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A Taxonomic Revision of Eastern North Pacific Softnose Skates (Arhynchobatidae: Bathyraja Ishiyama)

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A TAXONOMIC REVISION OF EASTERN NORTH PACIFIC SOFTNOSE SKATES (ARHYNCHOBATIDAE: *BATHYRAJA* ISHIYAMA)

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by

James D. S. Knuckey

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by

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APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

SAN JOSÉ STATE UNIVERISTY

May 2017

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ABSTRACT

A TAXONOMIC REVISION OF EASTERN NORTH PACIFIC SOFTNOSE SKATES (ARHYNCHOBATIDAE: *BATHYRAJA* ISHIYAMA)

by James D. S. Knuckey

Softnose skates (Rajiformes: Arhynchobatidae: *Bathyraja* Ishiyama) are the most diverse genus of skates, with 54 described species, and are readily distinguishable from their congeners by their relatively uncalcified and flexible rostral cartilages. Six species of *Bathyraja* are considered valid in the eastern North Pacific, including: deepsea skate, *B. abyssicola*, Aleutian skate, *B. aleutica*, sandpaper skate, *B. kincaidii*, fine-spined skate, *B. microtrachys*, Pacific white skate, *B. spinosissima*, and roughtail skate, *B. trachura*. As with other skate genera, the eastern North Pacific *Bathyraja* lacks a well-supported phylogeny, which leads to issues with setting catch limits and creating management plans. This study identifies and formally describes the softnose skates species in the eastern North Pacific based on morphometric and meristic measurements and includes an Alaskan species, Bering skate, *B. interrupta* due to its close morphological relationship to *B. kincaidii*. Multivariate tests determined that significant differences existed between the study species. Parsimonious phylogenetic trees showed that *B kincaidii* represents the basal condition, with *B. abyssicola* and *B. aleutica* being the most derived species in the study. The synonymized species *B. interrupta* and *B. kincaidii* were shown to be separate, as were the synonymized species *B. microtrachys* and *B. trachura.* An improved *Bathyraja* phylogeny will hopefully assist fisheries managers in developing conservation policies and easing the impacts of deepsea fishing expansion.

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Introduction

Chondrichthyans (sharks, rays, and chimaeras) are the extant members of an early offshoot of the vertebrate evolutionary tree and are one of two main divisions of surviving gnathostomes (jawed vertebrates), with the bony fishes being the sister group (Carroll, 1988; Naylor, Ryburn, Federigo & Lopes, 2005; Nelson, 2006). Due to their close relationship to bony fishes, chondrichthyans are taxonomically important and may represent the ancestral vertebrate condition (Aschliman et al., 2012). The class Chondrichthyes is subdivided into two major groups: Elasmobranchii (sharks and rays) and Holocephalii (chimaeras). Elasmobranchs are the larger of the two groups and are separated from holocephalans by the lack of a palatoquadrate fused to the neurocranium and by possessing teeth that are not fused into three plates (Didier, 1995; Lund & Grogan, 1997; Maisey, 1986).

Taxonomically, elasmobranchs have been studied for over 250 years, starting with Linnaeus (1758); however the taxonomic relationships among different groups of elasmobranchs are not well understood (Naylor et al., 2005). Other early research into elasmobranch taxonomy included works by Bloch and Schneider (1801), Duméril (1865), Günther (1870), Jordan and Evermann (1896), Müller and Henle (1841), and Rafinesque (1810), among others. Initial elasmobranch research sought to ascribe the known species into distinct groupings and to describe new species. Since these early studies, there have been numerous chondrichthyan classification schemes proposed based on the assignment of different weights to several morphological characters (e.g., Bigelow & Schroeder, 1948; 1953; Compagno, 1973; 1977; de Carvalho, 1996; Garman, 1913; Jordan, 1923;

Maisey, 1984a; 1984b; Schaeffer & Williams, 1977; 2012; Shirai, 1992; 1996). Even though there has been reasonably broad acceptance of the proposed family level classifications, many of the inter-relationships between taxa are debated, including the notion that elasmobranchs may not form a monophyletic group (Maisey, 1984a; Naylor et al., 2005; Nelson, 2006).

The monophyly of elasmobranchs has been upheld and is not in dispute, and while the higher level of classification, including order level, is relatively stable, the relationship of Batoidea (rays) within modern elasmobranchs remains unstable due to researchers disagreeing on what morphological characters are most important (Last et al., 2016; Maisey, 1984a; Naylor et al., 2005). The typical view places batoids as a sister group to sharks (Bigelow & Schroeder, 1948; 1953; Douady, Dosay, Shivji & Stanhope, 2003;Theis & Reif, 1985); however some research shows that batoids may in fact be a highly derived taxon within sharks (Shirai 1992). Shirai (1992) concluded that batoids were nested deep within a group that he called "Squalea," which is comprised of the hexanchoids, squaloids, *Squatina*, and pristiophorids. Other studies have placed Batoidea in various locations, including as a sister group to sawsharks (de Carvalho, 1996) and as a sister group to angelsharks (Compagno, 1973).

Batoids contain more than half of the chondrichthyan species diversity (633+ species of 1,193+ species) (Ebert, personal database, 2017; Last et al., 2016; Last & Yearsley, 2016), and much of the morphological disparity within Chondrichthyes, including departures from the typical shark ancestral body plan (Compagno, 1999; 2005). The wide spectrum of batoid body plans rivals that of many other groups of vertebrates (Aschliman et al., 2012). There is growing interest in batoid evolution, but the lack of a well-supported phylogeny has historically hampered the interpretation of studies such as life histories, behavior, and senses (Aschliman et al., 2012; Last et al., 2016). Current batoid taxonomy is provisional at best and awaits a well-supported phylogeny. Historically, five major groups were recognized within Batoidea: skates (Rajoidei), stingrays (Myliobatoidei), electric rays (Torpedinoidei), sawfishes (Pristoidei), and ‘‘guitarfishes,’’ which some authors suggested comprised an artificial group (Aschliman et al., 2012; Compagno, 2005; McEachran & Aschliman, 2004). More recent research suggests that only four major groups exist: skates (Rajiformes), electric rays (Torpediniformes), guitarfishes and sawfishes (Rhinopristiformes), and stingrays (Myliobatiformes), with the panrays (Zanobatidae) and thornback rays (Platyrhinidae) being sister groups to the stingrays and electric rays, respectively (Last et al. 2016; Last & Yearsley, 2016). There is debate over batoid inter-relationships, due to the high number of batoid phylogenies that have been proposed, and resolution within the skates and stingrays, which are the two largest clades within Batoidea, could be improved (e.g., Last et al. 2016; McEachran & Aschliman, 2004; Shirai, 1996).

The skates are the most diverse group within Batoidea, and consist of more genera (n = 38) and species (n = 288) than any of the other batoid suborders (Ebert, personal database, 2017; Ebert & Compagno, 2007; Last & Yearsley, 2016). The total number of skates represents over 24.1% of all known chondrichthyans and 43.4% of all known batoids. The greater degree of species diversity exhibited by skates is somewhat curious given their relatively conservative dorso-ventrally flattened body morphology and their restrictive habitat preference of soft bottoms. However, recent research has shown that skates can also inhabit rocky, high relief substrates (Ebert & Compagno, 2007; Kuhnz, Bizzarro, Chaney & Ebert, 2006; Monterey Bay Aquarium Research Institute (MBARI), unpublished video). Skates are benthic organisms with a worldwide distribution, a high rate of endemism, and greater diversity at higher latitudes and in deeper waters, whereas rays (family Myliobatiformes) are more commonly found in warmer, shallower waters (Ebert & Compagno, 2007; Ebert & Sulikowski, 2007; Ebert & Winton, 2010; White & Sommerville, 2010). For the most part skates are absent from freshwater environments, except for a single species that resides in Tasmanian estuaries (Last & Stevens, 2009).

The classification system of Rajiformes is still debated, with Compagno (1999) describing it as consisting of three families: Arhynchobatidae, Anacanthobatidae, and Rajidae (Compagno, 2001; 2005). Compagno (1999) is generally the most accepted phylogeny in the literature, while some authors place the Arhynchobatidae and Anacanthobatidae as subfamilies within the Rajidae (de Carvalho 1996; McEachran & Aschliman 2004). This thesis follows Last et al. (2016), which lists Rajiformes as being comprised of four families, with Gurgesiellidae being added to the three families described in Compagno (1999). As with Batoidea, the classification of skates is unresolved, due to the high morphological conservatism exhibited by species within this group. Because of the morphological similarities of skates, several early authors ascribed most species to the genus *Raja*, making identification for fisheries and research difficult (McEachran & Dunn, 1998). Subsequent taxonomic studies have since recognized numerous genera within the family, mostly based on external morphometric and meristic measurements (Ishiyama, 1952; McEachran & Dunn, 1998). Skate classification has typically been done on the basis of external characteristics, but descriptions of internal structures such as the rostral cartilage, neurocranium, claspers, counts of the vertebral column, and turns of the intestinal spiral valve have been shown to be much more useful for separation of species and genera (Bigelow & Schroeder, 1948; 1950; Ishihara & Ishiyama, 1985; Ishiyama, 1952; 1955). Even though skate systematics has been researched for over 100 years and the number of new species and genera has sharply increased in the last two decades (e.g., Bigelow & Schroeder, 1948; 1950; 1951; 1954; 1958; 1962; 1965; Ebert & Compagno, 2007; Ishihara, 1987; Ishihara & Ishiyama, 1985; 1986; Ishiyama, 1958; 1967; Ishiyama & Ishihara, 1977; Leigh-Sharpe, 1920; 1921; 1922; McEachran & Dunn, 1999), there has been relatively little taxonomic research done on the softnose skates belonging to Arhynchobatidae Fowler, 1934 (Ebert 2003; Ebert & Compagno, 2007; Last et al., 2016).

Softnose skates are readily distinguishable from their congeners by their relatively uncalcified rostral cartilages; hence their common name (Ebert, 2003). The flexible rostra of softnose skates are believe to be more advanced than that of the hard-nose skates (Ishiyama, 1952). Arhynchobatidae is currently comprised of 13 genera (Table 1), with the most speciose genus being *Bathyraja* with 54 species (Ebert, personal database, 2017; Last & Yearsley, 2016).

Table 1.

Valid Genera within Arhynchobatidae.

Genus	Author(s) and Year	Valid Species
Arhynchobatis	Waite, 1909	1
Atlantoraja	Menni, 1972	3
Bathyraja	Ishiyama, 1958	54
Brochiraja	Last & McEachran, 2006	8
Irolita	Whitley, 1931	2
Insentiraja	Yearsley & Last, 1992	2
Notoraja	Ishiyama, 1958	12
Pavoraja	Whitley, 1939	6
Psammobatis	Günther, 1870	8
Pseudoraja	Bigelow & Schroeder, 1954	1
Rhinoraja	Ishiyama, 1952	3
Rioraja	Whitley, 1939	1
Sympterygia	Müller & Henle, 1837	4

Note: Includes authors and the number of valid species per genus.

The genera *Breviraja* and *Rhinoraja* were two of the first softnose genera to be split from *Raja*, based mostly on their flexible rostral cartilages (Ishiyama, 1952). *Breviraja* and *Rhinoraja* differ from each other in multiple ways, including a segmented rostrum, large wings on the distal ends of the rostrum, and the tail being always longer than the disc length in the latter genus (Ishiyama, 1952). *Bathyraja* was considered a subgenus of *Breviraja*, until Ishiyama and Hubbs (1968) elevated it to full generic status based on morphometric measurements and distribution patterns. Members of *Breviraja* are typically found in the North Atlantic Ocean, whereas members of *Bathyraja* are typically found in the North Pacific and southwest Atlantic Oceans (Ishiyama & Hubbs, 1968). The closely-related genus, *Rhinoraja*, differs from *Bathyraja* by lacking a pseudosiphon and a rostral segment (Stevenson, Orr, Hoff & McEachran, 2004). Additionally, Ishiyama

(1958) proposed the subgenera *Arctoraja* and *Notoraja,* of which *Arctoraja* is currently a subgenus of *Breviraja* and *Notoraja* has been elevated to full generic status (Ishiyama, 1958; Stehmann, 1989). *Bathyraja* was originally separated from *Rhinoraja* by having a relatively short tail and intermediate vertebral counts, but some studies have indicated that the two genera are synonymous (Stevenson et al., 2004). Both *Breviraja* and *Bathyraja* share the characteristics of the extension of the inner pectoral radials to near the wing-like anterior appendices of the soft and slender, unsegmented rostral cartilage, generally prickly skin, and numerous vertebrae (Ishiyama & Hubbs, 1968), but differ in other respects.

The genus *Bathyraja* is a well-defined monophyletic genus (Hulley, 1972; Ishihara & Ishiyama, 1986; Ishiyama, 1958; 1967; Ishiyama & Hubbs, 1968; Ishiyama & Ishihara, 1977; Stehmann, 1970), and is distinguished from other softnose skates by differences in structures of the claspers, neurocranium, and egg cases (Ishihara & Ishiyama, 1985). *Bathyraja* is morphologically distinct from the genus that it once belonged to, *Breviraja,* in the following ways: the length of the cartilage and its relationship to the forward extension of the pectoral radials; the external morphology of the claspers, including the lack of large, thin, flake-like shield, the small ventral terminal that is hidden within the skin of the ventral lobe, and the presence of a pseudorhipidion and a pseudosiphon; the morphology of the rostral cartilage, including the small anterior notches that lie on either side of a short, anterior, free projection of the axis; the small appendices of the rostral cartilage that are broadly united with the subterminal part of the elongated axis, with each appendix extending backwards a short distance as a slender, unnotched process paralleling the axis; and the posterior wing of each appendix being separated from the axial rod by a notch about half as long as the whole appendix (Ishiyama & Hubbs, 1968). Ishihara and Ishiyama (1986) also found that the North Pacific bathyrajids had an anterior bridge on the scapulocoracoids, but there were differences in the shape and numbers of postdorsal and postventral foramina. The development of the rhipidion and the shield in the claspers of *Breviraja* and *Raja*, and the lack of these structures in *Bathyraja*, suggests that *Breviraja* and *Raja* have a closer relationship than *Bathyraja* and *Raja* (Ishiyama & Hubbs, 1968). Additionally, the rostral cartilage is more reduced in *Bathyraja* than in *Breviraja* (Ishiyama & Hubbs, 1968).

Eleven skate species are found in the Eastern North Pacific (ENP; which this study defines as the coasts of Washington, Oregon, and California), and have been formally ascribed to the genera *Amblyraja, Bathyraja,* and *Beringraja* based on internal and external anatomical characters (Ebert 2003; Ishihara, Treloar, Bor, Senou & Jeung, 2012; Zorzi & Anderson, 1988). This study concerns skates of the genus *Bathyraja*, Ishiyama, 1958, which is widely distributed throughout the North Pacific, and range from Alaska to northern Mexico (Brown, Bizzarro, Cailliet & Ebert, 2011). *Bathyraja* is the most abundant genus of skates in the North Pacific, possibly because the Bering Sea is a highly suitable habitat for skates, especially on the continental slope (Ishihara & Ishiyama, 1986). Six species of *Bathyraja* are considered valid in the ENP, including: deepsea skate, *B. abyssicola* (Gilbert, 1896), Aleutian skate, *B. aleutica* (Gilbert, 1896), sandpaper skate, *B. kincaidii* (Garman, 1908), fine-spined skate, *B. microtrachys* (Osburn

& Nichols, 1916), Pacific white skate, *B. spinosissima* (Beebe & Tee-Van, 1941), and roughtail skate, *B. trachura* (Gilbert, 1892).

