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In situ observations of deep-living skates in the eastern North Pacific

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ABSTRACT

We report on 18 years of *in situ* observations of seven skate species (2192 individual observations) in the eastern North Pacific (Vancouver Island, Canada to the Gulf of California, Mexico) between 200 and 3322 m depth. Biological (species, sex, maturity, behavior) and abiotic (geographic location, depth, habitat type, temperature, oxygen) data were evaluated for each species. This study extends the depth and geographic ranges of *Bathyraja microtrachys* and *B. trachura*. Additional species studied include *Amblyraja hyperborea*, *B. abyssicola*, *B. kincaidii*, *B. spinosissima,* and *Beringraja rhina*. *Bathyraja trachura* was shown to be uniquely tolerant of low oxygen environments and *B. spinosissima* is distinctive in that it was most frequently found actively swimming over lava fields. Our video recording of a potentially undescribed species at 3321 m represents the deepest reported *in situ* visual observation of a skate to date.

1. Introduction

Focused research on deep-sea benthic and demersal communities is becoming more common with new developments and improvements in marine technology. With the advent of remotely operated and autonomous underwater vehicles (ROVs and AUV's), long-deployment time-lapse cameras, baited remote underwater video systems (BRUVs), camera sleds, and other underwater imaging methods, *in situ* visual observations of deep-sea biological communities have become an important adjunct or replacement to traditional methods (e.g., trawling, baited traps, longlines) for assessing the presence, abundance, and diversity of animals living in deep areas of the ocean (Langlois et al., 2018; Ramirez-Llodra et al., 2010). These new methods facilitate more extensive sampling, long-term studies, and greater visual persistence in the deep-sea.

One benefit of increased research attention in the deep-sea is the opportunity for a greater understanding of marine organisms that are poorly known or difficult to collect by traditional means. One such group of organisms is the skates, a diverse order (Rajiformes) of primarily benthic and demersal elasmobranchs (Compagno and Ebert, 2007). Although they are morphologically conservative, skates have an extremely broad, cosmopolitan distribution, occurring from high latitude polar waters to low latitude equatorial seas from the intertidal to deep-sea at depths to 4156 m (Ebert and Winton, 2010; Stehmann, 1990; Weigmann, 2016).

The biology and species composition of deepwater skate assemblages are poorly understood, especially in the deep bathyal-abyssal environment. To date, there are about 125 skate species recognized from deep-sea environments, most from the families Arhynchobatidae and Rajidae (Priede, 2017). Some are known from only a small number of specimens (Kyne and Simpfendorfer, 2007). The difficulty and expense of sampling in the deep sea limits scientific investigation of skates; published data regarding their presence, depth range and geographic distribution is relatively sparse and frequently based on animals obtained as bycatch (Last et al., 2016). Anthropogenic changes are becoming recognized as likely drivers of changes in deep-sea environments (Smith et al., 2013); therefore, baseline data for deep-sea skates are essential to monitor future changes in distribution should warming temperatures, de-oxygenation, and acidification occur with predicted changes in climate (Ramirez-Llodra et al., 2010).

The Monterey Bay Aquarium Research Institute (MBARI) began archiving and annotating footage from its numerous ROV's in 1988 (> 6500 dives to date). These dives are generally focused beyond the continental shelf (> 200 m) depths and observations are archived in an accompanying database (Video Annotation and Reference System, VARS) (Schlining and Stout, 2006), presenting a unique opportunity to document information (e.g., depth and range extensions, habitat associations, behavior) about deep-living skates in the regions of the most dedicated study, the eastern North Pacific (ENP). A subset of skate observations for *Bathyraja kincaidii* and *Beringraja rhina* from this

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database were published previously in a paper on shallower-living ENP species (< 600 m depth, Bizzarro et al., 2014). This paper represents an analysis of seven species at depths > 200 m. We utilized this database to develop and investigate four primary research questions: 1) What are the distribution patterns of deepwater skates in the ENP, 2) How do distribution patterns differ among skate species, 3) What are the species-specific habitat associations, and 4) What behavioral patterns were observed for each species?

2. Materials and methods

2.1. Data collection

In situ observations of skates living deeper than 200 m were made throughout the ENP during research cruises by the MBARI from 2000 to 2017 using ROVs. Skates were encountered opportunistically during dives that were conducted for a variety of research objectives. Total horizontal distance observed varied greatly among MBARI ROV dives. Most benthic dives were conducted over 1500 m or less of seafloor and contained one to three habitat categories used in this study. Dives only occasionally covered > 1500 m.

R/V *Point Lobos,* R/V *Rachel Carson*, and R/V *Western Flyer* were used as platforms for the operation of ROVs *Ventana* (1800 m max working depth), *Tiburon* (4000 m max working depth), and *Doc Ricketts* (4000 m max working depth) from Vancouver Island (British Columbia, Canada, 45° 38′ 24″ N, 127° 39′ 54″ W) to the Gulf of California (Mexico, 23° 14′ 45.6″ N, 111° 28′ 30″ W) in water depths of 200–3992 m (Fig. 1). Cameras used on the ROVs included a Sony HDTV camera (prior to 2007) and Ikegami high-definition cameras (HDL40/45/57) fitted with HA10Xt.2 Fujinon lenses.

Annotations were detailed using MBARI's Video Annotation and Reference System (VARS) (Schlining and Stout, 2006). Because identification of organisms from video can be difficult, we were conservative in the assignment of presumptive species names. When we could establish redundancy, multiple observations of an individual skate were combined into one data point. To ensure consistency in annotations*, in situ* species accounts (S1) and a comprehensive observational key (S2) were developed for the species we observed: *Amblyraja hyperborea* (Collett, 1879), *Bathyraja abyssicola* (Gilbert, 1896), *Bathyraja kincaidii* (Garman, 1908), *Bathyraja microtrachys* (Osburn & Nichols, 1917), *Bathyraja* cf. *microtrachys*, *Bathyraja spinosissima* (Beebe & Tee-Van, 1941), *Bathyraja trachura* (Gilbert, 1892), *and Beringraja rhina* (Jordan & Gilbert, 1880). Descriptions were based on known external morphological characteristics (e.g. shape, thorn patterns and counts, fin positions, coloration) that can commonly be seen in video observations. The taxonomic status of *B. kincaidii* has been problematic with some authors (Ishihara and Ishiyama, 1985; Stehmann, 1986; Weigmann, 2016) treating it as a junior synonym of *Bathyraja interrupta* (Gill and Townsend, 1897), but without explanation. However, most authors (Compagno, 1999; Compagno and Ebert, 2007; Del Moral-Flores et al., 2016; Ebert et al., 2017; Eschmeyer and Herald, 1983) have long recognized these as distinct species. Recently, Knuckey (2017) investigated the issue using morphological, meristic, and statistical data, and concluded that *B. kincaidii* is a valid species. Furthermore, molecular research into the issue confirms the distinction between *B. kincaidii* and *B. interrupta*. (Pietsch and Orr, 2015).

Depth, temperature and oxygen levels were obtained from instruments attached to the ROV.

