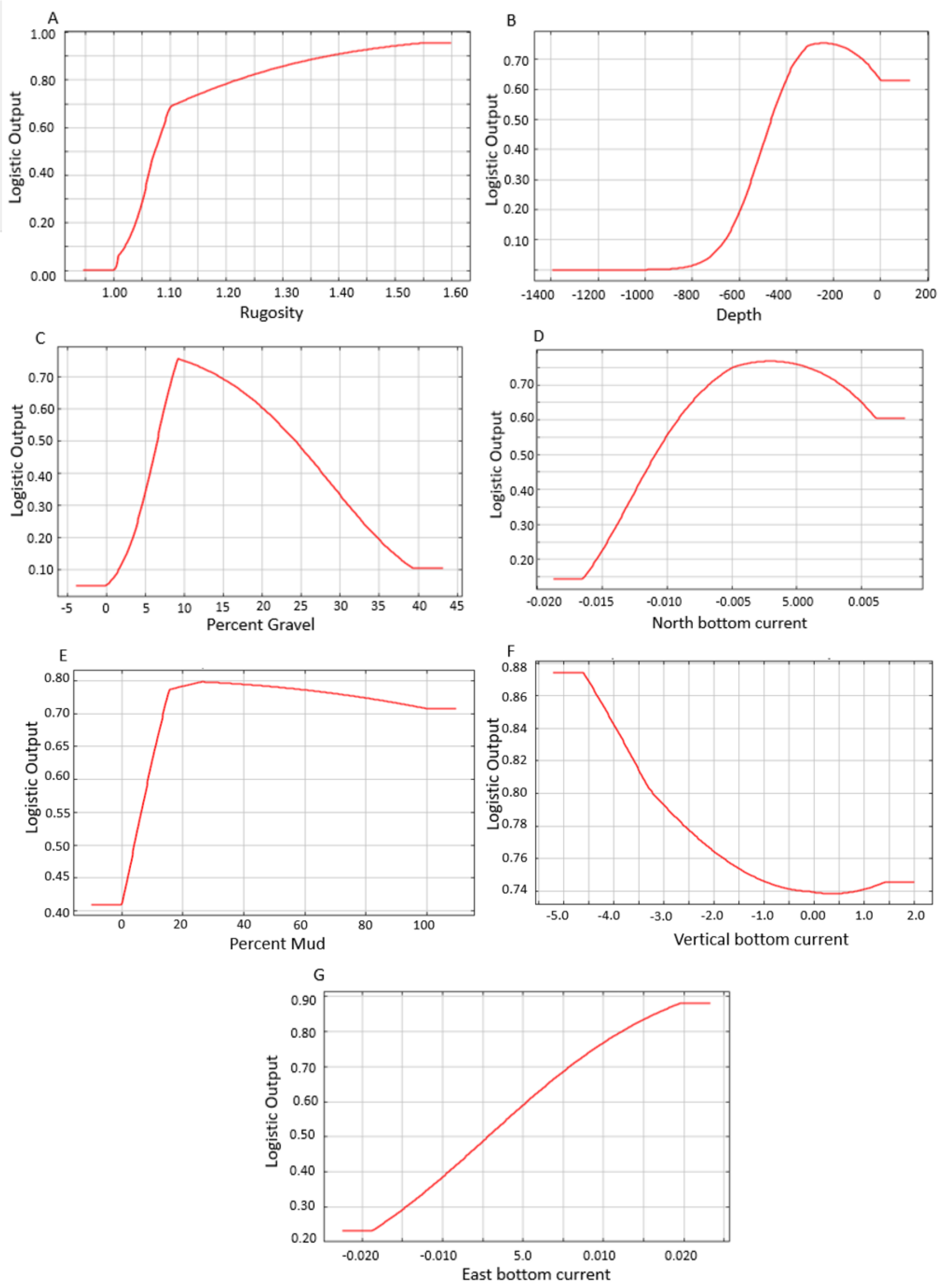

Figure 14. Response curves of environmental variables that were included in the final MaxEnt model of habitat suitability probability for *P. xaniurus* egg cases. Higher values indicate higher predicted presence of egg cases as a function of the environmental variables. Where A) = rugosity, B) = depth, C) = % gravel, D) = Northern bottom current velocity, E) = % mud, and F) = Vertical bottom current velocity and G) = Eastern bottom current velocity.