As with other skates, *Bathyraja* in the ENP lack a well-supported phylogeny. This is mostly due to confusion in the literature regarding similar looking species, unreliable morphological measurements, and the possible presence of cryptic speciation (Ebert & Sulikowski, 2007). Many skate species have not been well described, including those occurring in the ENP; this includes structures such as claspers and craniums, which are useful in separating closely related and possibly cryptic species (Ebert & Compagno, 2007). All but one of the species found in the ENP have not been further described based on additional data, with the exception being *B. abyssicola*, which was redescribed by Zorzi & Anderson (1988).

In addition to the lack of robust, contemporary descriptions of ENP bathyrajids, there are other specific taxonomic difficulties with synonymies within the genus (Ishihara & Ishiyama, 1985). Ishihara & Ishiyama (1985) synonymized *B. kincaidii* with Bering skate, *B. interrupta* (Gill & Townsend, 1897), which has a distribution in the Bering Sea and Gulf of Alaska. Ishihara & Ishiyama (1985) based the synonymy of these two species on a comparison of the structure of the claspers and neurocrania. *Bathyraja interrupta* is one of the most common skate species in Alaskan waters (Ainsley, 2009), but is likely not found off of the contiguous United States. While there are several additional species found in the Bering Sea and Alaska, none are considered in this study. *Bathyraja interrupta* is included in this study as it is closely related morphologically, and sometimes synonymized, with *B. kincaidii*, a species that inhabits the waters considered for this study.

As well as the possible synonymy between *B. interrupta* and *B. kincaidii*, Ishihara and Ishiyama (1985) followed Miller and Lea (1972) by synonymizing *B. microtrachys* with *B. trachura*, due to Carl L. Hubbs (Scripps Institute of Oceanography, San Diego, California) regarding *B. microtrachys* as a junior synonym of *B. trachura*. The agreement on synonymy in Ishihara and Ishiyama (1985) was based solely on the figure of *B. microtrachys* resembling *B. trachura* in the original description (Osburn & Nichols, 1916), with the condition that further investigations into the relationship should be conducted. Subsequent studies have since investigated the synonymy between *B. microtrachys* and *B. trachura* and have distinguished the two species as being separate and valid (Craig, 1993; Ebert, 2003; Ebert & Compagno, 2007; Last et al., 2016).

The present study examines the external and internal morphology of softnose skates from the ENP. The main objective of this study is to elucidate the morphological variation of these skates, through the descriptions of such anatomical features as claspers and cranial structures, in order to explain the systematics of ENP skates belonging to *Bathyraja*. Morphological and meristic differences will be reported, especially for the species in which their validity is doubted, such as the distinction between *B. interrupta* and *B. kincaidii*, and the distinction between *B. microtrachys* and *B. trachura*. Based on new material, these descriptions should help elucidate the complicated phylogeny of *Bathyraja*. Moreover, this study represents the first description of *B. microtrachys* claspers and the first description of cranial structures for several species. An improved phylogeny and identification of these skates will provide researchers better tools for identifying these vulnerable cartilaginous fishes, as well as allow fisheries managers to set informed catch limits. A simple taxonomic key for the species investigated in this study will be provided, with the intent of making it available for fisheries biologists. Because previous taxonomic studies have enhanced the identifications of other species of skates, it is hypothesized that a novel redescription of *Bathyraja* would describe previously undescribed features such as claspers and cranial structures, as well as generally improve the descriptions of other structures, which are known from poor or inadequate original descriptions.

The aim of the study, in addition to utilizing morphometric and meristic measurements to formally redescribe the genus *Bathyraja* from the ENP, was to address the following questions: 1) Can investigations into the differing morphological structures of claspers and/or neurocrania allow for the identification of ENP bathyrajids? Skeletonization and x-radiogram samples of the collected specimens were examined to identify defining character traits and answer this question; 2) Can morphological, meristic, and statistical data be used to validate the species included in this study?; 3) Is there any evidence of a synonymy between *B. interrupta* and *B. kincaidii*, or are they one species with a large geographic distribution? Examinations of both putative species were completed and the morphometrics of both species were compared to determine if they are distinct species. This, in addition to statistical analyses, allows for the identification of possible speciation; 4) Is there any evidence of a synonymy occurring between *B. microtrachys* and *B. trachura*, which Miller and Lea (1972) upholds, but other studies refute? As with the *B. kincaidii*/*interrupta* question, morphometrics and meristics of both species were compared and statistical analyses such as nMDS, ANOVA, PCA, were performed to determine if the morphological variations were significant.

For studies of the taxonomy and phylogenetics of ENP bathyrajids, the following hypotheses were tested:

H_1: The examination of the differing morphological structures of claspers and/or neurocrania will allow for the positive identification of ENP bathyrajids;

H_2: The use of morphological, meristics, and statistical data will allow for the validation and correct identification of species;

H_3: There will be evidence of speciation occurring between *Bathyraja interrupta* and *B. kincaidii*; they will be two separate, distinct species with different distributions;

H_4: There will be evidence of speciation occurring between *Bathyraja microtrachys* and *B. trachura*; they will occur as two separate and distinct species.

Materials and Methods

Specimens of four species of *Bathyraja* (*B. abyssicola*, *B. aleutica*, *B. kincaidii*, and *B. trachura*) were collected during trawl surveys conducted along the coasts of California, Oregon, and Washington by the National Marine Fisheries Service (NMFS) from June through October of 2011-2012 and 2014-2016 under IACUC Protocol #2014-D. These annual surveys seek to assess the diversity and abundance of groundfish from the western coast of the United States, with the aim of setting catch limits for the following year. Depths ranged from 119 m to 1,233.6 m for the specimens collected in this study. Most of the specimens were collected in deep, low relief environments that are ideal for bottom trawling. Trawl sample sizes were as follows: *B. abyssicola* (N = 14), *B. aleutica* (N = 12), *B. kincaidii* (N = 39), and *B. trachura* (N = 19). Specimens of *B. abyssicola*, *B. kincaidii*, and *B. trachura* were caught throughout the entirety of the survey's range. *Bathyraja aleutica* was not collected south of Cape Mendocino, which was expected due to similar reported ranges found in previous studies. After collection, the survey specimens were preserved onboard the collection vessels by freezing. Specimens were transported to the Moss Landing Marine Laboratories (MLML) and were housed in the ichthyological freezer for later processing.

Since some species were inadequately sampled by the NMFS surveys, additional specimens were obtained from supplementary sources. Dr. Jeff Drazen (University of Hawaii, Manoa, Hawaii) collected specimens of *B. microtrachys* (N = 5; depth range = 2,080-2,250 m) from Monterey Bay, California in April and October of 2009 during a National Science Foundation (NSF) Study. Specimens of *B. interrupta* (N = 16) were collected and measured in the Bering Sea in June and July of 2002. No fresh specimens of *B. spinosissima* were collected during the course of the study. As such, specimens of *B. spinosissima* (N = 4; depth range = 2,121-2,700 m) were obtained from the preserved collections of both Oregon State University (OSU), Newport, Oregon and the California Academy of Sciences (CAS), San Francisco, California. Additional preserved material was obtained from the CAS and sample sizes were as follows: *B. aleutica* (N = 3), *B. microtrachys* (N = 1), and *B. trachura* (N = 1). Preserved specimens from OSU and the CAS were first preserved in formalin and then moved into 70% ethanol.

Morphometric and meristic measurements were taken and follow Aschliman, Ebert & Compagno (2010), with some modifications, to determine if investigations into the differing morphological structures of ENP bathyrajids can be used to correctly separate species. Morphological and meristic measurements were taken after the specimens had thawed. Measurements were taken to the nearest 0.1 mm and are presented as a proportion of total length (TL). Meristic counts include vertebrae, teeth, spiral valve, fin radials, and thorns. Tooth counts were taken directly from the upper and lower jaws of the specimens. Spiral valve counts were taken directly from the specimens. Thorn counts were taken directly from the dorsal surface of the specimens. Pectoral and pelvic radial fin counts were taken directly from the specimens, after removing the skin. Skeletonization was performed, whereby the flesh was removed so that the skeleton was exposed. This was done in order to view and document the variation in the skates' skeletal anatomy, including the crania and claspers. Moreover, x-radiograms of each species were taken at the CAS to further illustrate differences in skeletal anatomy. Vertebral counts were taken from the x-radiograms obtained from the CAS. Utilization of the number, size, position, and orientation of skeletal traits, allows for the determination of suitable characters for identification. Based on previous studies, morphological structures are useful for identification purposes.

In order to define a species, and therefore determine whether separate and valid species exist in the ENP, this study follows the definitions put forth by Mayr (1996). Species are defined as having unequal rates of evolution and are subjected to reproductive isolation (Mayr, 1996). Species exhibit biological properties of individual specimens which prevent the interbreeding of populations, and therefore keep species isolated from other species (Mayr, 1996). Degree of morphological differentiation is often used as an indication of species (Mayr, 1996) because reproductive isolation and dissimilarities in evolutionary rates are often difficult to show.

For the purposes of visualizing the minute dermal denticles that bathyrajid species possess, images of denticles were taken via a Hitachi S-3400N-II scanning electron microscope (SEM). Skin samples were taken from just behind the eyes and from the first dorsal fin. The samples were washed, dried, and fixed on a stage by a bilateral adhesive tape, then sprayed with gold and examined. Images were taken at 30.0 kV with resolutions that ranged between 5.1-9.00 mm.

In order to present images of each species for comparison, photographs of specimens were taken on a digital camera and edited with GIMP 2 to remove the backgrounds and add scale bars. Additionally, maps of the catch locations were created with GIMP 2. Tables found throughout the study were created with Microsoft Excel.

Several multivariate methods were used to test for potential differences between and among the species and to elucidate the questions of synonymies and speciation. To visually determine if the putative bathyrajid species were different from each other based on their morphometric characters, expressed as % TL, study specimens were subjected to non-metric multi-dimensional scaling (nMDS) ordinations (Clarke & Gorley, 2006). The different assemblages identified using nMDS represented the different species in this study. Normalization transformations were conducted before the calculation of the resemblance matrix. Euclidean distance matrices were constructed for all morphological traits, which were followed by the execution of the nMDS (Clarke & Gorley, 2006).

An analysis of similarities (ANOSIM) was calculated to test for differences between species. The null hypothesis of the ANOSIM was that no differences exist between species. The result, expressed as R, compared the mean of ranked dissimilarities among groups to the mean of ranked dissimilarities between groups. An R-value near 1.0 implied a high degree of dissimilarity, whereas a value nearer to -1.0 indicated little or no degree of dissimilarity. R-values that occur below 0 suggest that the dissimilarities within groups are greater than those between groups (Clarke & Gorley, 2006). A similarity percentage analysis (SIMPER) was calculated to determine the morphological trait that contributed the largest differences between species. The results of the SIMPER analysis identified the relative importance of the morphological characters. All multivariate statistical analyses were performed using PRIMER software, version 6 (Plymouth Routines in Multivariate Ecological Research, 6.0).

Following the nMDS ordinations, individual one-way analyses of variances (ANOVAs) were conducted to test for differences in specific characters among the study species. The ANOVAs were used to compare the means and a Tukey-Kramer HSD *post hoc* test was utilized to establish the significance of the means. A sequential Bonferroni adjustment was used after the initial ANOVAs to correct for type I errors. A series of bar plots were constructed that depicted the means and standard errors of characters that appear to be driving the variations across species. Besides total length and thorn counts, the means and standard errors were taken from the measurements expressed as a percentage of total length. The bar plots, ANOVAs, and Tukey-Kramer HSD tests were performed using JMP Pro software, version 12.

In a subsequent analysis, a principal components analysis (PCA) was used to ascertain which morphological traits were correlated with each other, thereby reducing the number of variables tested (Abdi & Williams, 2010). PCA models the variation in certain variables in terms of a smaller number of independent combinations (the principal components) of those variables (Clarke & Gorley, 2006), with the first principal component having the largest variance. The PCA was used to visualize which characters were causing the separation of the putative species on the nMDS axes. Only data containing the full complement of measurements were included in this particular analysis. PCA can describe the data as completely as possible, while using the fewest possible variables. The goal of the PCA was to find a way that best explains the correlation and variance within the data set (Abdi & Williams, 2010). The PCAs were performed using JMP Pro software, version 12.

A maximum parsimony-based method was used to create a phylogenetic tree of the ENP bathyrajids, with the intention of visualizing the relations between the species. Parsimony selects trees that minimize the total tree length, and thereby the evolutionary steps, to explain a data set (Swofford, Olsen, Waddell & Hillis, 1996). As parsimony analysis requires discrete characters, continuous morphological characters were binned and analyzed as discrete character states. A closely-related species (California skate, *Beringraja inornata*) was used as an outgroup to root the tree. The choice of outgroup polarizes character states which can be interpreted evolutionarily (Swofford et al., 1996).

Multiple trees of shortest length represent the parsimonious hypotheses of evolutionary relationships among ENP bathyrajids, based upon both similarities and differences in their physical characteristics. The module PARS within Phylogeny Inference Package (PHYLIP) 3.695 (Felsenstein, 2005) was utilized to construct the rooted parsimony phylogenetic trees, which was further analyzed and edited using the software, TreeGraph2 (Stöver & Müller, 2010).

Systematics

Bathyraja Ishihara, 1958

Type species. *Raja isotrachys* Günther 1877, by original description.

Diagnosis. Small to large skate; rhomboidal in shape, often with rounded pectoral fins. Mature males possess concave anterior margins on the pectoral fins. Relatively slender and uncalcified rostral cartilages, possessing small anterior notches that lie on either side of short, anterior, free projections of the axis; small appendices of the cartilage that are broadly united with the subterminal part of the elongated axis, with each appendix extending backwards a short distance as a slender, unnotched process paralleling the axis; and the posterior wing of each appendix separated from the axial rod by a notch about half as long as the whole appendix. Disc width larger than disc length. First four gill slits always longer than fifth gill slit. Often possessing an anterior bridge on the scapulocoracoids. Tail is relatively long and often possesses only one row of thorns down its length. Claspers lack a large, thin, flake-like shield, the small ventral terminal that is hidden within the skin of the ventral lobe, and possess a pseudorhipidion and a pseudosiphon. Coloration is often lighter on ventral side, with a dark brown, grey, or black dorsal side. Dorsal surface often possesses darker blotches or spots.

Teeth are similar in both the upper and lower jaws with each tooth having a single, large rear-pointing cusp. Tooth rows on upper jaws numbering 22-42 and lower jaws numbering 11-38. Mature males possess alar thorns, but lack malar thorns.

Common name. Softnose skates, refers to the short, flexible snout.

Distribution. Softnose skates inhabit continental and insular shelves and slopes in tropical, temperate, and arctic waters. Globally, they range in depth from 17-2,952 m (Orlov, Tokranov & Fatykhov*,* 2006; Stehmann & Merrett, 2001). In the ENP, softnose skates range from the Bering Sea south to Mexico.

Etymology. The generic name derives from the Greek *bathos*, meaning deep, and *raja*, meaning skate, which is a reference to the depth range.