We described the habitat within ~10 m of each observed skate. Habitat types included: active hydrothermal vent^{1}, boulder field^{4}, carbonate crust^{3}, clay^{3}, cobble^{3}, cold seep^{1}, gravel^{3}, inactive hydrothermal vent^{4}, interface between hard and soft substratum^{3}, pillow or aa lava

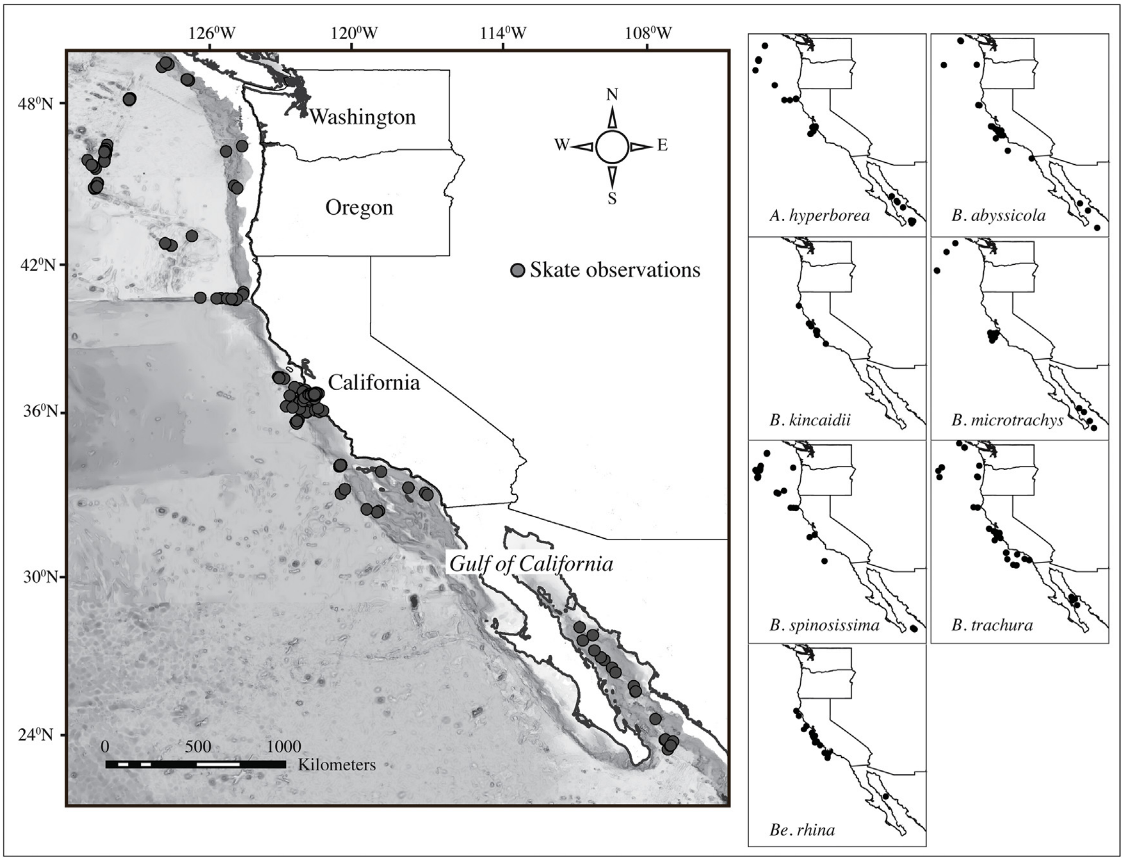

Fig. 1. Eastern North Pacific, showing the locations of skate observations by Monterey Bay Aquarium Research Institute's remotely operated vehicles at depths > 200 m between 2000 and 2017. Skate genera are defined as: *A.* = *Amblyraja*, *B.* = *Bathyraja*, *Be.* = *Beringraja*.

field[2], sediment[5], silt[5], pebble[3], sand[5], scarp[4], rock outcrop[4], talus slope[4], water column[na], and whale fall[1]. Habitats were later condensed into five major categories ([1]chemosynthetic, [2]lava, [3]mixed substrate, [4]hard substrate, and [5]sediment) for statistical analysis.

Because *B. kincaidii and Be. rhina* have depth distributions that are primarily shallower than 600 m (Tolimieri and Levin, 2006), additional already published observations from 200 to 599 m during the same ROV time series (n = 794) were included for context. These data were used to more fully demonstrate depth zones, determine habitat associations, summarize behaviors, and estimate temperature and oxygen preferences (Bizzarro et al., 2014).

When possible, sex was determined for observed skates. The assignment of sex in large males (M) was straightforward and based on the presence of claspers. A close view of the pelvic region of an animal was necessary to distinguish small males from females. When this wasn't possible, these relatively small specimens were identified as juveniles of unknown sex (J, unknown sex). Female (F) skates were distinguished by an obvious absence of claspers. Sex was listed as unknown (U) when skates were viewed from too far a distance, when the pelvic region was not viewed, or the size of the animal made an assignment ambiguous.

The behavior of each individual skate was recorded among the following categories: resting when encountered, swimming when encountered, hovering, presumed feeding activity, or sediment burial. Regional co-occurrence was noted when more than one species of skate, or more than one life stage of a specific species, was observed on the same ROV dive (most frequently within a distance < 1500 m).

2.2. Data analysis

Relationships between all abiotic variables were first tested against one another to determine their degree of correlation using Pearson Product Moment Correlation (Systat v. 13). Highly correlated variables ($r > 0.60$, $p < 0.05$) were removed prior to analysis. *G*–test for Goodness-of-fit tests then were used to test the relationship between observed vs. expected frequencies for environmental variables among seven species (S3), with the range of values and division of categories established from the combined data for all species.

Parametric ordination techniques were used to associate species and environmental variables in PRIMER 7 (Clarke and Gorley, 2015). A metric multidimensional scaling (mMDS) ordination was created using a Bray Curtis similarity index and averaged values for all environmental values, as depicted with an overlain segmented bubble plot, to investigate differences in interspecific habitat use. Non-transformed percent occurrence data (for habitat categories), and ranked values from 1 to 10 (for depth and oxygen categories) were used to conduct the mMDS. Although normalized Euclidean distance is typically used with continuous physical data of different scales, re-scaling enables depth and oxygen data to be combined with the habitat data using Bray-Curtis similarity (Purcell et al., 2014).

3. Results

We observed 2192 skates > 200 m depth from 1781 ROV dives (Table 1). Because they were distant, only partially visible (sometimes due to burial), or represented uncommon morphotypes, 83 skates could not be identified to species. For dives where skates were present, only a single species was observed 78% percent of the time. The greatest species richness on a single dive (four species) was near a whalefall on a sediment seafloor at ~2900 m depth in the axis of Monterey Canyon. Similar species richness was also observed at 2050 m depth in the Canyon on sedimented slopes with rock outcrops. A relatively large number of *B. spinosissima* were observed at Endeavor Ridge (northern Juan de Fuca Ridge), amongst highly sedimented elongate pillow lavas and near inactive hydrothermal chimneys from 2050 to 2150 m depth (12 animals in one dive). We observed the co-occurrence of males and females, and small skates presumed to be juveniles amongst all seven species (Table 1).

The number of measured environmental variables used in this study was reduced from three (depth, temperature, oxygen) to two following the results of correlation tests. Depth and temperature were highly correlated ($r = 0.923$, $p = < 0.001$) therefore, these two variables were never used in the same analysis. Oxygen was not highly correlated with either depth ($r = 0.527$) nor temperature ($r = 0.230$).

3.1. Interspecific comparisons

Species were largely segregated by depth (Fig. 2) with *B. kincaidii* and *Be. rhina* occurring on the upper continental slope, whereas all other species occupied progressively deeper ranges in bathyal and deep bathyal regions. *Bathyraja trachura*, *B. abyssicola* and *A. hyperborea* occupied the widest depth ranges (each > 2200 m). The deep-bathyal/abyssal sightings of *B.* cf. *microtrachys* represented a different morphotype or a potentially new species. The null hypothesis for the G-test for Goodness of Fit for depth (that the expected and the observed distributions would be the same across all levels) was rejected and distributions were non-random for six of the seven species. *Bathyraja abyssicola* did not exhibit a significant preference across its observed depth range (p = 0.141).