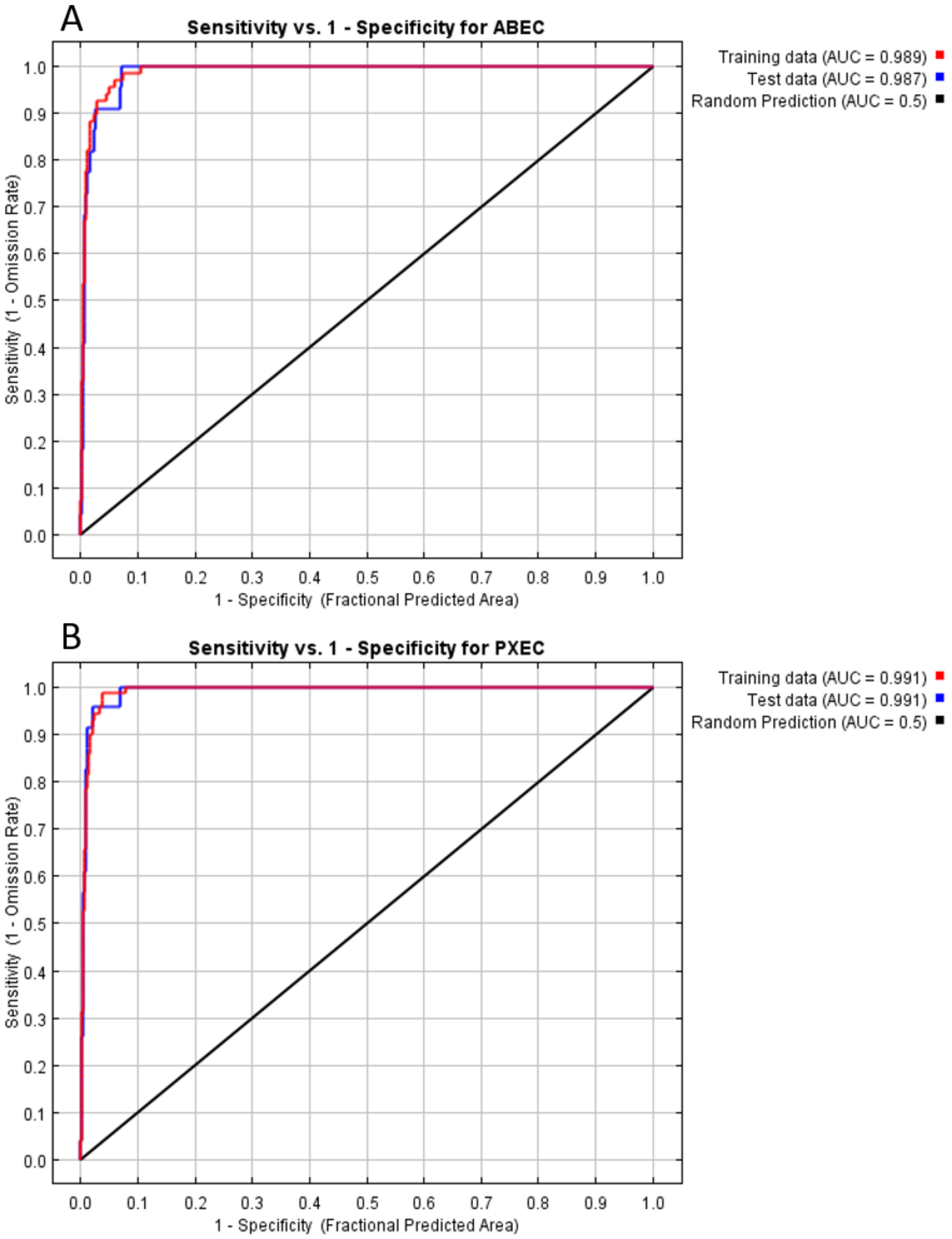

Figure 15: Receiver operating characteristic (ROC) curve for A) *A. brunneus* egg case (ABEC) and B) *P. xaniurus* egg case (PXEC) final MaxEnt models. AUC = Area under the curve. AUC measures the model's performance by plotting test data ROC against a random prediction of AUC = 0.5.