Bathyraja abyssicola (Gilbert, 1896)

Description. A large, flabby-bodied skate with a rhomboidal disc, 1.03-1.55 times as broad as long; disc length very triangular; disc length and width larger than all conspecific species, except *B. spinosissima*; anterior margin strongly triangular, moderately concave in adult males, straight to moderately convex beside and just forward of eyes; apex rounded; posterior margin convex and broadly rounded; free rear tip broadly rounded (Figures 1-2; Table 2). Head length (29.7.5-27.8% TL) and preorbital snout length (12.4-16.8% TL) significantly longer than all of its congeners ($F_{6,104}$ = 10.23, $p < 0.0001$ and $F_{6,104}$ = 12.41, $p < 0.0001$, respectively (see Statistical Results section for further detail)). Preoral length relatively long 12.0-17.3% TL and prenarial length significantly larger than all of the conspecific species ($F_{6,104}$ = 16.24, $p < 0.0001$ (see Statistical Results section for further detail)). Snout tip narrowly pointed; possessing no fleshy process at apex. Eye length relatively small 2.0-4.6% TL. Spiracles average 1.9-3.4% TL; oval shaped. Nasal curtain length large 2.7-9.1% TL, width average 6.3-9.7% TL, its posterior margin fringed at the corners; anterior margin of curtain lobe-like. Internarial distance 5.5-8.6% TL; gills roughly equivalent in length, except for a smaller fifth gill slit; first gill slit length 1.6-2.6% TL; fifth gill slit length 1.3-2.4% TL; distance between first gill slits 12.0-18.0% TL, and distance between fifth gill slits 10.0-13.7% TL. Upper jaw moderately well arched, possessing a symphysis; lower jaw convex. Teeth similar in both jaws; teeth unicuspid, with a strong, bluntly pointed posteriorly directed cusp; arranged in longitudinal rows; upper and lower teeth moderate in number (27-39 and 24-34, respectively).

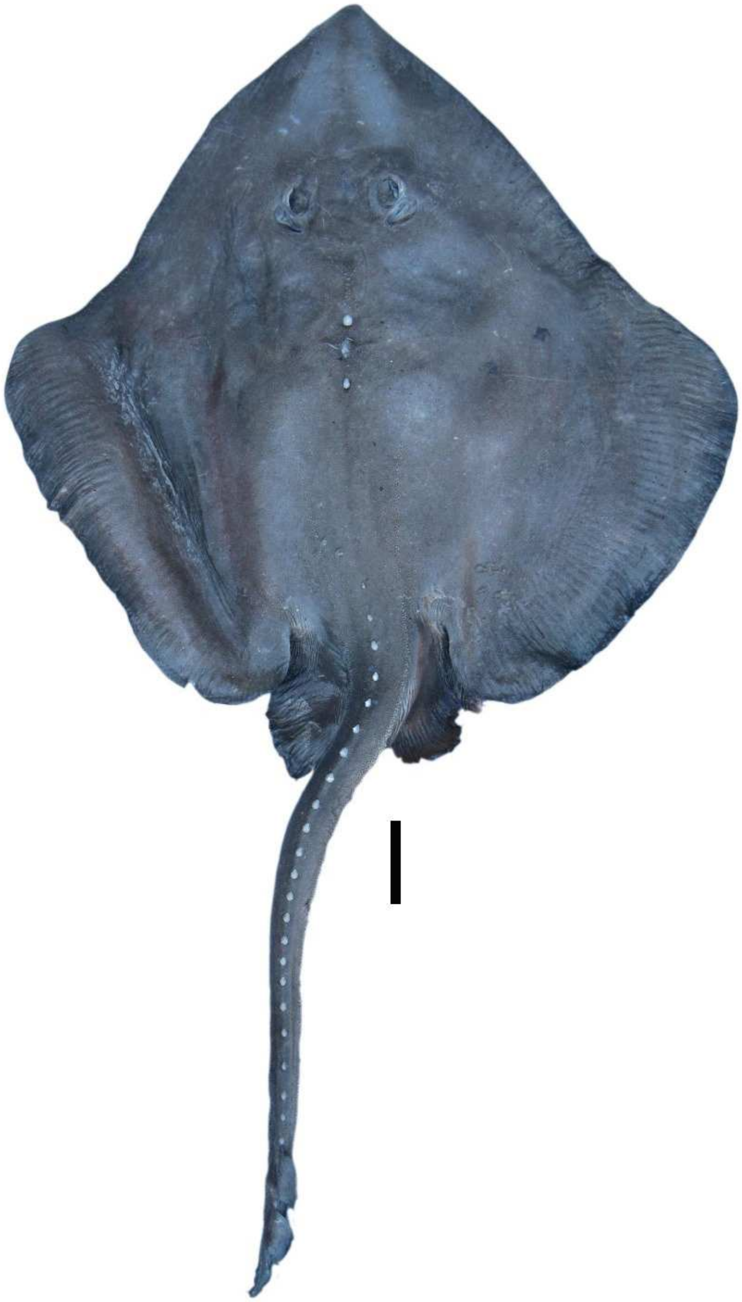

Figure 1. *Bathyraja abyssicola*, PSRC Baby 110813-1, 1125 mm TL, female, dorsal view, after freezing. Photo by J.D.S. Knuckey. Scale bar = 70 mm.

Figure 2. *Bathyraja abyssicola*, PSRC Baby 110813-1, 1125 mm TL, female, ventral view, after freezing. Photo by J.D.S. Knuckey. Scale bar = 70 mm.

Table 2.

Morphometric and Meristic Data for Bathyraja abyssicola (N = 14) Specimens.

Measurements	**% TL**
Total length (mm)	498 - 1386
Disc length	28.5 - 54.8
Disc width	44.2 - 63.7
Anterior disc length	35.2 - 46.7
Anterior anterior disc length (males only)	22.9 - 30.2
Anterior posterior disc length (males only)	9.6 - 17.6
Posterior disc length	25.0 - 32.8
Inner disc length	4.4 - 9.4
Disc base length	7.1 - 15.0
Snout to maximum disc width	29.0 - 37.1
Head length	19.7 - 27.8
Preorbital snout length	12.4 - 16.8
Eye length	2.0 - 4.6
Interorbital width	3.5 - 5.2
Spiracle length	1.9 - 3.4
Interspiracular width	2.0 - 6.4
D1 origin to tail tip	10.1 - 15.1
D1 base length	3.1 - 4.0
D1 vertical height	1.8 - 3.1
D2 base length	2.7 - 4.2
D2 vertical height	1.9 - 2.6
Interdorsal space	0.4 - 1.7
Caudal base length	0.6 - 4.4
Caudal vertical height	0.2 - 1.0
Lateral tail fold length	16.5 - 22.4
Preoral snout length	12.0 - 17.3
Mouth width	4.6 - 9.3
Prenarial snout length	9.8 - 14.3
Internarial width	5.5 - 8.6
Nasal curtain length	2.7 - 9.1
Nasal curtain width	6.3 - 9.7
Snout to 1st gill slit	19.7 - 24.8
Snout to 5th gill slit	27.3 - 31.8
1st gill slit length	1.6 - 2.6

2nd gill slit length	1.9 - 2.5
3rd gill slit length	1.6 - 2.8
4th gill slit length	1.9 - 2.6
5th gill slit length	1.3 - 2.4
Space between the 1st gill slits	12.0 - 18.0
Space between the 5th gill slits	10.0 - 13.7
Pelvic length	11.8 - 19.7
Pelvic posterior lobe length	7.2 - 12.8
Pelvic anterior lobe length	4.9 - 10.4
Inner anterior lobe length	2.9 - 8.6
Clasper inner length	8.3 - 30.7
Clasper outer length	4.5 - 20.8
Clasper base length	0.9 - 1.9
Precaudal length	94.3 - 99.3
Tail length	52.1 - 61.7
Interdorsal thorn count	0 - 1
Middorsal thorn count	0 - 2
Nuchal thorn count	2 - 4
Orbital thorn count- right side	0
Orbital thorn count- left side	0
Rostral thorn count	0
Scapular thorn count- right side	0 - 2
Scapular thorn count- left side	0 - 2
Tail thorn count	15 - 30
Alar thorn count- rows- right side (males only)	3 - 6
Alar thorn count- rows- left side (males only)	3 - 5
Alar thorn count- columns- right side (males only)	20 - 22
Alar thorn count- columns- left side (males only)	21 - 23
Malar thorn count- rows- right side (males only)	0
Malar thorn count- rows- left side (males only)	0
Malar thorn count- columns- right side (males only)	0
Malar thorn count- columns- left side (males only)	0
Upper teeth- total count	27 - 39
Lower teeth- total count	26 - 34
Spiral valve count	8 - 9
Pectoral fin radial count	82
Pelvic fin radial count	19
Vertebral count	139

Rostral cartilage length	46.6
Prefontanelle rostral length	47.2
Cranial width	78.9
Least interorbital width	20.1
Anterior prefontanelle length	19.5
Posterior prefontanelle length	26.5
Rostral appendices length	18.9

Note: Includes the ranges of the measurements. Total length is the actual measurement in millimeters; all other measurements are expressed as a percentage of total length (% TL).

Pelvic fins large, posterior lobe 7.2-12.8% TL, anterior lobe 4.9-10.4% TL, and inner margin deeply incised 2.9-8.6% TL. Tail moderately long 52.1-61.7% TL, rather slender; wider at base, tapering to the first dorsal fin origin, not expanded in the middle. Lateral tail fold small, 16.5-22.4% TL, similar in both sexes; not obviously broader at any point along its length. Dorsal fins moderate in size and shape, first dorsal fin slightly taller than second dorsal fin, 1.8-3.1% TL and 1.9-2.6% TL, respectively; bases of both dorsal fins are similar in length, 3.1-4.0% TL for first dorsal fin and 2.7-4.2% TL for second dorsal fin; anterior margins of both fins concave, apices rounded; free rear tip rounded; interdorsal space short 0.4-1.7% TL, with larger individuals having a larger interdorsal space, rear tip of first dorsal fin not overlapping base of second dorsal fin. Caudal fin small, low, height 0.2-1.0% TL; its dorsal margin weakly concave; not connected to second dorsal fin by a small membranous ridge. Tail relatively long 52.1-61.7% TL.

Scapular, middorsal, nuchal, interdorsal, and tail thorns present, males with a well-developed set of alar thorns; malar thorns absent; thorns vary in size, from very short to well developed. Middorsal thorns weakly developed or absent (0-2); nuchal thorns strongly developed (2-4); tail thorns moderate (15-30) and go down the length of the tail; interdorsal thorns weakly developed and small in number (0-1). Alar thorn patches possess 3-6 rows and 20-23 columns on both pectoral fins. No multiple rows of thorns on body. Middorsal thorn count is significantly lower than all of its congeners ($F_{6,104} = 16.20$, $p < 0.0001$ (see Statistical Results section for further detail)).

Mature claspers very slender and long, base length 0.9-1.9% TL, inner length 20.4-30.7% TL, tip of clasper conspicuously bulbous and wider than the rest of the structure (Figure 3). Clasper fully developed with squared tip, its length 35.7-49.7% of tail length. Very large and wide pseudosiphon present near the outer lateral edge of dorsal lobe, its length 20.0% of clasper length; inner surface of dorsal lobe with a distinct, curved pseudorhipidion; inner surface possesses a clearly defined V-shaped cleft; ventral lobe possesses a rounded projection.

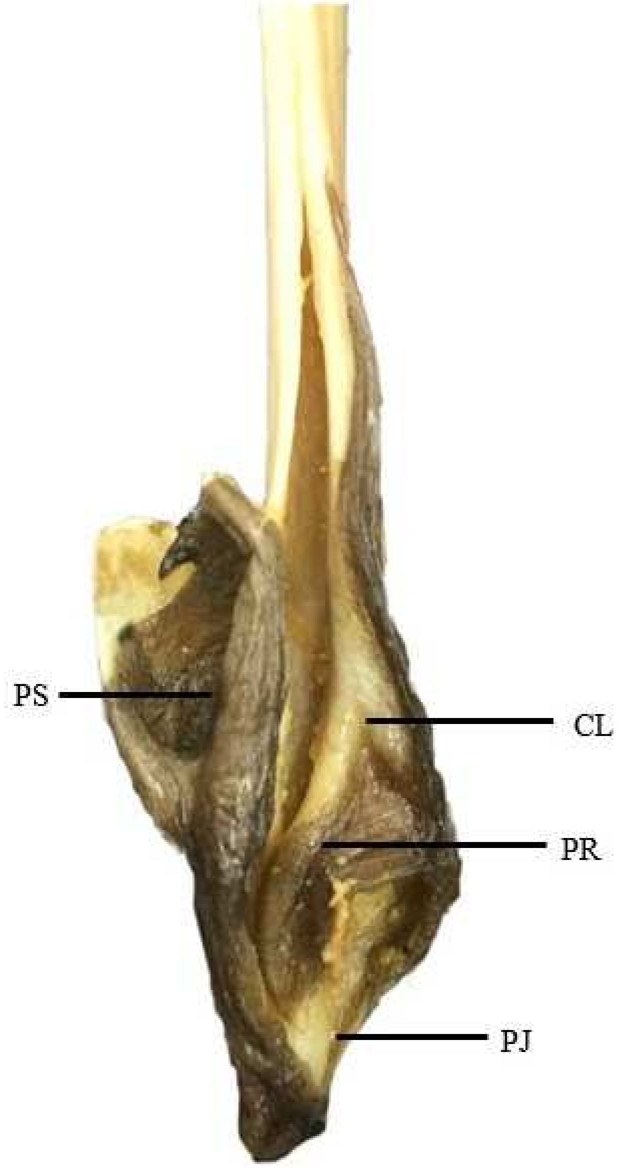

Figure 3. Components of the clasper for *Bathyraja abyssicola*. CL- cleft, PJ- projection, PS- pseudosiphon, PR- pseudorhipidion. Photo by J.D.S. Knuckey.

Clasper skeleton consists of 3 dorsal terminal, 1 accessory terminal, ventral terminal and axial cartilages; dorsal terminal 1 squared with a notch on the inner edge; dorsal terminal 1 curves around the axial onto ventral side and connected with ventral terminal, forming the relatively large pseudosiphon externally; tip of dorsal pointed, forming the pseudorhipidion externally; ventral terminal long, leaf-shaped, and overlying the tip of ventral marginal and accessory terminal 1; tip of ventral marginal pointed, forming a rounded projection externally.

Dermal denticles possess 3-4 points to the base and are well developed on posterior third of the dorsal surface; denticles on the first dorsal fin long, needle-like, posterior-oriented; denticles on head stouter and strongly curved (Figure 4).