Temperatures associated with skates varied by depth and by region. The lowest temperature (1.58 °C) was recorded at 3200 m just SW of Monterey Bay, with the highest measured in a relatively shallow area in the Gulf of California (13.2 °C, 275 m). *Bathyraja kincaidii*, *B. trachura* and *Be. rhina* exhibit distributions in the mid-range of temperatures whereas *A. hyperborea*, *B. abyssicola*, *B. microtrachys*, *B. spinosissima* show a strong association with relatively cold temperatures (Fig. 3).

Oxygen levels ranged from a low of 0.13 ml l^{-1} for *B. trachura* to a high of 3.45 ml l^{-1} for *B. microtrachys* (Fig. 4). The null hypothesis for the G-test for Goodness of Fit for oxygen (that the observed data were sampled from a population with the expected frequencies across all levels) was rejected and distributions were non-random for six of the seven species. *Bathyraja trachura* was observed in very low-oxygen habitats nearly 80% of the time. *Bathyraja kincaidii* and *Be. rhina* were predominantly found in levels below 1.2 ml l^{-1}, and *B. hyperborea*, *B. microtrachys*, and *B. spinosissima* primarily utilized areas with oxygen levels above 1.8 ml l^{-1}. *Bathyraja abyssicola* utilized areas with a wide range of oxygen levels (Fig. 4).

Most skate species were found mainly on sediment, but interspecific variability in habitat associations was evident (Fig. 5). Quantitative information on the relative amount of each habitat was unavailable for these data, therefore G-tests for Goodness of Fit were not conducted. Sediment, hard substrate and mixed substrate were the most common habitats observed, with chemosynthetic and lava habitats showing restricted representation in this data set. All species but *B. spinosissima* were mainly found on sediment, with *Be. rhina*, *B. kincaidii*, and *B. microtrachys* using additional habitat types and *A. hyperborea*, *B. abyssicola*, and *B. trachura* using all habitat types (Fig. 5). Habitat diversity was especially pronounced for *B. trachura* (Fig. 5). In marked contrast to the other study species, *B. spinosissima* was mostly observed in association with lava fields.w

The mMDS bi-plot shows that *B. spinosissima* strongly separates from other species in that it was uniquely found over lava fields at low temperatures and in a relatively compressed deep depth range (1539–2917 m, Fig. 6). This is especially conspicuous given that the relative amount of lava habitat was limited in this study. Amongst the overall cluster of the remaining species, *B. microtrachys* separates, as it was observed over sediment-laden deep-bathyal areas (Fig. 6). *Bathyraja trachura* is unique in that it can inhabit mixed-substrate chemosynthetic environments (which was also very limited in terms of area as it was largely restricted to chemosynthetic biological communities (CBC's), and low oxygen areas (Fig. 6). *Bathyraja abyssicola* and *A. hyperborea* have somewhat similar habitat associations; with the later

Table 1
Number of in-situ observations (n = 2192) made in years 2000–2017 between 200 and 3322 m water depth, and the percentage of observed skates by sex or life stage (male, female, unknown, juvenile). Co-occurrence refers to animals observed within about 1.5 km of each other on the same date. BS = *Bathyraja spinosissima*, BA = *B. abyssicola*, BM = *B. microtrachys*, BT = *B. trachura*, AH = *Amblyraja hyperborea*, Be = *Beringraja rhina*, BK = *B. kincaidii.*

Taxa	Number of observations	% male	% female	% unk	% juv	Sexes co-occur	Species co-occur	Max distance from shore (km)	Geographic min/max latitude longitude
Bathyraja kincaidii	332	27.1	35.5	23.5	13.9	Y	BeR, BA	35	34° 17′ 13.2″ N/39° 34′ 30″ N 119° 53′ 56.4″ W/123° 57′ 18″ W
Beringraja rhina	1103	13.4	25.1	33.7	27.8	Y	BK, BA	200	28° 23′ 56.4″ N/40° 47′ 13.2″ N 112° 22′ 22.8″ W/124° 35′ 42″ W
Bathyraja trachura	291	35.9	32.4	9.7	22.1	Y	BA, AH, BS	540	26° 45′ 14.4″ N/49° 16′ 44.4″ N 111° 10′ 12″ W/126° 50′ 20.4″ W
Bathyraja abyssicola	109	15.3	50.5	17.1	17.1	Y	BT, AH, BM, BeR, BK, BS	470	23° 14′ 45.6″ N/45° 56′ 38.4″ N 108° 37′ 4.8″ W/127° 43′ 12″ W
Amblyraja hyperborea	77	19.5	40.3	10.4	29.9	Y	BS, BA, BM, BT	516	23° 33′ 3.6″ N/44° 33′ 25.2″ N 108° 37′ 4.8″ W/130° 25′ 26.4″ W
Bathyraja spinosissima	95	47.9	43.8	3.1	5.2	Y	AH, BA, BM, BT	520	23° 26′ 49.2″ N/45° 38′ 24″ N 108° 29′ 24″ W/129° 5′ 34.8″ W
Bathyraja microtrachys	102	10.1	50.5	12.1	27.3	Y	AH, BA, BS	500	23° 24′ 28.8″ N/45° 23′ 34.8″ N 108° 31′ 1.2″ W/127° 51′ 46.8″ W
Unidentified skates	83	9.6	6.0	60.2	24.1	na	na	na	within the boundaries listed above for individual species
Total	**2192**								

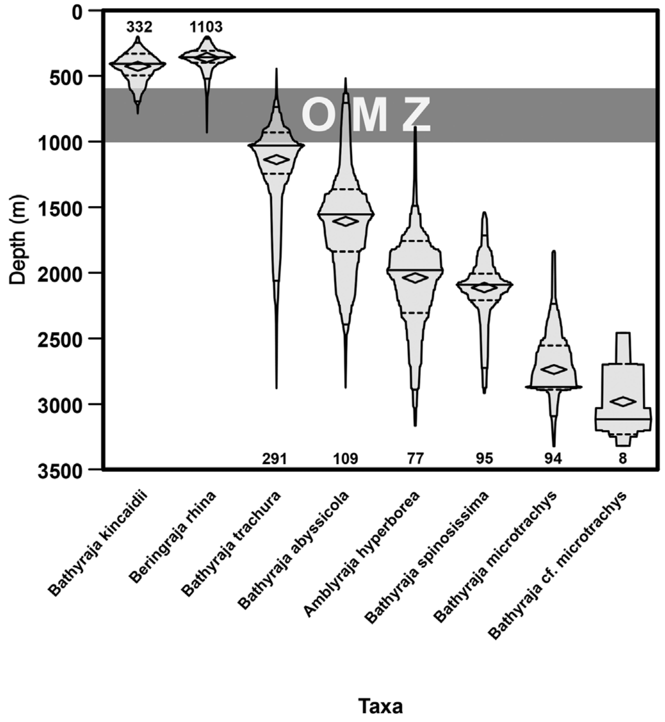

Fig. 2. Kite diagram showing depth distribution of skates observed by MBARI ROVs at depths of > 200 m between 2000 and 2017. Note that observations are not normalized by ROV effort. Mean (◇), median (−), and 1st and 3rd quartiles (− − −) are shown for each species. Change in percentage of observations by depth is indicated by the variable width of each plot. The number of observations associated with each species are listed. The oxygen minimum zone (600–1000 m) is shown as a dark gray bar. *B. kincaidii and Be. rhina* have depth distributions that are primarily shallower than 600 m; therefore, additional published data from observations at shallower depths were used in this analysis. All species exhibited non-random distributions ($p = < 0.001$, Goodness of fit test), expect *B. abyssicola* which utilized a wide range of depths ($p = 0.141$).

more tolerant of deeper depth (and thus higher temperatures; Fig. 6). *Bathyraja kincaidii* and *Be. rhina* are linked in their habitation of relatively shallow depths, high oxygen levels, and highly sedimented areas (Fig. 6).

3.2. Species accounts

The majority of skates did not actively move away from the ROV. Most skates were resting when encountered (78.6%, n = 1767, Table 2) and could be approached closely without any apparent disturbance. A small number (1.8%, n = 29) were buried or partially buried. None of the skates studied here formed large aggregations and no mating or egg deposition behaviors were observed. Over approximately 6500 ROV dives, most of which included video during ascents and descents, skates were preponderantly benthic/demersal with few skates observed in the water column (n = 3). Species-specific behavioral descriptions are not intended to be unique but rather reflect the best information available for each species.

3.2.1. Amblyraja hyperborea (Collett, 1879) arctic skate (S.1, S1.1)

The 77 animals (15M:31F:8U:23J) observed in this study ranged from Washington to central California and the Gulf of California at depths of 890–3167 m (Fig. 1, Table 2). Individuals of this species were observed as far as 516 km offshore (Oregon), and were frequently encountered in the axis of Monterey Canyon and at Davidson Seamount, southwest of Monterey Bay. *Amblyraja hyperborea* was only observed in the southern Gulf of California, however, we made relatively few ROV dives in the northern part of the Gulf. This species was primarily observed on sediment (64%), but was found on high rugosity lava fields and mixed substrates as well. It was seen over volcaniclastic sediments, on ponded sediment near lava, over lava tumulus slopes and boulders, and off canyon walls (rock outcrops) but rarely observed near CBC's and whale falls. *Amblyraja hyperborea* was found largely in cold water regions (Fig. 3) and across a broad range of oxygen levels (Fig. 4).

Amblyraja hyberborea was observed swimming approximately a third of the time (Table 2). The swimming activity of subadults and adults was typically slow and deliberate; they skim the seafloor, with locomotion resulting from a combination of undulatory swimming and punting. This skate frequently lifts its tail when it begins to swim from a resting position. It sometimes punts when it initiates swimming from a resting position, and uses pelvic fins (walking legs) to assist in settling back to the seafloor. One animal was partially buried. Early juveniles swim quickly relative to larger animals, with a distinctive flapping motion of the pectoral fins.

3.2.2. Bathyraja abyssicola (Gilbert, 1896) deepsea skate (S1, S.1.2)

Individuals of this species were encountered 109 times (16M:55F:19U:19J), almost exclusively on the slopes of Monterey

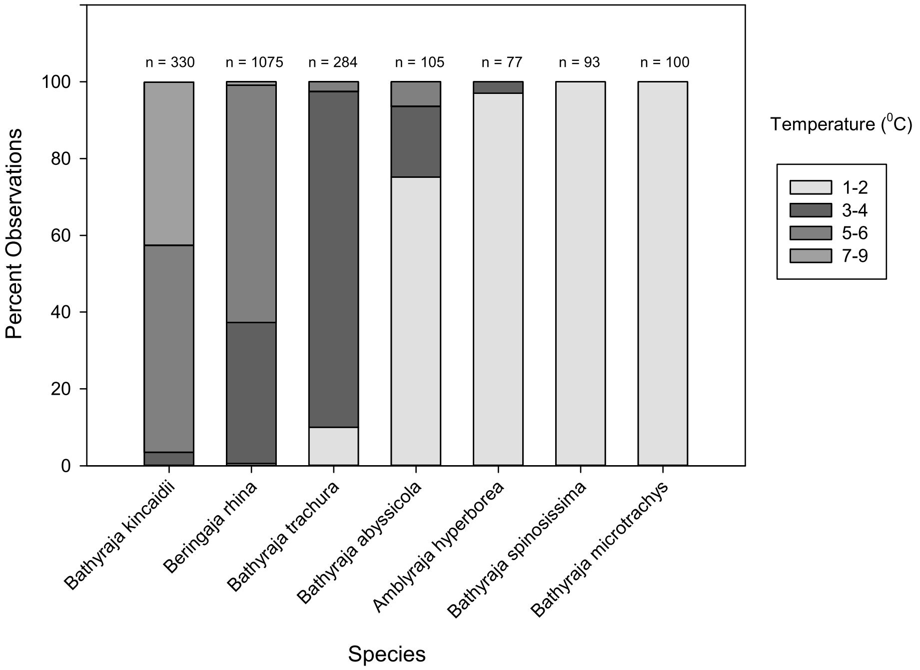

Fig. 3. Temperature associations for the skate species observed. n = the number of observations used in the analysis, * = statistically significant by G-tests for Goodness of Fit/Exact tests indicating that observed distributions that differed from expected.

Canyon (Fig. 1, Table 2). They also occurred at Pioneer Seamount (NW of Monterey Bay), the Mendocino Ridge/Gorda Escarpment, and as far north as western margin off of Vancouver Island. We observed two adults in the mid Gulf of California in 2012. Although most individuals were found relatively close to shore (18–114 km), we found three 470 km off the Oregon coast at Axial Seamount. Depth ranged from 600 to 2876 m. *Bathyraja abyssicola* was closely associated with flat, sedimented areas (71%), but also occurred in higher rugosity areas near canyon walls with rock out crops, mixed substrates, cobble, volcaniclastic sediments, authigenic carbonate crust, and over lava. It was rarely seen at CBC's and whalefalls. *Bathyraja abyssicola* were observed in association with relatively cold water (Fig. 3) and across a wide variety of oxygen levels (Fig. 4).

Approximately one-third of all identified *B. abyssicola* were observed to be swimming (Table 2). Swimming generally occurred above the height at which the pelvic fins could be used to assist by punting, but within ~0.5 m of the seafloor. *Bathyraja abyssicola* often does, however, use its walking legs to move along the seafloor, to assist in generating lift off the seafloor, and to maneuver up the walls of submarine canyons. It is frequently found on medium to steep mud and