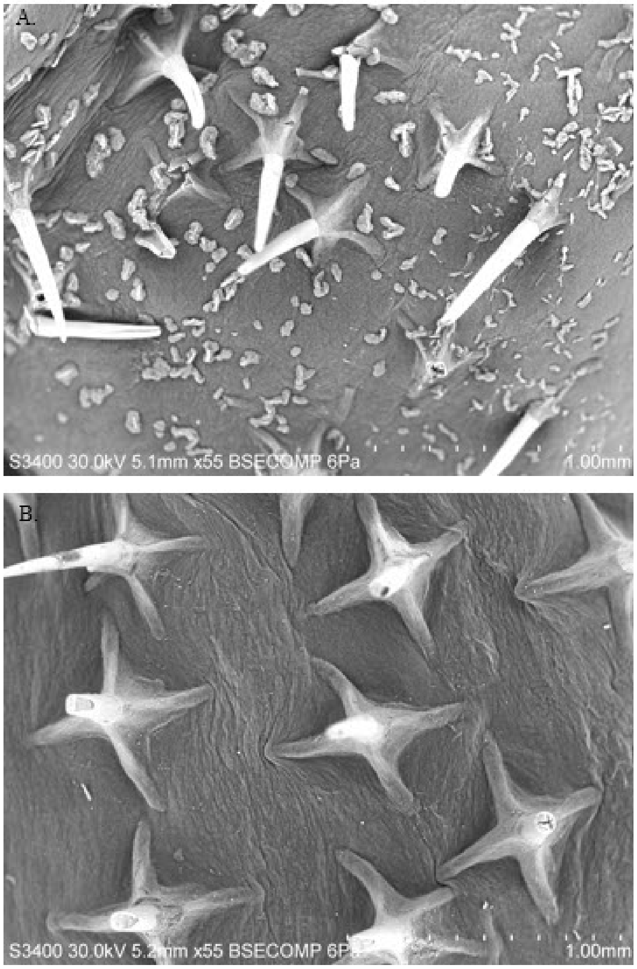

Figure 4. Scanning electron microscope images of the dermal denticles of *Bathyraja abyssicola* from A. the first dorsal fin and B. the head region, behind the eyes. Photos by Justin Cordova (MLML).

Length of rostral cartilage 51.1% of cranial length; prefontanelle rostral length 46.7%; cranial width 61.4%; least interorbital width 18.5%; length of anterior prefontanelle 14.1%; length of rostral appendices 16.2%. Rostral cartilage abruptly tapering near its broad base; rostral appendices long, its length 38.4% of the length of rostral cartilage; anterior fontanelle spade-shaped (Figure 5).

Figure 5. Ventral view X-radiogram of *Bathyraja abyssicola*, CAS 38289, female. X-radiogram by Jon Fong (CAS).

Size and sexual maturity. Size at maturity for males 109-120 cm TL; 145 cm TL for females. Males grow to at least 135 cm TL; females grow to at least 161 cm TL. Size at birth is uncertain, although the smallest free-swimming specimen measured 34 cm TL (Ebert, 2003). Maximum is size is 135 cm TL and 157 cm TL for males and females, respectively (Matta et al. 2006).

Coloration. Dorsal coloration dark brown or black to grey, occasionally with small dark blotches scattered on body. Snout semi-translucent. Spiracles pale white to pink. Pectoral fin edges are darker than the rest of the body; pelvic fins darker, often with whitish anterior tips. Ventral coloration slightly darker than dorsal surface; often possessing white coloration around mouth, gills, and cloaca; irregular pale blotches and numerous dark spots often scattered on body. Claspers brown to grey; cloaca sometimes possesses a dark ring around it. Thorns on dorsal surface are very pale. Possesses very fine prickles on the dorsal surface.

Distribution. *Bathyraja abyssicola* has been verified as occurring in the North Pacific, specifically from the Bering Sea, south to northern Baja California, Mexico, and as far west as Japan (Ebert, 2003). It occurs at depths of 362-2,906 m (Ebert, 2003); the specimens included in this study were found no shallower than 968 m and not deeper than 1,212.3 m. The relatively shallow depth for the specimens in this study is due to the maximum survey depth, not because the species does not occur at those depths.

Etymology. The species was named after the Greek *abyssos*, meaning bottomless, and *cola*, meaning living at depths, referring to its deep sea habitat.

Common name. Deepsea skate.

Comparisons. *Bathyraja abyssicola* is one of the largest bathyrajid species that occurs in the ENP and can easily be differentiated from the smaller-bodied species in its geographic range. *Bathyraja kincaidii* is significantly smaller in body size than *B. abyssicola* (46-50 cm TL and 109-145 cm TL at maturity, respectively). The dorsal coloration of *B. kincaidii* is light brown to beige, with dark blotches across the surface and a pale ventral surface. *Bathyraja abyssicola* possesses dark brown coloration on both the dorsal and ventral surfaces. *Bathyraja kincaidii* possess a significantly smaller head length than *B. abyssicola* (15.9-21.3% TL and 19.7-27.8% TL, respectively).

Bathyraja interrupta, which is a medium-sized skate, is differentiated from *B. abyssicola* based on its coloration and pelvic fin measurements. *Bathyraja abyssicola* is uniformly dark on both surfaces, whereas *B. interrupta* is beige on the dorsal surface and pale ventrally, but with brown blotching on the tail. *Bathyraja abyssicola* possesses smaller pelvic fin measurements than *B. interrupta*, specifically for the posterior lobe length (7.2-12.8% TL and 10.4-23.4% TL, respectively) and the anterior lobe length (4.9-10.4% TL and 7.7-11.6% TL, respectively).

Bathyraja microtrachys is a smaller-bodied species that differs from *B. abyssicola* in its thorns counts and coloration. *Bathyraja abyssicola* possesses thorns in the middorsal, nuchal, and scapular region. These thorns are consistently absent in *B. microtrachys*. Further differences exist in that *B. abyssicola* is darker on the dorsal and ventral surfaces, whereas *B. microtrachys* has a pale ventral surface, with dark edges to the fins. *Bathyraja abyssicola* is separated due to its uniform dark coloration on both surfaces.

Bathyraja trachura is a darkly colored softnose skate that shares a similar range to *B. abyssicola*, but lacks middorsal and scapular thorns, features that *B. abyssicola* possesses. *Bathyraja trachura* is further differentiated based on a significantly smaller to often non-existent interdorsal space (0.0-2.8% TL, compared to 0.4-1.7% TL) and a smaller head length (14.9-24.1% TL, compared to 19.7-27.8% TL).

Bathyraja abyssicola is of a similar size to *B. spinosissima*, but is clearly differentiated based on coloration. *Bathyraja spinosissima* is the only ENP bathyrajid to display pale coloration on both the dorsal and ventral surfaces. Additionally, *B. abyssicola* possesses a much smaller interspiracular width, when compared to *B. spinosissima* (2.0-6.4% TL and 9.1-12.2% TL, respectively).

Bathyraja abyssicola is compared to *B. aleutica*, as the two are similar in size, coloration, and distribution. *Bathyraja abyssicola* possesses dark ventral and dorsal coloration, whereas *B. aleutica* possesses a pale ventral side, with dark brown edges to the fins. *Bathyraja aleutica* possesses a significantly longer interdorsal space (1.3-3.1% TL, compared to 0.4-1.7% TL). *Bathyraja abyssicola* has the longest snout to body size of any species in this study and can be further separated from *B. aleutica* based on the head length and preorbital snout length. *Bathyraja abyssicola* possesses a head length of 19.7-27.8% TL and a preorbital snout length of 12.4-16.8% TL. This is compared to the head length and preorbital length of *B. aleutica*, 16.7-24.3% TL and 9.7-16.9% TL, respectively.

Bathyraja aleutica (Gilbert, 1896)

Description. A large skate with a rhomboidal disc, 1.13-2.05 times as broad as long; anterior margin moderately concave in adult males, straight to slightly convex beside and just forward of eyes; pectoral fin apices broadly rounded; posterior margin slightly convex; free rear tip broadly rounded (Figures 6-7; Table 3). Head length long 16.7-24.3% TL, preorbital snout length long 9.7-16.9% TL; preoral length relatively long 11.8-17.5% TL. Snout tip broadly triangular; possessing no fleshy process at apex. Deeply concave space directly behind eyes, eye length relatively small 2.6-5.0% TL. Interorbital width short 3.3-5.3% TL. Spiracles average 1.6-3.7% TL; oval shaped. Mouth width short 6.2-10.0% TL. Nasal curtain length average 2.8-4.5% TL, width average 7.0-9.0% TL, its posterior margin fringed at the corners; anterior margin of curtain lobe-like. Internarial distance 6.6-7.7% TL; first gill slit length 1.2-2.5% TL; fifth gill slit length 0.7-2.1% TL; distance between first gill slits large 14.7-20.2% TL, and distance between fifth gill slits 10.1-13.4% TL. Upper jaw moderately well arched, possessing a symphysis; lower jaw convex. Teeth similar in both jaws; teeth unicuspid, with a strong, bluntly pointed posteriorly directed cusp; arranged in longitudinal rows; upper and lower teeth high in number (34-42 and 32-38, respectively).

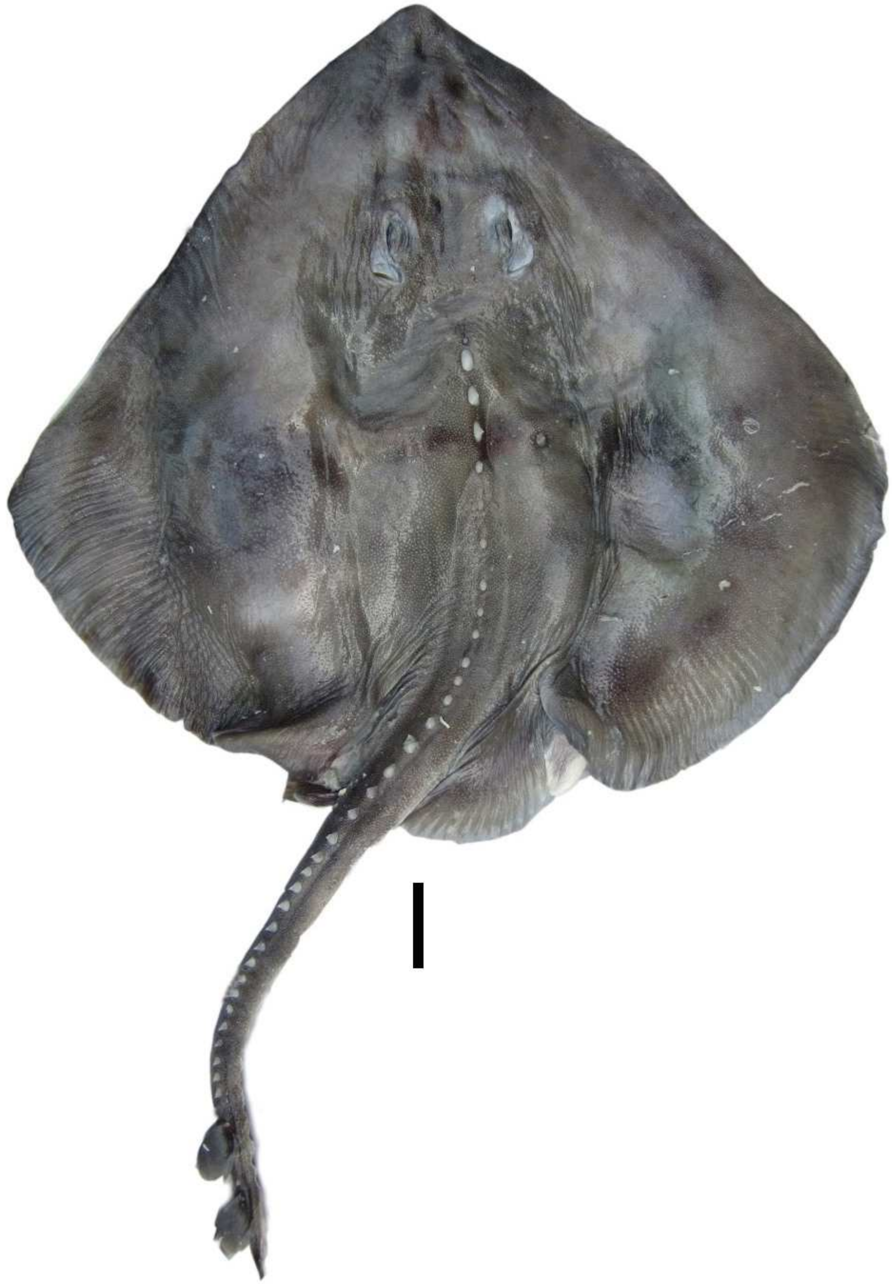

Figure 6. Bathyraja aleutica, PSRC Bale 070313-1, 908 mm TL, immature male, dorsal view, after freezing. Photo by J.D.S. Knuckey. Scale bar = 60 mm.

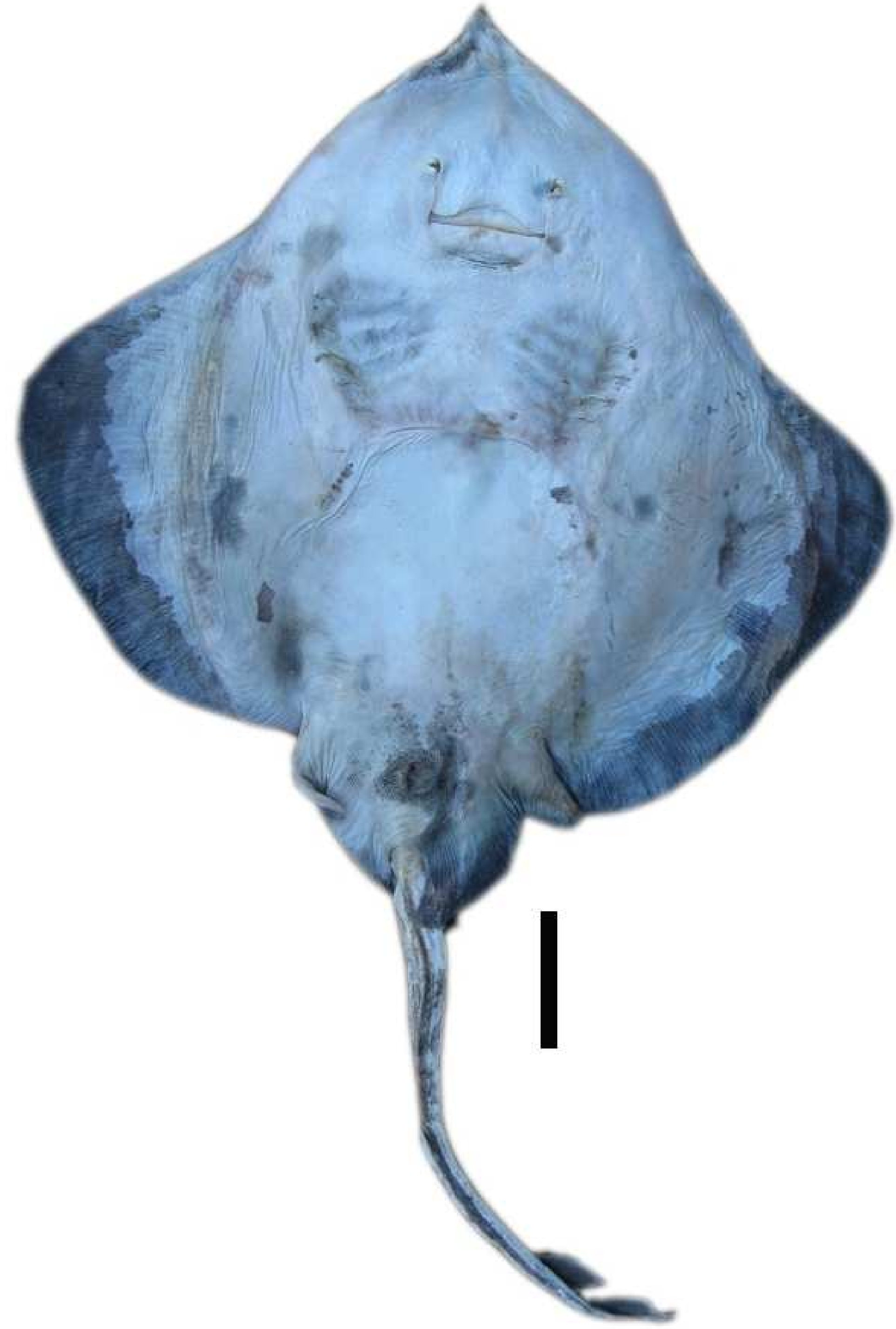

Figure 7. Bathyraja aleutica, PSRC Bale 062812-1, 1198 mm TL, female, ventral view, after freezing. Photo by J.D.S. Knuckey. Scale bar = 130 mm.