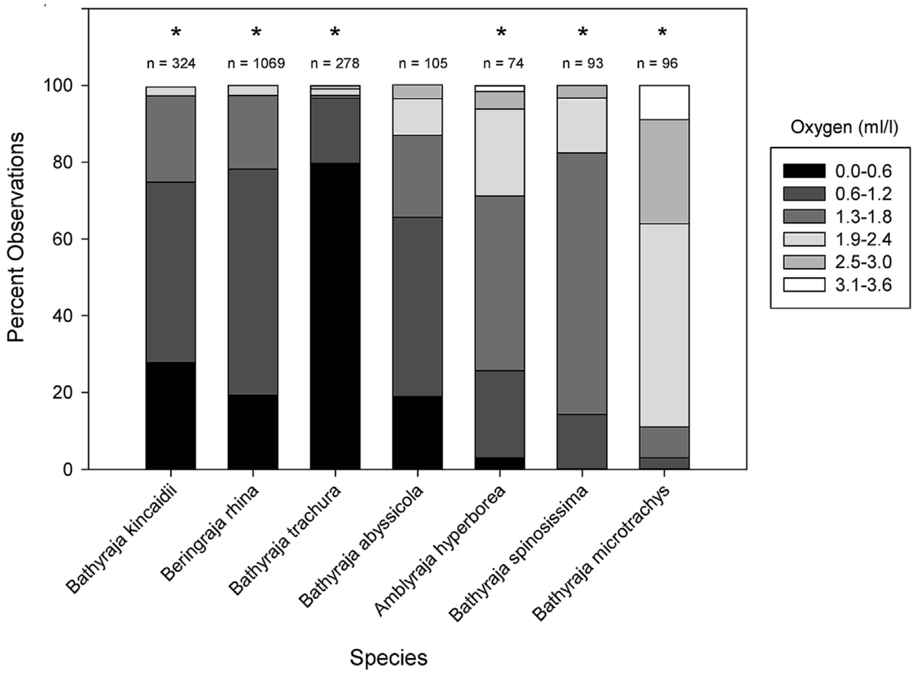

Fig. 4. Oxygen associations for each skate species observed. n = the number of observations used in the analysis, * = statistically significant by G-tests for Goodness of Fit/Exact tests indicating that observed distributions that differed from expected.

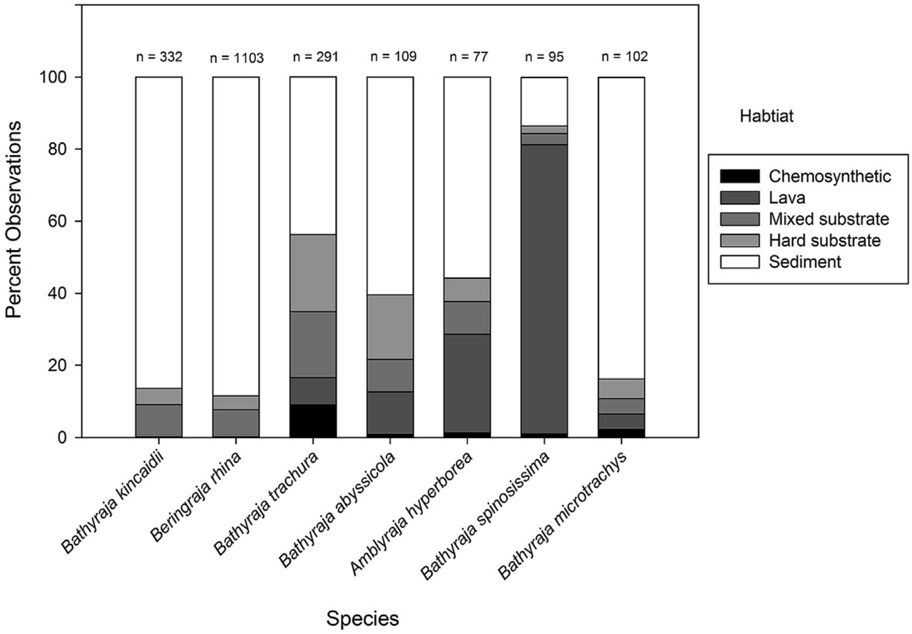

Fig. 5. Observed habitat associations for each species. G-tests for Goodness of Fit/Exact were not conducted for these data as no information on the relative amount of each habitat in the study area was available.

rock slopes, and was always observed facing up slope. Six animals were observed buried or partially buried. It is able to swim upward quickly (e.g. following rock outcrops).

3.2.3. *Bathyraja kincaidii* (Garman, 1908) sandpaper skate (S1, S.1.3)

Our dataset includes 332 observations of *B. kincaidii* (90M:118F:78U:46J). This species was observed from the Eel Canyon area off northern California to the Santa Barbara Channel to the south (Fig. 1, Table 2) and from 200 to 784 m depth. A relatively nearshore species, we found these skates 2–35 km from the closest coastline. *Bathyraja kincaidii* was strongly associated with flat, sediment environments (92%), but occasionally found on mixed substrates, authigenic carbonate crust, and hard substrates. It was observed exclusively in water temperatures above 4.6 °C and at relatively low oxygen concentrations (Fig. 4).

Bathyraja kincaidii was strongly associated with the benthos and rarely observed swimming (Table 2). When it did swim, it skimmed the bottom with a distinctive, highly undulatory butterfly-like motion. It also remained in contact with the benthos when punting with the pelvic limbs, a common form of locomotion for this species, essentially lurching across the seafloor. When startled by the ROV, this skate typically punted away rapidly without incorporating thrust from the fins or tail. It was never observed swimming in the water column, and very rarely ventured more than a few centimeters off the benthos.

3.2.4. *Bathyraja microtrachys* (Osburn & Nichols, 1917) finespined skate (S1, S.1.4)

This very deep-living species was observed 102 times (11M:52F:12U:27J) between 1126 and 3322 m, constituting an extension of both the minimum and maximum reported depths. In this study *B. microtrachys* occurred from northern Washington to the Gulf of California (geographic range extension), and from 13 to 500 km offshore (Fig. 1, Table 2). It inhabited mostly flat, sedimented areas (88%) but was occasionally found over higher-rugosity lava and rock outcrops and occasionally seen near whalefalls. *Bathyraja microtrachys* was mostly observed at relatively low temperature and high oxygen levels (Figs. 3 and 4).

The morphology of eight individuals does not strictly correspond to

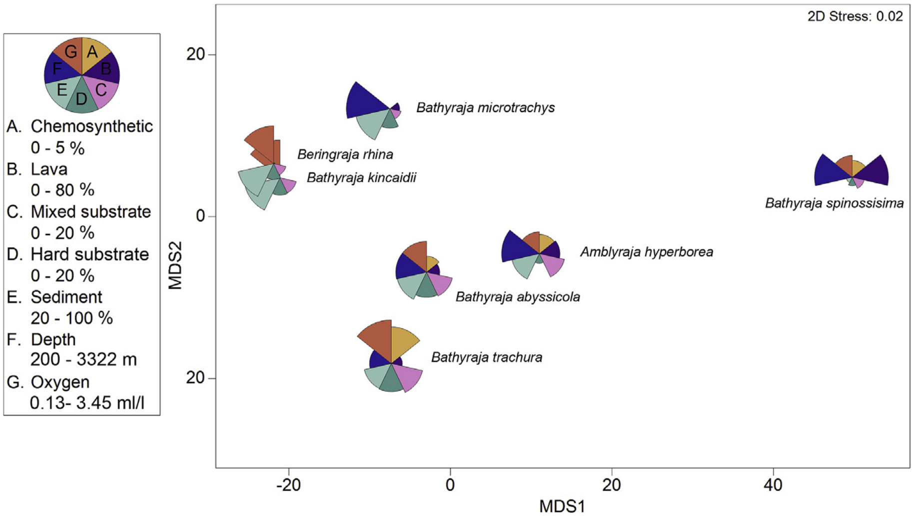

Fig. 6. mMDS plot depicting average habitat association, depth, and oxygen. The overlain segmented bubbles show the relative contribution of each parameter in the Bray-Curtis-based similarity ordination. Habitat associations (A–E) were calculated on the percent occurrence for each species. Physical variables (F–G) were ranked. Labels indicate the overall range in original units. The stress value of 0.02 indicates that this is a good representation of the data.

Table 2
Select behaviors observed for the seven study species. Agile = observed making fast turns or swimming upward quickly. Height above seafloor indicates the observed swimming position (skim = 0–30 cm, med = 30–100 cm, high = 100 cm–10 m).