Table 3.

Morphometric and Meristic Data for Bathyraja aleutica (N = 12) Specimens.

Measurements	**% TL**
Total length (mm)	258 - 1198
Disc length	31.2 - 57.5
Disc width	55.8 - 65.5
Anterior disc length	39.9 - 47.1
Anterior anterior disc length (males only)	29.4
Anterior posterior disc length (males only)	17.5
Posterior disc length	25.3 - 35.0
Inner disc length	6.8 - 10.7
Disc base length	9.7 - 17.4
Snout to maximum disc width	28.7 - 37.0
Head length	16.7 - 24.3
Preorbital snout length	9.7 - 16.9
Eye length	2.6 - 5.0
Interorbital width	3.3 - 5.3
Spiracle length	1.6 - 3.8
Interspiracular width	4.3 - 7.0
D1 origin to tail tip	11.6 - 15.9
D1 base length	2.8 - 5.0
D1 vertical height	1.9 - 3.0
D2 base length	2.8 - 5.0
D2 vertical height	1.7 - 3.8
Interdorsal space	1.3 - 3.1
Caudal base length	2.2 - 3.7
Caudal vertical height	0.5 - 2.1
Lateral tail fold length	13.9 - 24.0
Preoral snout length	11.8 - 17.5
Mouth width	6.2 - 10.0
Prenarial snout length	9.5 - 13.7
Internarial width	6.6 - 7.7
Nasal curtain length	2.8 - 4.5
Nasal curtain width	7.0 - 9.0
Snout to 1st gill slit	17.4 - 25.2
Snout to 5th gill slit	23.9 - 33.3
1st gill slit length	1.2 - 2.5

2nd gill slit length	1.1 - 2.9
3rd gill slit length	1.1 - 2.8
4th gill slit length	1.1 - 2.8
5th gill slit length	0.7 - 2.1
Space between the 1st gill slits	14.7 - 20.2
Space between the 5th gill slits	10.1 - 13.4
Pelvic length	12.4 - 18.8
Pelvic posterior lobe length	7.2 - 15.7
Pelvic anterior lobe length	6.9 - 9.9
Inner anterior lobe length	5.0 - 8.9
Clasper inner length	3.5 - 23.1
Clasper outer length	1.9 - 12.9
Clasper base length	0.8 - 1.3
Precaudal length	92.2 - 97.5
Tail length	51.1 - 60.9
Interdorsal thorn count	1 - 2
Middorsal thorn count	4 - 11
Nuchal thorn count	3 - 5
Orbital thorn count- right side	0
Orbital thorn count- left side	0
Rostral thorn count	0
Scapular thorn count- right side	1 - 2
Scapular thorn count- left side	1 - 2
Tail thorn count	18 - 30
Alar thorn count- rows- right side (males only)	7
Alar thorn count- rows- left side (males only)	8
Alar thorn count- columns- right side (males only)	21
Alar thorn count- columns- left side (males only)	24
Malar thorn count- rows- right side (males only)	0
Malar thorn count- rows- left side (males only)	0
Malar thorn count- columns- right side (males only)	0
Malar thorn count- columns- left side (males only)	0
Upper teeth- total count	34 - 42
Lower teeth- total count	32 - 38
Spiral valve count	8 - 9
Pectoral fin radial count	90
Pelvic fin radial count	22
Vertebral count	152

Rostral cartilage length	47.2
Prefontanelle rostral length	48.4
Cranial width	87.3
Least interorbital width	18.3
Anterior prefontanelle length	11.1
Posterior prefontanelle length	11.1
Rostral appendices length	20.6

Note: Includes the ranges of the measurements. Total length is the actual measurement in millimeters; all other measurements are expressed as a percentage of total length (% TL).

Pelvic fins average overall; anterior lobe short 6.9-9.9% TL, posterior lobe relatively long 7.2-15.7% TL, and similar between sexes and maturities, inner margin deeply incised. Tail relatively long 51.1-60.9% TL, rather slender; wider at base, tapering to the first dorsal fin origin, not expanded in the middle. Lateral tail fold length 13.9-24.0% TL, similar in both sexes; not obviously broader at any point along its length. Dorsal fins moderate in size and shape, both dorsal fins similar in height, 1.9-3.0% TL and 1.7-3.1% TL, respectively; bases of both dorsal fins are the same length, 2.8-5.0% TL; anterior margins of both fins concave, apices rounded; free rear tip rounded, occasionally pointed; interdorsal space significantly larger than all of its congeners 1.3-3.1% TL ($F_{6,104} = 15.27$, $p < 0.0001$ (see Statistical Results section for further detail)), with larger individuals having a shorter interdorsal space, rear tip of first dorsal fin not overlapping base of second dorsal fin. Caudal fin moderate, low, height 0.5-2.1% TL; its dorsal margin weakly concave; connected to second dorsal fin by a small membranous ridge.

Dorsal surface covered with fine prickles, with larger prickles on the tail; ventral surface smooth. Scapular, middorsal, nuchal, interdorsal, and tail thorns present, males with a well-developed set of alar thorns; malar thorns absent; thorns vary slightly in size, from moderate to well developed. Middorsal thorns well developed and high in number

(4-11); nuchal thorns very well developed and high in numbers (3-5); 1-2 scapular thorns present on either side; tail thorns average (25-30); interdorsal thorns weakly developed (1-2). Alar thorn patches range between 7-8 rows and 21-24 columns on both pectoral fins. No multiple rows of thorns on body. Middorsal thorns are significantly higher in number than all of its congeners ($F_{6,104} = 16.21$, $p < 0.0001$ see Statistical Results section for further detail)).

Mature claspers relatively short and stubby, base length 1.3% TL, inner length 23.1% TL, and tip of clasper rounded and not bulbous (Figure 8). Clasper inner length 42.6% of tail length; weakly defined pseudosiphon present, its length 30.8% of the clasper length; inner surface of dorsal lobe possesses a short pseudorhipidion; U-shaped cleft; inner surface of ventral lobe has a rounded projection.

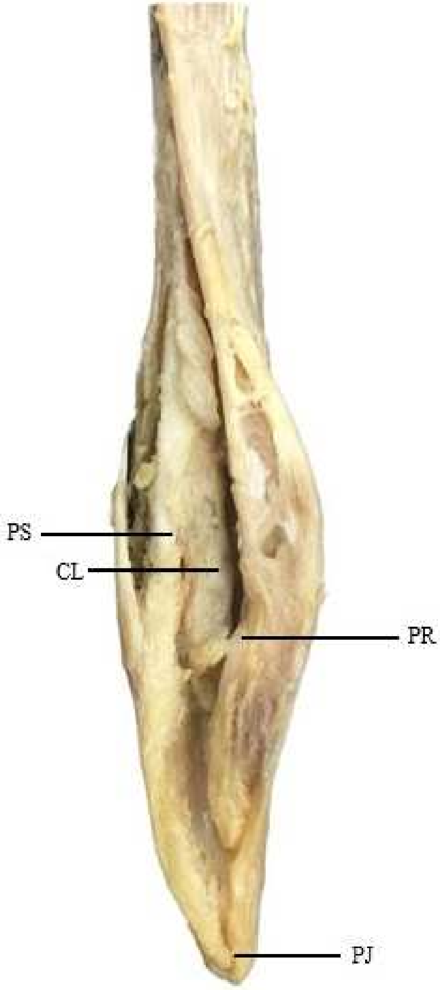

Figure 8. Components of the clasper for *Bathyraja aleutica*. CL- cleft, PJ- projection, PR- pseudorhipidion, PS- pseudosiphon. Photo by J.D.S. Knuckey.

Clasper skeleton consists of 3 dorsal terminal, 1 accessory terminal, ventral terminal and axial cartilages; dorsal terminal 1 large, taking up most of the dorsal surface; dorsal terminal 1 forms a weakly defined pseudosiphon externally; the tip of the dorsal marginal is round, and forms a thick, short, but poorly defined pseudorhipidion externally; ventral terminal curved and pointed, possessing a tip that forms the projection externally; accessory terminal 1 almost as long as the ventral terminal; tip of accessory terminal 1 is pointed.

Dermal denticles possess 4-7 points at the base; developed on the posterior third of the dorsal surface; denticles on the first dorsal fin strong curved, claw-like; denticles on head wider than dorsal fin; found in high density patches (Figure 9).

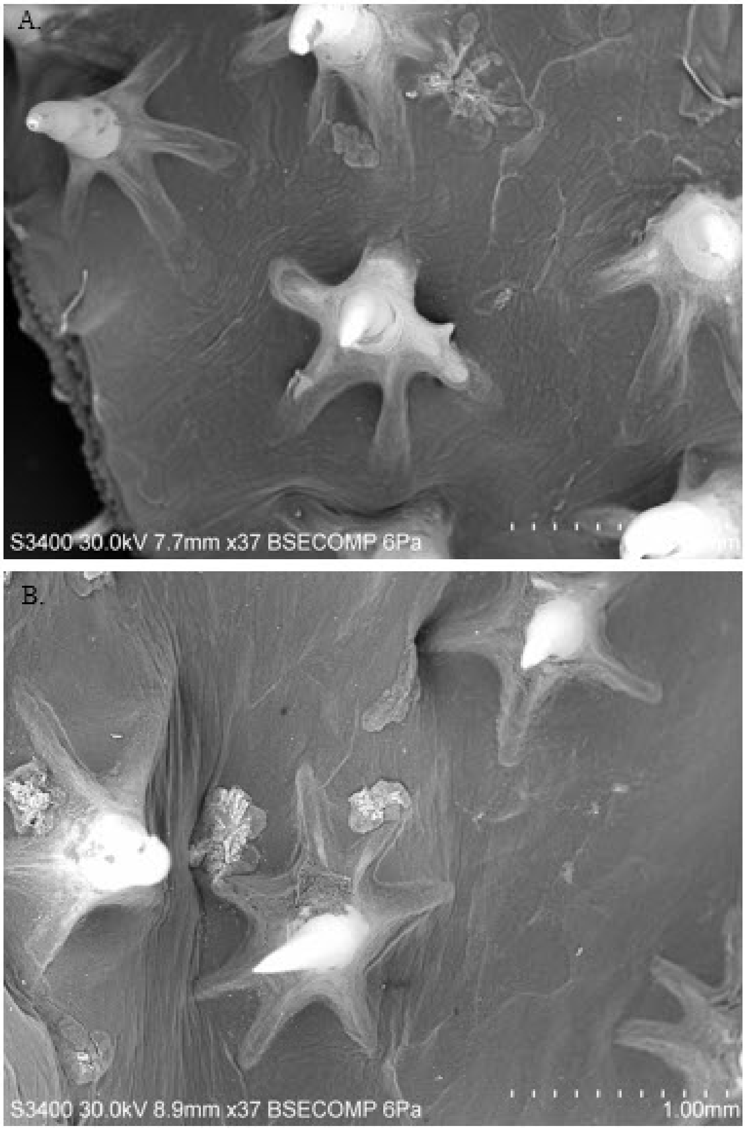

Figure 9. Scanning electron microscope images of the dermal denticles of *Bathyraja aleutica* from A. the first dorsal fin and B. the head region, behind the eyes. Photos by Justin Cordova (MLML).

Length of rostral cartilage 47.2% of cranial length; prefontanelle rostral length 48.4%; cranial width 87.3% least interorbital width 18.3%; length of anterior prefontanelle 11.1%; length of posterior prefontanelle 11.1%; length of rostral appendices 20.6%. Rostral cartilage nearly straight; the two fontanelles are equal in length (Figure 10).

Figure 10. Ventral view X-radiogram of *Bathyraja aleutica*, CAS 243646, immature female. X-radiogram by Jon Fong (CAS).

Size and sexual maturity. Size at maturity for males 113 cm TL; 125 cm TL for females. Males grow to at least 150 cm TL; females grow to about 154 cm TL. Size at birth is 12-15 cm TL (Ebert, 2003; 2005). Maximum size is at least 154 cm TL (Haas, 2011; Haas, Ebert & Cailliet, 2016).

Coloration. Dorsal coloration dark brown to grey, with dark spots on pectoral fins, often darker at the disc margins. One ocellus on either pectoral fin is present in some specimens. Spiracles often pale in coloration. Ventral coloration white, including the claspers, but with dark brown to dark grey coloration on the snout, gills, posterior disc margins, pelvic fins, cloaca, and underside of the tail. Thorns on dorsal surface pale.

Distribution. *Bathyraja aleutica* has been verified as occurring in the North Pacific, specifically from the Bering Sea, south to Cape Mendocino, northern California, and as far west as northern Japan (Ebert, 2003). It occurs at depths of 15-1,602 m (Kyne et al., 2012); the specimens included in this study were all from the shallow portion of the species' depth range (379-730 m).

Etymology. The species was named after the Aleutian Islands, where the holotype was collected.

Common name. Aleutian skate.

Comparisons. *Bathyraja aleutica* is a relatively large skate that can be easily separated from other smaller-bodied skates in its range (e.g., *B. interrupta*, *B. kincaidii*, *B. microtrachys*, and *B. trachura*) based on coloration, thorn counts, and morphological measurements. Of the smaller-bodied skates, only *B. microtrachys* possesses similar dorsal and ventral coloration, but can be differentiated from *B. aleutica* by its lack of middorsal, nuchal, and scapular thorns.

The two species most similar in size to *B. aleutica*, and that possess the same range, are compared. *Bathyraja spinosissima* is the easiest to differentiate, based on its pale coloration on both sides of its disc. *Bathyraja aleutica* possesses thorns in the middorsal, nuchal, and scapular region; *B. spinosissima* lacks thorns in those regions. Moreover, *B. spinosissima* can be identified from to its significantly larger interspiracular width and interorbital width. *Bathyraja spinosissima* possesses an interspiracular width of 9.1-12.2% TL and an interorbital width of 4.9-9.5% TL. *Bathyraja aleutica* possesses widths of 4.3-7.0% TL and 3.3-5.3% TL for the interspiracular and interorbital widths, respectively.

Bathyraja abyssicola shares a similar range to *B. aleutica* and is of similar coloration and size. Thorn count differences exist between the two species, with *B. abyssicola* possessing 0-2 middorsal thorns and *B. aleutica* possessing 4-11 in the same region. *Bathyraja abyssicola* is characterized as having long, thin mature claspers, whereas *B. aleutica* possesses shorter, stubbier claspers. The clasper morphology of *B. abyssicola* can be further used to separate it from *B. aleutica* as it possesses a strong, V-shaped cleft, compared to the weak, U-shaped cleft in *B. aleutica*. The geographic distribution varies somewhat between species, as *B. abyssicola* is found south of Cape Mendocino, which is the southern extent of the range for *B. aleutica*.