Taxa	n	Swimming Freq. (%)	Swimming Behavior	Swimming Height	Walking (w) Punting (p)	Burial
Bathyraja kincaidii	332	13.9	slow pace, short bursts	low	w	yes
Beringraja rhina	1103	11.3	medium pace, agile	low-med	w, p	yes
Bathyraja trachura	291	25.1	medium pace	med		yes
Bathyraja abyssicola	109	33.0	medium pace, agile	med	w, p	yes
Amblyraja hyperborea	77	36.4	slow pace, deliberate	low	w, p	yes
Bathyraja spinosissima	95	74.7	slow pace, continuous pace; hovers	high		yes
Bathyraja microtrachys	102	46.8	medium pace, continuous pace	low-med		no
Total	**2109**					

the known characteristics of *B. microtrachys* and we herein refer to them *Bathyraja* cf. *microtrachys*. These individuals, all female and present on low-relief mud at least 36 km from shore in the Monterey Canyon and fan valley, represent either an alternate morph of this species or an undescribed species. *Bathyraja* cf. *microtrachys* is mottled gray with a dark ventral surface, has a tail that is shorter than typically reported and thicker at the base, and the body is generally more robust than typical *B. microtrachys*. Individuals corresponding to *B.* cf. *microtrachys* were observed from 2460 to 3321 m depth; some of them appear to have circular-shaped markings on the dorsal surface (S1.5).

Bathyraja microtrachys was usually observed swimming, typically within a few centimeters to about a meter above the seafloor, but occasionally higher in the water column when transiting across steep terrain (e.g., ridges, scarps, canyons) (Table 2). Juveniles swim relatively quickly and with a distinctive flapping motion. Subadults and adults appear to utilize a combination of swimming behaviors. When cruising above the seafloor, *B. microtrachys* modifies the frequency of waves along its highly flexible pectoral fins to adjust speed; however, this mode of locomotion is relatively slow. To increase its speed, it incorporates an additional rapid flapping motion of the wings.

3.2.5. Bathyraja spinosissima (Beebe & Tee-Van, 1941) pacific white skate (S1, S.1.6)

Ninety-five *B. spinosissima* (46M:41F:3U:5J) individuals were observed at depths of 1539–2917 m, but were predominately found around 2000 m (Fig. 2). We recorded them between northern Washington and the southern Gulf of California (Fig. 1, Table 2). Although most specimens were observed far offshore in the northern part of our range (up to 520 km), some were < 50 km offshore in the deep axis of Monterey Canyon, and off the Eel Canyon in northern California. Seventy-three percent of observations were over high-rugosity lava (lobate and pillow lava, talus slopes, jumbled sheet flows), with the remaining over muddy and volcaniclastic sediments (Fig. 3). *Bathyraja spinosissima* was relatively abundant along a 2700 m-long transect over lava flows near Endeavor ridge (off Washington). This species was occasionally found near inactive hydrothermal chimneys; one animal was observed swimming next to an active hydrothermal vent. It inhabits relatively cold water and mid-range oxygen levels (Figs. 3 and 4).

Bathyraja spinosissima appears to be a slow but largely active swimmer that was occasionally found resting on the seafloor (23%). It also was occasionally observed to be hovering or gliding in the water column (Table 2). This species tends to swim higher off the seafloor than the other skates studied here, and was frequently observed swimming 10s of meters above calderas and lava channels. It can extend its walking legs to land, although this behavior was only observed once. It lifts its tail when it begins to swim from a resting position on the benthos, and sometimes swims with back arched and its tail lowered.

3.2.6. Bathyraja trachura (Gilbert, 1892) roughtail skate (S1, S.1.7)

Bathyraja trachura was observed in all regions of the study area (Fig. 1, Table 2) and in relatively high abundance (291 sightings, 104M:94F:64J:29U). Observations in the mid-Gulf of California extend the known geographic range of this species. The observed depths (600–2880 m) and distances from shore (8–540 m) ranged widely, with the deepest recorded specimen constituting a depth extension. *Bathyraja trachura* was mainly found in sedimented areas (62%), but also was observed in a variety of habitats: rock out crops, mixed substrates, authigenic carbonate crust, lava and near CBC's. One individual was sighted at an active hydrothermal vent. We found most of these skates in 1–3 °C water temperatures (89%) and at very low oxygen levels (80%).

The great majority of *B. trachura* individuals were observed to be lying motionless on the seafloor (Table 2). One individual in this condition seemed undisturbed by a large *Paralomis* crab that walked over its pectoral fin. *Bathyraja trachura* occupies uneven rocky substrates in addition to soft sediment regions, and was commonly found resting on sediment at the base rocky slopes, bedded walls, and rock outcrops. When off the bottom, *B. trachura* was sometimes observed to be drifting or gliding in currents.

3.2.7. Beringraja rhina (Jordan & Gilbert, 1880) longnose skate (S1, S.1.8)

Beringraja rhina was observed 1103 times (148M:277F:372U:306J) from the Eel Canyon area off northern California to the mid-Gulf of California (Fig. 1) at depths of 200–929 m. Another relatively nearshore species, we found that individuals ranged 2–200 km from the closest coastline, predominately over sediment, but also in association with rock out crops, authigenic carbonate crust, and mixed substrate areas. It inhabited areas with 3–6 °C temperatures and was mostly associated with oxygen levels between 1.2 and 1.8 $\mathrm{ml\,l^{-1}}$, but was capable of utilizing a broad concentration range (Fig. 4).

Although *Be. rhina* was mainly observed lying on the seafloor (Table 2), it was the strongest and most agile swimmer of the studied skates. Most swimming individuals were observed just above the seafloor, and were capable of relatively rapid motion and abrupt turns. This species is also quite adept at punting, moving rapidly along the seafloor solely with this form of locomotion, supplementing forward movement while swimming, and using the walking legs independently to turn and pivot. *Beringraja rhina* sometimes used the pectoral fins to initiate a swimming sequence from a resting position on the seafloor. Several feeding strikes were observed at the benthos but resulting mud clouds prevented us from determining their success.

4. Discussion

We present the first detailed distribution, habitat, and behavioral information for a suite of poorly known, deep-water skates in the eastern North Pacific, facilitated through the use of an extensive, long-term database of annotated *in situ* video. Imaging technology can be used as a tool to supplement traditional sampling methods and may provide important data in habitats that are inaccessible to study or for animals that are difficult to capture. *In situ* investigations also provide more specific and reliable information on distribution, behavior, and habitat information than traditional sampling methods (e.g., trawl, longline). In this study, species-specific observations and measurements of depth, temperature, and oxygen levels provided evidence of the habitat associations and behaviors of seven deepwater skate species. We report broader depth (two species) and geographic ranges (two species), and more specific habitats (lava fields, chemosynthetic biological communities, whalefalls) and temperatures for these skates than were previously reported. New information on species-specific oxygen level associations may be a potentially important abiotic factor to consider, especially since marked declines have been reported for deep-water fishes in oxygen minimum zones of the California Current (Koslow et al., 2011). We document *in situ* observations of skates > 3000 m, an area of the ocean where chondrichthyans do not commonly occur (Priede et al., 2006; Treberg and Speers-Roesch, 2016). We also made observations of some very deep-living skates with morphologies that are not consistent with known species occurring in the region of study and may represent an undescribed species.

4.1. Geographic and depth distributions

Because of the relative stability and environmental homogeneity (high pressure, low temperature, absence of light, food limitation) of the deep-sea, species occupying this region tend to have broader geographic ranges than those with relatively shallow distributions (Cotton and Grubbs, 2015). This trend was generally supported by our results with a few notable exceptions. *Bathyraja abyssicola* and *B. spinosissima* have eastern North Pacific distributions that extend from boreal regions to the equator (Cerutti-Pereyra et al., 2018; Ebert, 2003; Mecklenburg et al., 2002). *Amblyraja hyperborea* has a cosmopolitan distribution at mainly high latitudes, though it has been reported as far south as Panama in the eastern Pacific (Stevenson and Orr, 2005; Zorzi and Anderson, 1988). The geographic ranges of the deepest (*B. microtrachys*, Vancouver Island to central Baja (Orr et al., 2019) and one of the shallowest (*B. kincaidii*, Southeast Alaska to northern Baja) (Ebert, 2003) dwelling species were comparable; however, deep-water skate species are poorly documented and the range of *B. microtrachys* is likely to expand further with more exploration of the deep sea. For example, the geographic ranges of four species were extended or refined to include the southern Gulf of California based on our observations. *Beringraja rhina* and *B. trachura* have similar distributions, ranging from the Bering Sea to the Gulf of California, although the depth range of *B. trachura* is nearly 1600 m deeper (Last et al., 2016).

Bathymetric and spatial segregation has been widely documented for skate species (e.g., sex, size, maturity stage) (Kyne and Simpendorfer, 2010) and skate assemblages (Bizzarro and Vaughn, 2009; Ebert and Compagno, 2007; Stevenson et al., 2008), including the continental shelf and outer slope assemblage off the U.S. Pacific (Bizzarro et al., 2014); however, a lack of abundance information and the pooling of data from a long time period preclude any such investigations in this study. Published literature on deep-sea chondrichthyans typically consider deep-sea fauna to consist of any species that solely or predominantly occupy depths > 200 m (Cotton and Grubbs, 2015; Dulvy et al., 2014; Simpfendorfer and Kyne, 2009). The 200 m depth isobath we used to distinguish deep-water species is related to the bathymetric segregation of U.S. Pacific continental shelf and upper continental slope fauna, consisting of four hardnose (*Beringraja binoculata* (Girard, 1855)*, Be. rhina, Be. inornata* (Jordan & Gilbert, 1881)*, Be. stellulata* (Jordan & Gilbert, 1880), Rajidae) and one softnose (*B. kincaidii*; Arhychobatidae) species, and deep-water fauna, consisting primarily of the four additional softnosed (*Bathyraja* spp.) and one hardnosed species (*Amblyraja hyperborea*) included in this study. The depth distributions of *Be. rhina* and *B. kincaidii* span these two faunal groups but both species are primarily distributed in waters < 400 m (Bizzarro, 2015; Tolimieri and Levin, 2006). The only other deep-water species that occurs off the U.S. Pacific coast is the Aleutian skate, *B. aleutica* (Gilbert, 1896), but this species was not observed in MBARI videos and appears to be uncommon south of British Columbia.

Skates are one of the most specialized chondrichthyan taxa to deep-sea environments, and, *Bathyraja* spp., especially, often have very deep minimum depths (Kyne and Simpendorfer, 2010). The deepest verified chondrichthyan occurrence is a Bigelow's Skate, *Rajella bigelowi* Stehmann, 1986, captured at 4156 m in the north Atlantic (Stehmann, 1990; Weigmann, 2016). Our video recording of a *B.* cf. *microtrachys* at 3322 m represents the next deepest record and the deepest *in situ* observation of a skate. We observed nearly 300 skates in deep-bathyal areas (> 2000 m) and 15 at abyssal depths (> 3000 m), although MBARI's ROV effort in these regions has been relatively limited compared to shallower depths (200–2000 m). Other known deep-bathyal skates include *Bathyraja pallida* (Förster, 1967) (3280 m, Priede et al., 2006) and *Bathyraja richardsoni* (Garrick, 1961) (3055 m, Orlov et al. 2006) both occurring along the Mid-Atlantic Ridge. The deepest shark occurrences were documented at 3366 m (*Centrophorus squamosus* (Bonnaterre, 1788)), 3675 m (*Centroscymnus coelolepis* Barbosa, du, Bocage, de, Brito & Capello, 1864), and 3700 m (*Isistius brasiliensis* Quoy and Gaimard, 1824) (Weigmann, 2016). *Etmopterus princeps* Collett, 1904, which has been reported to 4500 m, does not have any verified occurrence records below 2213 m (Weigmann, 2016). The virtual absence of chondrichthyans at depths > 4000 m is not considered to be a function of insufficient sampling (Priede et al., 2006). For example, at an established abyssal study site (4000 m depth) in the northeast Pacific, which has been regularly monitored during the last 30 years using trawls, camera sleds, multiple 6–12 month-long time-lapse camera deployments, and video transects, no chondrichthyans have been encountered, even during periods when the abundance of megafauna was extremely high (Jacobsen Stout et al., 2019; Kuhnz et al., 2014).

Considerable recent study has been devoted to investigating the reason(s) that chondrichthyans have been largely unable to colonize abyssal and hadal regions of the deep-sea. This depth limitation is not universal among fishes, as several teleost taxa (e.g., ophidiid, liparid, macrourid) may occur to 8145 m (Linley et al., 2016). The following explanations have been proposed for the relative lack of deep-sea penetration by chondrichthyans: 1) their urea-based osmoregulatory system may conflict with the interactive effects of low temperature and high pressure on membrane function (Treberg and Speers-Roesch, 2016), 2) energetic limitations imposed by the use of the liver for dual purposes of lipid storage and buoyancy control (i.e., energetic advantage of a swim bladder in teleosts) (Priede et al., 2006), 3) dietary limitations on the amount of nitrogen available to synthesize trimethylamine N-oxide (TMAO) to stabilize proteins in the presence of high urea concentrations (Laxson et al., 2009), and 4) trophic limitations (i.e., elevated energetic needs as upper trophic level predators, less efficient at using and storing available food, absence of typical chondricthyan trophic guilds) (Musick and Cotton, 2015). Based on the totality of available evidence, there appears to be a temperature/pressure-related depth limit to homeostasis and, ultimately physical function for chondrichthyans. This factor, combined with competitive disadvantages in an oligotrophic environment imposed by food limitation and energetic constraints seem to preclude the establishment of viable chondricthyan populations in abyssal and hadal regions of the deep-sea.

4.2. Habitat associations

Temperature associations among species are largely reflective of depth distributions since these two environmental factors are highly correlated in the study region. For central California and sites off Washington and Vancouver Island, temperatures declined from 7 °C to 2 °C between depths of 200–1500 m. Although *B. kincaidii* and *Be. rhina* have similar depth ranges and are restricted to waters < 1500 m, *B. kincaidii* was observed in warmer waters (5–9 °C; *Be. rhina*, 3–6 °C). Quantitative analysis, however, indicated similar temperature ranges for these species off the U.S. Pacific (Bizzarro et al., 2014). The four species with all or the bulk of their observed depth range > 1500 m were largely associated with temperatures < 2 °C. *Bathyraja trachura* occupied a depth and temperature range that was intermediate between these shallow and deep groupings (1–4 °C). Relatively higher temperatures are present at similar depths in the Gulf of California (GOC), and *A. hyperborea*, *B. abyssicola*, and *B. spinosissima* were all found in higher temperatures in the GOC compared to the U.S. Pacific Coast. Temperature ranges reported here for *A. hyperborea* are slightly higher than those reported from the Barents Sea (0 °C) (Dolgov et al., 2005) but within established limits (< 4 °C) (Bigelow and Schroeder, 1953).