Bathyraja interrupta (Gill & Townsend, 1897)

Description. A medium-sized skate with a rhomboidal disc, 1.21-1.34 times as broad as long; anterior margin strongly concave in adult males, convex beside and just forward of eyes; apex rounded; posterior margin slightly convex; free rear tip broadly rounded (Figures 11-12; Table 4). Head length moderate 18.4-21.4% TL, preorbital snout length 10.5-14.6% TL; preoral length 10.5-13.4% TL. Snout tip triangular and rounded; possessing no fleshy process at apex. A flat to moderately concave area between the eyes; interorbital width short 2.5-5.1% TL. Spiracle length 1.9-3.2% TL; oval shaped; interspiracular space short 5.5-6.8% TL; mouth width short 6.7-9.0% TL. Nasal curtain length 2.9-6.6% TL, its posterior margin fringed at the corners; anterior margin of curtain lobe-like. Internarial distance 3.2-7.4% TL. Upper jaw moderately well arched, possessing a symphysis; lower jaw convex. Teeth similar in both jaws; teeth unicuspid, with a strong, bluntly pointed posteriorly directed cusp; arranged in longitudinal rows; upper teeth and lower teeth relatively low in number (22-32 and 23-32, respectively).

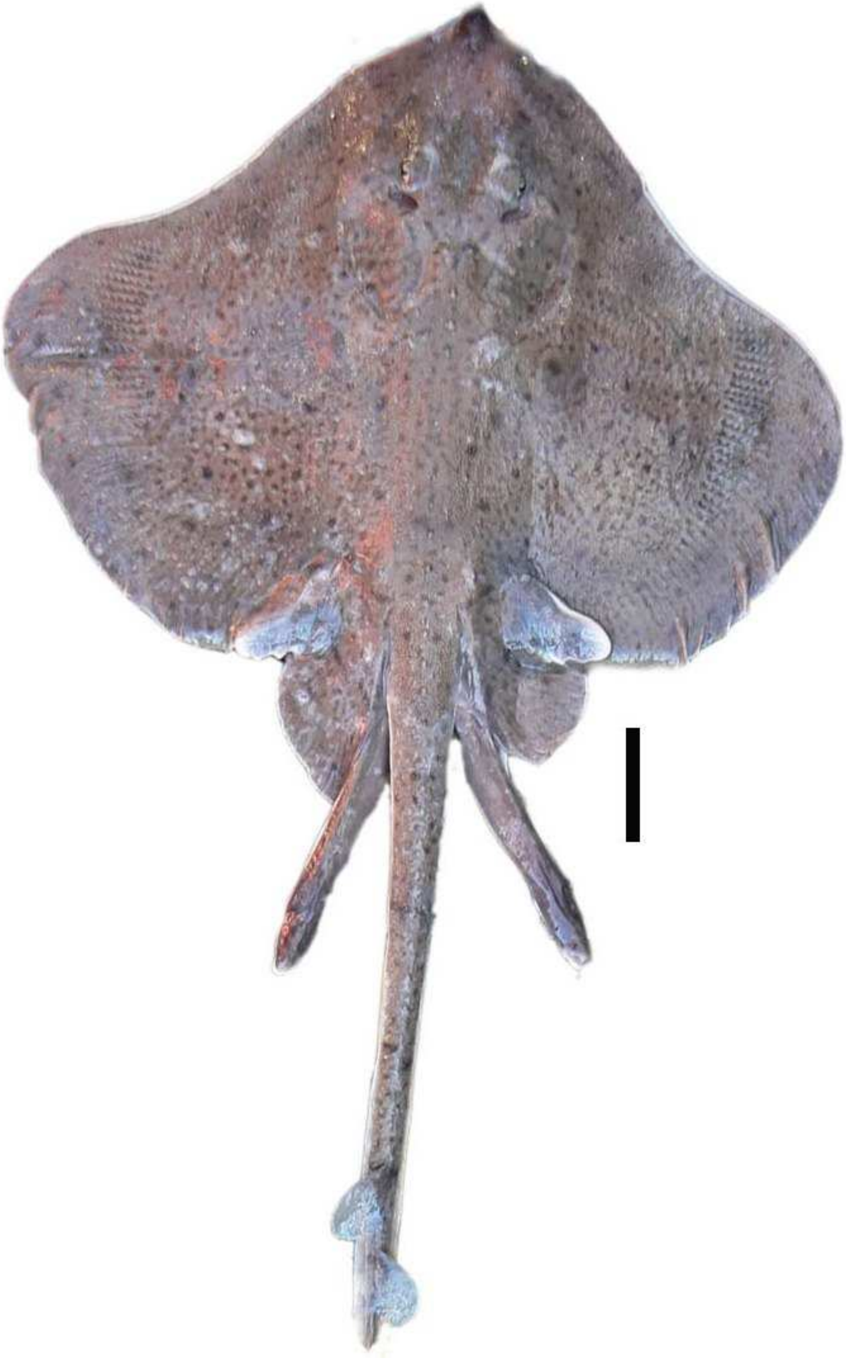

Figure 11. *Bathyraja interrupta*, PSRC BSPP-A 01, 710 mm TL, mature male, dorsal view, fresh. Photo by Diane Haas (MLML). Scale bar = 70 mm.

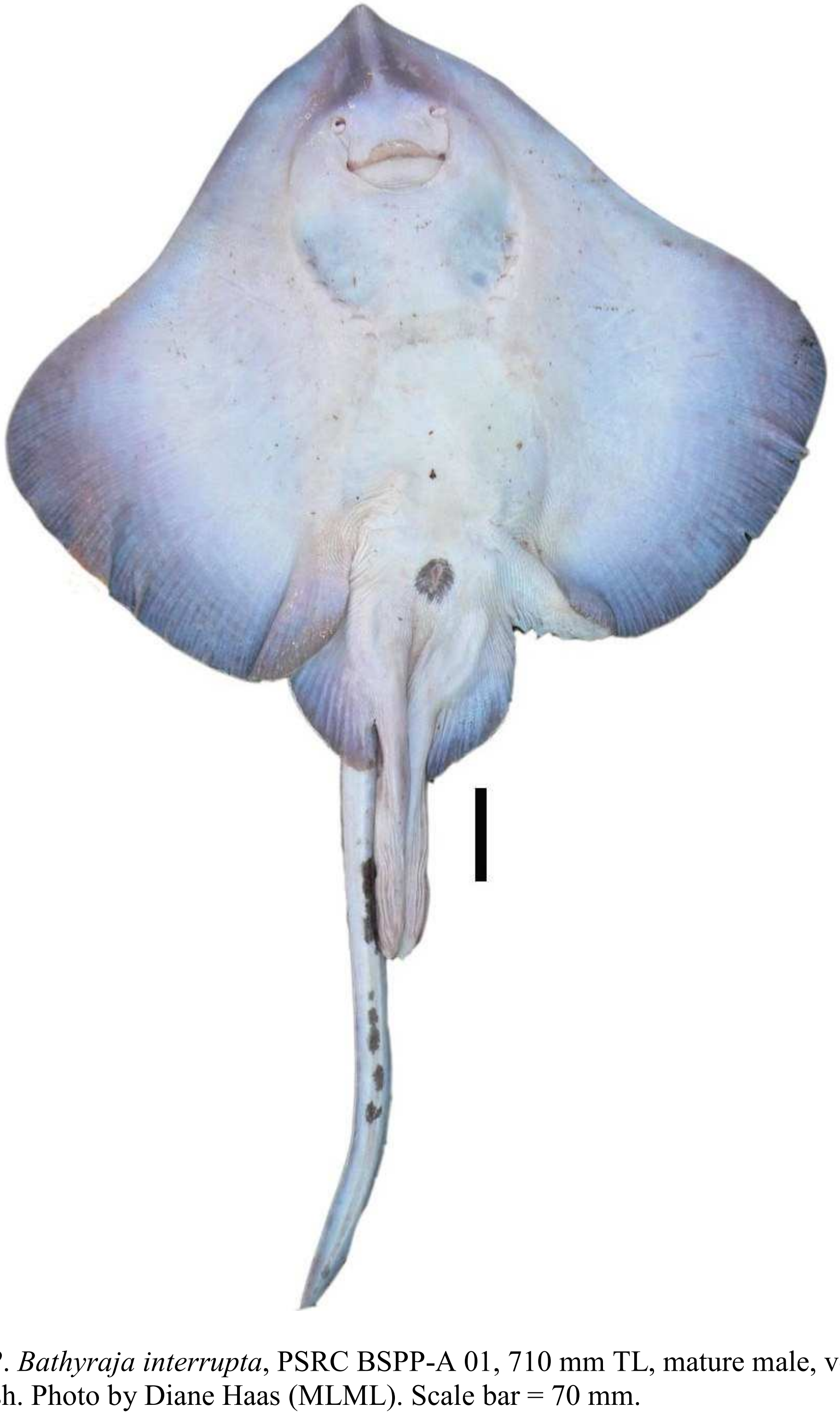

Figure 12. *Bathyraja interrupta*, PSRC BSPP-A 01, 710 mm TL, mature male, ventral view, fresh. Photo by Diane Haas (MLML). Scale bar = 70 mm.

Table 4.

Morphometric and Meristic Data for Bathyraja interrupta (N = 16) Specimens.

Measurements	**% TL**
Total length (mm)	289 - 768
Disc length	47.7 - 54.0
Disc width	61.2 - 67.0
Snout to maximum disc width	28.1 - 33.6
Head length	18.4 - 21.4
Preorbital snout length	10.5 - 14.6
Interorbital width	2.5 - 5.1
Spiracle length	1.9 - 3.2
Interspiracular width	5.5 - 6.8
D1 origin to tail tip	10.1 - 16.0
D1 base length	3.8 - 5.2
D1 vertical height	1.7 - 5.2
D2 base length	3.4 - 4.6
D2 vertical height	2.1 - 2.9
Interdorsal space	0.2 - 1.8
Caudal base length	1.9 - 4.2
Caudal vertical height	0.6 - 1.1
Lateral tail fold length	16.6
Preoral snout length	10.5 - 13.4
Mouth width	6.7 - 9.0
Prenarial snout length	8.5 - 11.8
Internarial width	3.2 - 7.4
Nasal curtain length	2.9 - 6.6
Snout to 1st gill slit	17.7 - 21.4
Pelvic posterior lobe length	10.4 - 23.4
Pelvic anterior lobe length	7.7 - 11.6
Inner anterior lobe length	2.7 - 9.3
Clasper inner length	5.5 - 26.0
Clasper outer length	2.8 - 17.7
Clasper base length	1.0 - 2.8
Precaudal length	44.5 - 51.1
Tail length	39.4 - 60.2
Interdorsal thorn count	0 - 1
Middorsal thorn count	1 - 8

Nuchal thorn count	2 - 5
Orbital thorn count- right side	0
Orbital thorn count- left side	0
Rostral thorn count	0
Scapular thorn count- right side	0 - 2
Scapular thorn count- left side	0 - 2
Tail thorn count	18 - 26
Alar thorn count- rows- right side (males only)	4 - 6
Alar thorn count- rows- left side (males only)	4 - 6
Alar thorn count- columns- right side (males only)	18 - 22
Alar thorn count- columns- left side (males only)	18 - 22
Malar thorn count- rows- right side (males only)	0
Malar thorn count- rows- left side (males only)	0
Malar thorn count- columns- right side (males only)	0
Malar thorn count- columns- left side (males only)	0
Upper teeth- total count	22 - 32
Lower teeth- total count	23 - 32
Vertebral count	133
Rostral cartilage length	46.6
Prefontanelle rostral length	47.2
Cranial width	78.9
Least interorbital width	20.1
Anterior prefontanelle length	19.5
Posterior prefontanelle length	26.5
Rostral appendices length	18.9

Note: Includes the ranges of the measurements. Total length is the actual measurement in millimeters; all other measurements are expressed as a percentage of total length (% TL).

Pelvic fins large overall; anterior lobe 7.7-11.6% TL, posterior lobe significantly longer than all of its congeners 10.4-23.4% TL ($F_{6,104} = 25.46$, $p < 0.0001$ (see Statistical Results section for further detail)) and similar between sexes and maturities, inner margin deeply incised. Tail length 39.4-60.2% TL, relatively short and stout; wider at base, tapering to the first dorsal fin origin, not expanded in the middle. Precaudal length significantly shorter than all of its conspecifics 44.5-51.1% TL ($F_{6,104} = 86.70$, $p < 0.0001$

(see Statistical Results section for further detail)). Dorsal fins moderate in size and shape, the first dorsal fin displays a wider range than second dorsal fin, 1.7-5.2% TL and 2.1-2.9% TL, respectively; bases of both dorsal fins similar in size and length, 3.8-5.2% TL and 3.4-4.6% TL, respectively; anterior margins of both fins concave, apices rounded; free rear tip rounded; interdorsal space relatively short 0.2-1.8% TL, with larger individuals having a shorter interdorsal space, rear tip of first dorsal fin not overlapping base of second dorsal fin. Caudal fin height 0.6-1.1% TL; its dorsal margin weakly concave; not connected to second dorsal fin by a small membranous ridge.

Dorsal surface covered in uniform, small, sandpaper-like prickles. Scapular, middorsal, nuchal, interdorsal, and tail thorns present, males with a well-developed set of alar thorns; malar thorns absent; thorns vary slightly in size, from short to well developed. Middorsal thorns range from low to high in number (1-8); nuchal thorns well developed and average in number (2-5); tail thorns moderate in number (18-26); scapular thorns absent in some specimens and present in others (0-2); interdorsal thorns weakly developed (0-1); tail thorns present (18-26). Thorns in a single, non-continuous row; no multiple rows of thorns on body. Alar thorn patches range between 4-6 rows and 8-22 columns on both pectoral fins.

Mature claspers relatively long and robust, base length 1.8-2.8% TL, inner length 25.5-26.0% TL, tip of clasper rounded and not bulbous (Figure 13). Clasper inner length 46.5-47.0% of tail length; pseudosiphon is absent; inner surface of dorsal lobe with a relatively weak, but long pseudorhipidion and a U-shaped cleft; inner surface of ventral lobe possesses a rounded projection that conspicuously protrudes from the tip of the clasper; a very large sentina; sentinel present; clasper relatively robust overall.

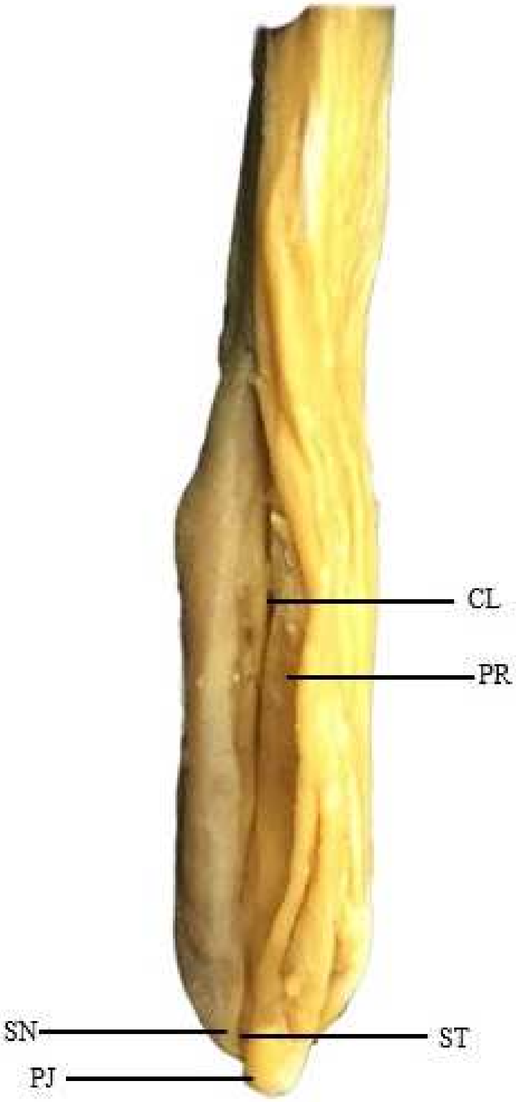

Figure 13. Components of the clasper for *Bathyraja interrupta*. CL- cleft, PJ- projection, PR- pseudorhipidion, SN- sentina, ST- sentinel. Photo by J.D.S. Knuckey.

Clasper skeleton consists of 3 dorsal terminal, 1 accessory terminal, ventral terminal and axial cartilages; dorsal terminal 1 shaped like a long, rounded leaf, and possessing a long shaft; unlike most bathyrajids in the ENP the dorsal terminal 1 does not form an external pseudosiphon; the tip of the dorsal marginal is pointed, and forms a long, thin pseudorhipidion externally; ventral terminal curved, possessing a blunt tip that forms the exposed projection; accessory terminal 1 nearly as long as the ventral terminal; tip of accessory terminal 1 is rounded; very large sentina located above the projection; sentinel present next to the sentina.

Dermal denticles possess 3-5 base points and are moderately developed on the posterior third of the dorsal surface; denticles on the first dorsal fin not curved, posterior-oriented, found in low densities across surface (Figure 14).

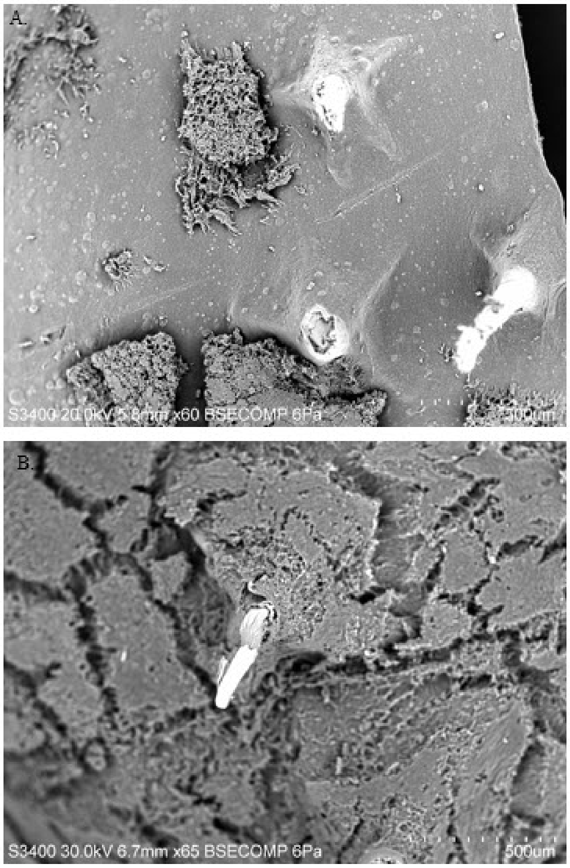

Figure 14. Scanning electron microscope images of the dermal denticles of *Bathyraja interrupta* from A. the first dorsal fin and B. the head region, behind the eyes. Photos by Justin Cordova (MLML).

Length of rostral cartilage 46.6% of cranial length; prefontanelle rostral length 47.2%; cranial width 78.9%; least interorbital width 20.1%; length of anterior prefontanelle 19.5%; length of posterior prefontanelle 26.5%; length of rostral appendices 18.9%. Rostral cartilage nearly straight; fontanelles rectangular in shape; the posterior fontanelle larger (Figure 15).

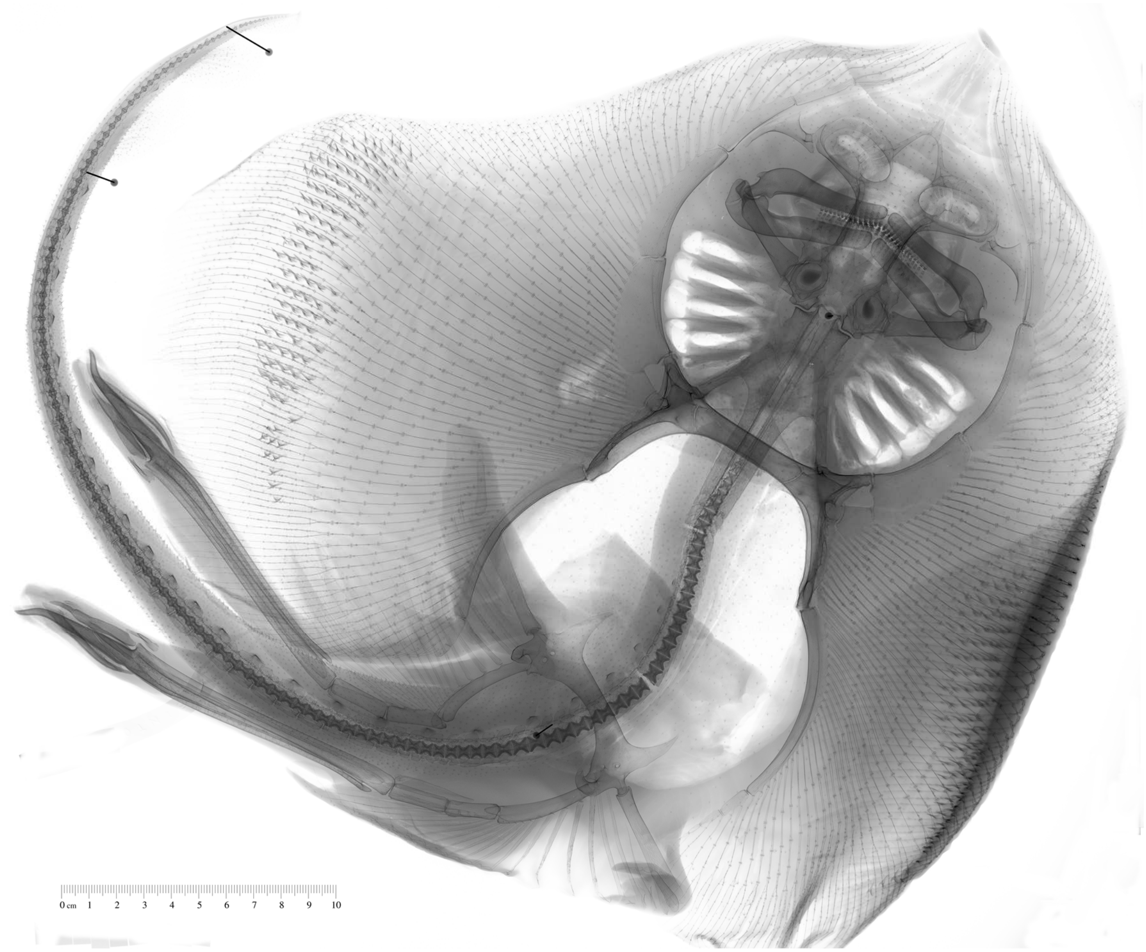

Figure 15. Ventral view X-radiogram of *Bathyraja interrupta*, CAS 243647, mature male. X-radiogram by Jon Fong (CAS).

Size and sexual maturity. Size at maturity for males is 69-70 cm TL and 71-72 cm TL for females, with a maximum size of at least 89 cm TL (Ainsley, 2009; Ainsley, Ebert, Natanson & Cailliet, 2014).

Coloration. Dorsal coloration dark brown to brown grey, with numerous small dark spots on body. Snout and edges of usually darker than the rest of the body. Ventral coloration white, usually with small to large dark brown blotches on underside of tail. After preservation the dark spots on dorsal surface tend to disappear.

Distribution. *Bathyraja interrupta* has been verified as occurring in the eastern North Pacific, specifically from the Bering Sea, Alaska south to British Columbia, Canada (Kyne et al., 2012). This species is most common on the continental shelf-slope break at around 200-500 m, but is possibly found down to 1,372 m (Bizzarro et al. 2014; Mecklenburg, Mecklenburg & Thorsteinson, 2002).

Etymology. The species name comes from the interrupted row of thorns down the middorsal and tail.

Common name. Bering skate.

Comparisons. *Bathyraja interrupta* is a medium-bodied skate that can be separated relatively easily from its congeners based on coloration, size, thorn counts, and distribution. *Bathyraja abyssicola, B. aleutica*, *B. spinosissima*, and *B. trachura* all display markedly different colorations. *Bathyraja microtrachys* has a geographic range that is much further south and does not possess middorsal, nuchal, and scapular thorns, whereas *B. interrupta* does.

Bathyraja interrupta is very closely related to *B. kincaidii*, which is a smaller-bodied species found in a more southern geographic range than *B. interrupta*. The two species may form a larger species complex that ranges from northern Mexico to the Bering Sea.

Bathyraja interrupta differs from its congener in that it possesses a shorter interdorsal space than *B. kincaidii* (0.2-1.8% TL and 0.6-3.3% TL, respectively). The pelvic fins are a useful separator of the two species, as *B. interrupta* has a much larger posterior lobe length (10.4-23.4% TL) and inner anterior pelvic lobe length (2.7-9.3% TL) than *B. kincaidii* does (8.1-14.9% TL and 5.5-8.5% TL, respectively). The mature claspers of both species differ, as *B. interrupta* has more robust, stockier claspers than *B. kincaidii*. Furthermore, *B. interrupta* has a pointed projection that conspicuously protrudes out past the tip of the clasper, whereas *B. kincaidii* has a rounded projection that does not protrude past the tip. The cleft of *B. interrupta* is V-shaped and the cleft is U-shaped and curved in *B. kincaidii*. The sentina on the mature clasper is very large in *B. interrupta*, but average in *B. kincaidii*.

***Bathyraja kincaidii* (Garman, 1908)**

Description. A small skate with a rhomboidal disc, 1.24-2.11 times as broad as long; anterior margin strongly concave in adult males, convex beside and just forward of eyes; apex rounded; posterior margin slightly convex; free rear tip broadly rounded (Figures 16-17; Table 5). Disc length and width are smaller than all of its congeners 29.0-54.1% TL and 61.2-67.3% TL, respectively. Head length relatively short 15.9-21.3% TL, preorbital snout length short 9.9-14.0% TL; preoral length 9.0-14.3% TL. Snout tip triangular and rounded; possessing no fleshy process at apex. Eye length moderate 2.3-5.6% TL; a flat to moderately concave area between the eyes; interorbital width short 3.6-5.3% TL. Spiracles average 1.9-3.6% TL; oval shaped; interspiracular space short 5.4-6.8% TL; mouth width short 5.9-8.2% TL. Nasal curtain length average 2.4-3.9% TL, width average 6.2-8.9% TL, its posterior margin fringed at the corners; anterior margin of curtain lobe-like. Internarial distance significantly shorter than all of its congeners 5.2-6.7% TL ($F_{6,104} = 21.86$, $p < 0.0001$ (see Statistical Results section for further detail)); first gill slit length 1.5-2.7% TL; fifth gill slit length 1.1-2.4% TL; distance between first gill slits short 11.6-16.4% TL, and distance between fifth gill slits short 8.0-10.7% TL. Upper jaw moderately well arched, possessing a symphysis; lower jaw convex. Teeth similar in both jaws; teeth unicuspid, with a strong, bluntly pointed posteriorly directed cusp; arranged in longitudinal rows; upper teeth and lower teeth relatively low in number (22-31 and 18-31, respectively).

Figure 16. Bathyraja kincaidii, PSRC Bkin 020612-1, 575 mm TL, mature male, dorsal view, fresh. Photo by J.D.S. Knuckey. Scale bar = 55 mm.

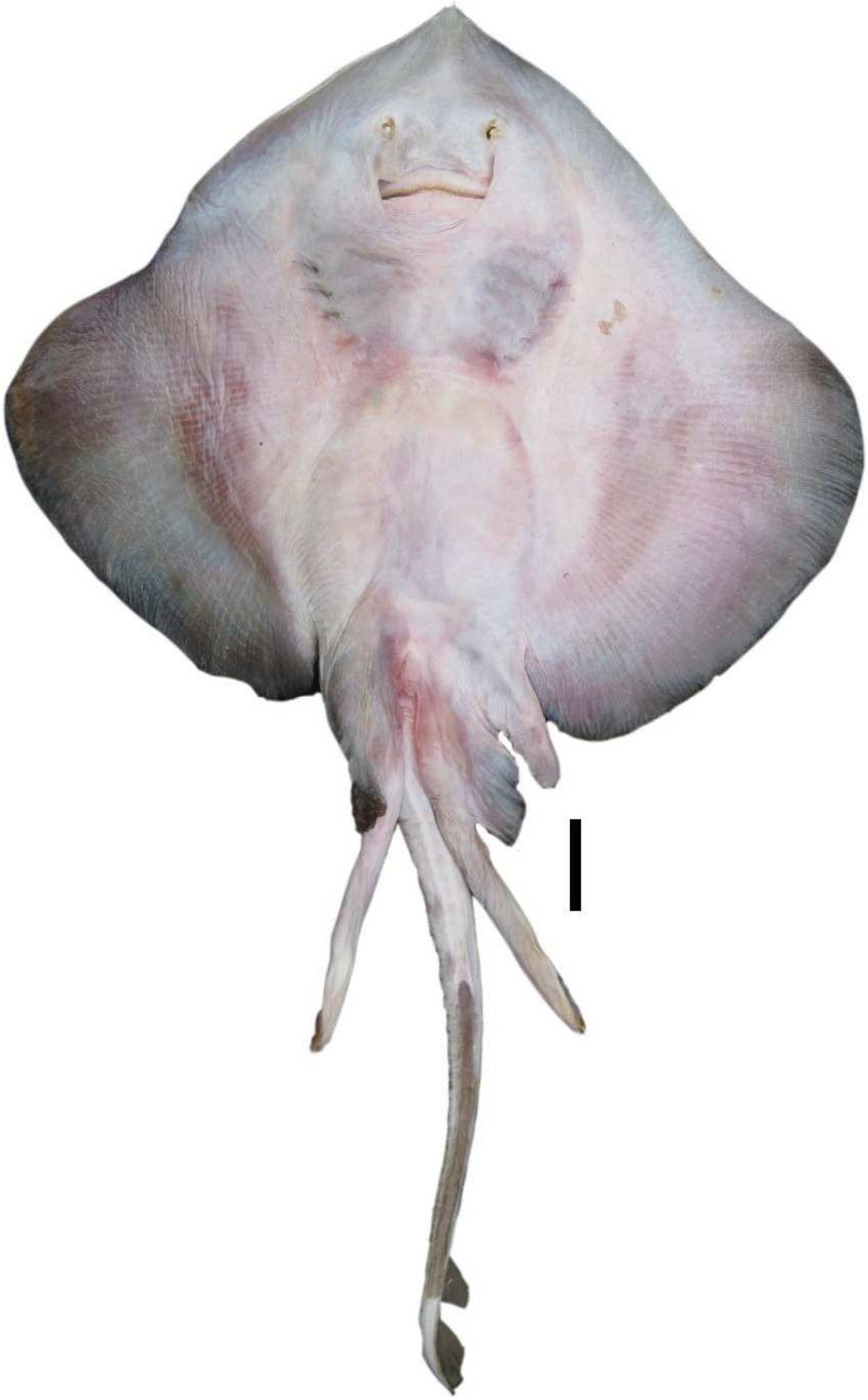

Figure 17. Bathyraja kincaidii, PSRC Bkin 020612-1, 575 mm TL, mature male, ventral view, fresh. Photo by J.D.S. Knuckey. Scale bar = 55 mm.

Table 5.