Most observations in this study occurred in central California beneath the California Current where the oxygen minimum zone (OMZ, defined as levels $< 0.5\,\text{ml}\,\text{l}^{-1}$) (Levin, 2003) was evident between approximately 450–1000 m depth. Oceans in the tropics, and specifically the GOC, are generally hypoxic. The OMZ in the GOC occupies a tall vertical swath from 40 to 1000 m water depth in many areas (Gallo and Levin, 2016). While all other skates were in observed within specific ranges, *B. abyssicola* appears to be an oxygen generalist, able to function in all oxygen concentration categories observed in this study. The extreme tolerance of low oxygen exhibited by *B. trachura* makes it capable of inhabiting the oxygen minimum zone. This ability may confer a strong adaptive advantage in a changing deep-sea environment (Gilly et al., 2013), either as a predatory avoidance strategy or to reduce resource competition with other species. Studies suggest that the vertical structure of the oxygen minimum zone is expanding due to climate change (Gilly et al., 2013; Levin, 2003; Stramma et al., 2010). This change may lead to habitat compression in shallower skate species and an increase in habitat for species that can survive at low O_2 levels. Changing conditions might also lead to decreased or altered benthic megafaunal and infaunal communities, impacting the food supply of skates, also leading to changes in the future depth and geographic distribution of these animals.

All skates utilized heavily sedimented areas but their association with this habitat type varied widely among species. Although no quantitative data were available, soft sediment habitats comprised the great majority of the surveyed region. Uneven sampling among habitats could be responsible for the relative lack of mixed habitat use observed for *B. kincaidii* and especially *Be. rhina* in this study compared to that of prior reports (Bizzarro et al., 2014; Ebert, 2003). The range of habitat associations was widest for *B. trachura*, and it was observed in association with CBC environments more often than other species. In Monterey Bay, CBC's are present in nearly the entire depth range of this study (300–2900 m) (Jacobsen Stout et al., 2019). The type and number of megafauna and infauna organisms present at them may represent a rich, concentrated food source.

Use of rocky habitats by skates, as evidenced in this study, is becoming more widely acknowledged (Bizzarro et al., 2014). Although *A. hyperborea* and *B. abyssicola* were primarily observed on soft substrate, they also were frequently observed on rock (lava, outcrops) and mixed habitats. *Bathyraja spinosissima* had a novel and distinct habitat association, occurring mainly in association with lava fields. This strong association with volcanic habitats extends to early life stages, as egg cases have been observed in close proximity to hydrothermal vents, presumably using the elevated temperatures to shorten embryo development time (Kyne and Simpendorfer, 2010; Salinas-de-León et al., 2018).

4.3. Behavioral patterns

Most of the published literature on deep-water chondrichthyans consists of taxonomic descriptions or catch/occurrence records (Cotton and Grubbs, 2015); therefore, behavioral observations provided novel insights into the biology of the studied skates. Rapid locomotory capacity, like that exhibited by *Be. rhina*, is believed to be restricted to shallower-dwelling chondrichthyans, with those living mainly ≥1000 m exhibiting greatly reduced metabolic rates and slower movement patterns (Childress, 1995; Rigby and Simpfendorfer, 2015). Our findings support this concept as related to speed of movement but not overall activity, as the deeper-dwelling skates in this study were more often observed swimming than the shallower species. Swimming behaviors also appears to be related to ecology. For instance, *B. kincaidii* lives in close proximity to the seafloor whereas *B. spinosissima* occupies benthopelagic habitats.

In addition to swimming, punting (synchronous movements of the anterior pelvic fin lobes, or crura) (Koester and Spirito, 2006) and walking (alternating movements of the crura; Holst and Bone, 1993; Jung et al., 2018) behaviors provided an additional form of locomotion, sometimes used alone and sometimes incorporated to supplement swimming. Observations indicated that punting was used to initiate swimming from a resting position for several species. The dual function of chondrichthyan livers for buoyancy and lipid storage presents physiological constraints on deep-water skates, and the deepest dwelling skates may therefore not be neutrally buoyant (Laxson et al., 2011; Treberg and Speers-Roesch, 2016). Pelvic fins may be necessary to generate lift off the seafloor for these species. *Beringraja rhina* and *B. abyssicola* used both modes of pelvic locomotion commonly to navigate terrain and seemingly to hunt for prey.

4.4. Caveats and future study

There are some caveats and considerations related to our study that should be mentioned. Because skates typically were observed on ROV dives that had other intended purposes, no quantitative assessment of effort exists. This lack of presence-absence data precludes an evaluation of abundance and diversity patterns or more detailed spatial analysis. One of the weaknesses of relying solely on video and imagery data is the inability to determine if unusual morphotypes, such as the *B.* cf. *microtrachys* observed in this study, represent undescribed species. Taxonomic designations require whole specimens (ideally) or at least viable tissue samples in addition to video footage. Biological (age and growth, reproduction, trophic) and molecular (genetics, stable isotope and fatty acid analysis) samples and physiological data currently cannot be obtained during ROV dives, severely limiting potential for more comprehensive, quantitative studies. eDNA studies are expanding, however for now the short time period that DNA remains viable in seawater and the sheer volume of water that would need to be collected and processed in order to detect skates in the sparsely populated deep-sea negates the usefulness of this technology.

In the near future, quantitative studies and a more persistent presence in the deep sea (time-lapse cameras, autonomous imaging vehicles) will help answer questions about biodiversity and population dynamics of deepwater species. The regular use of measuring tools (stereo cameras, lasers) can provide baseline data to enable assessments of potential ontogenic patterns and biomass estimates. Long-term, persistent observational data collection may also provide answers to questions regarding the ecological roles of the deepest living skates and whether they consistently inhabit these areas, or only utilize them during temporary forays. As technological developments occur and more consistent deep ocean imaging work is possible, the use of comprehensive observational keys like the one developed for this study can help ensure that data is reported by researchers are accurate and consistent, lending higher value to information available through information aggregators like the Ocean Biogeographic Information System (OBIS) and regulatory agencies.

5. Conclusions

We comprehensively observed seven deep-water skate species in their natural environments by utilizing MBARI's VARS database, greatly enriching the available distributional and biological information on the eastern North Pacific deep-water skate fauna. We noted that, much like the shallower fauna in the same region (Bizzarro et al., 2014), these deep-water skates exhibited bathymetric segregation and variable habitat associations, including use of volcanic rock (*B. spinosissima*) and low oxygen (*B. trachura*) habitats. This result further supports the emerging concept of skates having highly differentiated rather than analogous habitat niches. Although hundreds hours of video and years of near-continuous time lapse images have been collected at depths > 3500 m, the deepest skate observation (*B.* cf. *microtrachys*) was at 3322 m, reinforcing the notion that chondrichthyans are largely restricted to depths < 3000 m (Priede et al., 2006). Because chondrichthyans become more vulnerable to exploitation with increasing depth (Rigby and Simpfendorfer, 2015; Simpfendorfer and Kyne, 2009) and because they are largely restricted to depths > 1000 m, *A. hyperborea*, *B. spinosissima*, and *B. microtrachys* should not be commercially exploited. However, with a deep-water (1280–3500 m) commercial fishing ban in place throughout the U.S. Pacific Coast (National Marine Fisheries Service, 2006), an absence of deep-water (> 500 m) fisheries in the northern Mexican Pacific (Sosa-Nishizaki et al. in press), and Least Concern IUCN Red List status for all assessed species (IUCN 2018), there are no direct anthropogenic threats to deep-water skates in the study region.

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Appendix A. Supplementary data

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