Morphometric and Meristic Data for Bathyraja kincaidii (N = 39) Specimens.

Measurements	**% TL**
Total length (mm)	210 - 616
Disc length	29.0 - 54.1
Disc width	61.2 - 67.3
Anterior disc length	36.1 - 54.1
Anterior anterior disc length (males only)	22.4 - 29.0
Anterior posterior disc length (males only)	11.7 - 21.3
Posterior disc length	27.7 - 35.6
Inner disc length	6.4 - 11.0
Disc base length	10.1 - 15.9
Snout to maximum disc width	25.4 - 33.9
Head length	15.9 - 21.3
Preorbital snout length	9.9 - 14.0
Eye length	2.3 - 5.6
Interorbital width	3.6 - 5.3
Spiracle length	1.9 - 3.6
Interspiracular width	5.4 - 6.8
D1 origin to tail tip	9.9 - 14.5
D1 base length	2.9 - 4.9
D1 vertical height	2.0 - 4.0
D2 base length	2.3 - 5.3
D2 vertical height	1.4 - 2.9
Interdorsal space	0.6 - 3.3
Caudal base length	1.7 - 4.8
Caudal vertical height	0.6 - 1.9
Lateral tail fold length	6.2 - 9.7
Preoral snout length	9.0 - 14.3
Mouth width	5.9 - 8.2
Prenarial snout length	7.6 - 11.8
Internarial width	5.2 - 6.7
Nasal curtain length	2.4 - 3.9
Nasal curtain width	6.2 - 8.9
Snout to 1st gill slit	17. 2 - 21.0
Snout to 5th gill slit	24.0 - 29.3
1st gill slit length	1.5 - 2.7

2nd gill slit length	1.7 - 2.7
3rd gill slit length	1.5 - 2.7
4th gill slit length	1.5 - 2.6
5th gill slit length	1.1 - 2.4
Space between the 1st gill slits	11.6 - 16.4
Space between the 5th gill slits	8.0 - 10.7
Pelvic length	13.1 - 18.4
Pelvic posterior lobe length	8.1 - 14.9
Pelvic anterior lobe length	7.9 - 11.8
Inner anterior lobe length	5.5 - 8.5
Clasper inner length	3.8 - 27.5
Clasper outer length	1.9 - 18.0
Clasper base length	0.7 - 2.8
Precaudal length	92.0 - 98.1
Tail length	37.1 - 62.3
Interdorsal thorn count	0 - 2
Middorsal thorn count	0 - 9
Nuchal thorn count	3 - 7
Orbital thorn count- right side	0
Orbital thorn count- left side	0
Rostral thorn count	0
Scapular thorn count- right side	0 - 2
Scapular thorn count- left side	0 - 2
Tail thorn count	14 - 22
Alar thorn count- rows- right side (males only)	2 - 4
Alar thorn count- rows- left side (males only)	2 - 4
Alar thorn count- columns- right side (males only)	8 - 20
Alar thorn count- columns- left side (males only)	14 - 22
Malar thorn count- rows- right side (males only)	0
Malar thorn count- rows- left side (males only)	0
Malar thorn count- columns- right side (males only)	0
Malar thorn count- columns- left side (males only)	0
Upper teeth- total count	22 - 31
Lower teeth- total count	18 - 31
Spiral valve count	5 - 9
Pectoral fin radial count	69 - 72
Pelvic fin radial count	17 - 19
Vertebral count	132

Rostral cartilage length	45.8
Prefontanelle rostral length	45.8
Cranial width	78.3
Least interorbital width	18.1
Anterior prefontanelle length	20.5
Posterior prefontanelle length	25.3
Rostral appendices length	18.1

Note: Includes the ranges of the measurements. Total length is the actual measurement in millimeters; all other measurements are expressed as a percentage of total length (% TL).

Pelvic fins small, posterior lobe 8.1-14.9% TL, anterior lobe 7.9-11.8% TL, and inner margin deeply incised 5.5-8.5%. Tail moderate 37.1-62.3% TL, relatively stout; wider at base, tapering to the first dorsal fin origin, not expanded in the middle. Lateral tail fold short 6.2-9.7% TL, similar in both sexes; not obviously broader at any point along its length. Dorsal fins relatively moderate in size and shape, the first dorsal fin taller than second dorsal fin, 2.0-4.0% TL and 1.4-2.9% TL, respectively; bases of both dorsal fins similar in size and length, 2.9-4.9% TL and 2.3-5.3% TL, respectively; anterior margins of both fins concave, apices rounded; free rear tip rounded; interdorsal space average 0.6-3.3% TL, with larger individuals having a shorter interdorsal space, rear tip of first dorsal fin not overlapping base of second dorsal fin. Caudal fin large, low, height 0.6-1.9% TL; its dorsal margin weakly concave; not connected to second dorsal fin by a small membranous ridge. Tail relatively short 37.1-62.3% TL.

Dorsal surface covered in uniform, small, sandpaper-like prickles. Scapular, middorsal, nuchal, interdorsal, and tail thorns present, males with a well-developed set of alar thorns; malar thorns absent; thorns vary slightly in size, from short to well developed. Middorsal thorns range from absent to high in number (0-9); nuchal thorns well developed and high in numbers (3-7); tail thorns few in number (14-22); scapular thorns absent in some specimens and present in others (0-2); interdorsal thorns weakly developed (0-2). Thorns in a single, continuous row; no multiple rows of thorns on body. Alar thorn patches range between 1-4 rows and 8-22 columns on both pectoral fins. Tail thorn count is significantly lower than all of its congeners ($F_{6,104} = 24.02$, $p < 0.0001$ (see Statistical Results section for further detail)).

Mature claspers relatively long and thin, base length 1.3-1.9% TL, inner length 20.6-27.5% TL, tip of clasper rounded and not bulbous (Figure 18). Clasper inner length 28.2-58.0% of tail length; pseudosiphon is absent; inner surface of dorsal lobe with an average pseudorhipidion that does not conspicuously project out from the tip of the clasper; V-shaped cleft; inner surface of ventral lobe possesses a projection and an average sentina; projection is pointed; clasper thin overall.

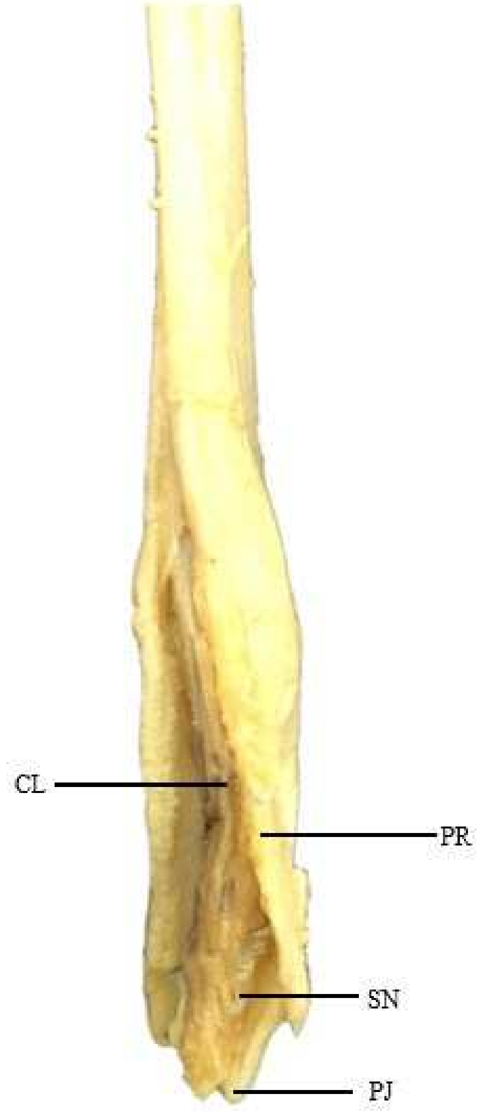

Figure 18. Components of the clasper for *Bathyraja kincaidii*. CL- cleft, PJ- projection, PR- pseudorhipidion, SN- sentina. Photo by J.D.S. Knuckey.

Clasper skeleton consists of 3 dorsal terminal, 1 accessory terminal, ventral terminal and axial cartilages; dorsal terminal 1 shaped like a long, narrow leaf, and possessing a long shaft; unlike most congeners the dorsal terminal 1 does not form a pseudosiphon externally; the tip of the dorsal marginal is pointed, and forms a long, thin pseudorhipidion externally; ventral terminal curved, possessing a blunt tip that forms the projection externally; accessory terminal 1 nearly as long as the ventral terminal; tip of accessory terminal 1 is pointed; average-sized sentina located above the projection; sentinel present, but fairly small.

Dermal denticles possess 4-5 points on the base of the denticle; moderately developed on posterior third of the dorsal surface; denticles on the first dorsal strongly curved posteriorly and relatively narrow; denticles on head stouter (Figure 19).

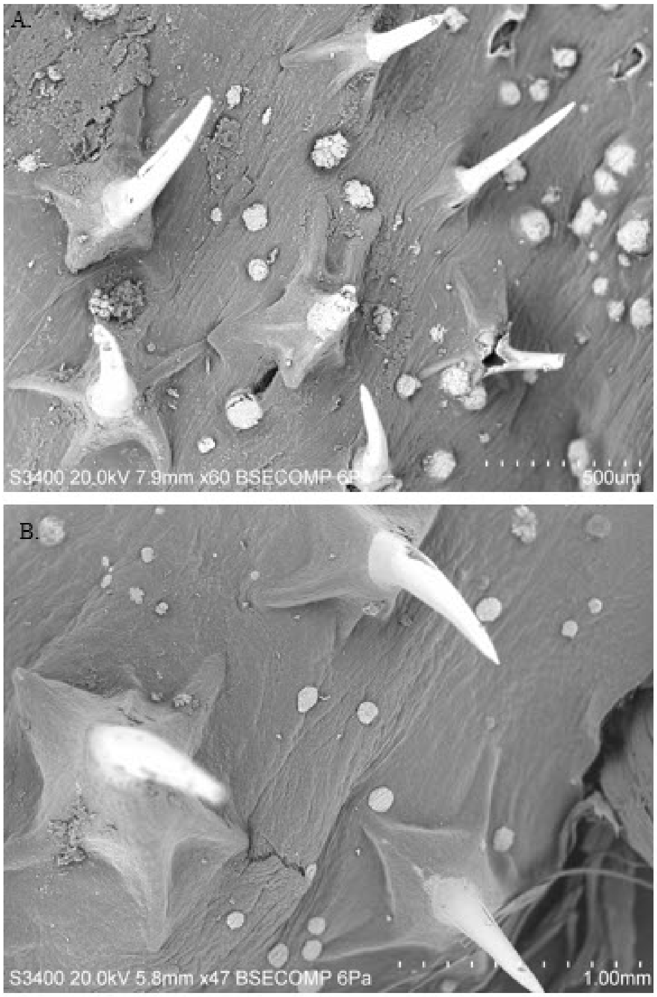

Figure 19. Scanning electron microscope images of the dermal denticles of *Bathyraja kincaidii* from A. the first dorsal fin and B. the head region, behind the eyes. Photos by Justin Cordova (MLML).

Length of rostral cartilage 45.8% of cranial length; prefontanelle rostral length 45.8%; cranial width 78.3%; least interorbital width 18.1%; length of anterior prefontanelle 20.5%; length of posterior prefontanelle 25.3%; length of rostral appendices 18.1%. Rostral cartilage nearly straight; anterior fontanelle spade-shaped; posterior fontanelle gourd-shaped; the posterior fontanelle larger (Figure 20).

Figure 20. Ventral view X-radiogram of *Bathyraja kincaidii*, CAS 243648, immature female. X-radiogram by Jon Fong (CAS).

Size and sexual maturity. Size at maturity for males 48 cm TL; 46-50 cm TL for females. Males grow to 62 cm TL; females grow to 58 cm TL. Size at birth is 12-16 cm TL (Ebert, 2003). Maximum size is at least 62 cm TL (Perez, 2005; Perez, Cailliet & Ebert, 2011).

Coloration. Dorsal coloration mottled dark brown to brown-grey, with numerous small dark spots on body. Snout semi-translucent; snout and edges of fins sometimes purple. Ventral coloration white, usually with small to large dark brown blotches on underside of tail; edges of fins sometimes purple. After freezing the dark spots on dorsal surface turn pale.

Distribution. *Bathyraja kincaidii* has been verified as occurring in the eastern North Pacific, specifically from British Columbia, Canada, south to Baja California, Mexico (Ebert, 2003). Its range may extend up to Alaska, but confusion with *B. interrupta* means that the northern extent of its range cannot be verified. It is reported to occur most commonly on the continental shelf-slope break at around 200-500 m, but is possibly found down to 1,372 m at the southern end of its range (Kyne et al., 2012); however this study shows an increased depth range of 119-1050.4 m. Most specimens occurred in the shallow portion of the species range, as there were only three specimens collected at 1050.4 m; the rest were captured at 119-458.3 m.

Etymology. The species was named in honor of Dr. Trevor Kincaid, University of Washington. Dr. Kincaid collected the holotype specimen.

Common name. Sandpaper skate.

Comparisons. *Bathyraja kincaidii* is easily distinguished from most softnose skate species in the ENP. *Bathyraja abyssicola, B. aleutica*, and *B. spinosissima* all possess large disc lengths and widths, in addition to obvious color differences. *Bathyraja microtrachys*, which is similar in size and coloration, lacks middorsal, nuchal, and scapular thorns. *Bathyraja trachura* is a darkly colored species that has much larger dermal denticles on the dorsal surface and a short to absent interdorsal space (0.0-2.8% TL), compared to the long space between the fins in *B. kincaidii* (0.6-3.3% TL).

Bathyraja interrupta is very closely related to *B. kincaidii* and is compared in detail to describe characters that are useful for identification. Besides the morphological traits listed in the prior comparison for *B. interrupta*, dermal denticles can be used to separate the two species, as *B. interrupta* has three points on the denticle base and the denticles are posteriorly oriented, with little to no curve along the length. *Bathyraja kincaidii* possesses four to five points with strongly curved denticles, especially for those on the head region. Some of the best indicators for species identification of softnose skates are the thorn counts. *Bathyraja kincaidii* has a higher middorsal and nuchal thorn count than *B. interrupta* (0-9 and 3-7 for *B. kincaidii*, respectively and 1-8 and 2-5 for *B. interrupta,* respectively). *Bathyraja kincaidii* possesses a single, uninterrupted row of thorns down the midline of the dorsal surface. *Bathyraja interrupta* has an interrupted row of thorns with a noticeable gap between the middorsal and tail thorns.

Bathyraja microtrachys (Osburn & Nichols, 1916)

Description. A moderately-sized skate with a rhomboidal disc, 1.15-1.38 times as broad as long; anterior margin strongly concave in adult males, convex beside and just forward of eyes; apex broadly rounded; posterior margin slightly convex; free rear tip broadly rounded (Figures 21-24; Table 6). Head length moderate 18.3-21.2% TL, preorbital snout length 9.8-14.3% TL; preoral length 9.9-13.7% TL. Snout tip triangular, flabby, and pointed; possessing no fleshy process at apex. Eye length moderate 2.9-5.5% TL. Spiracles small 0.8-3.0% TL; oval shaped. Nasal curtain length average 2.0-4.09% TL, its posterior margin not fringed at the corners; anterior margin of curtain lobe-like. Internarial distance relatively large 7.3-8.67% TL; first gill slit length moderate 0.6-2.4% TL; fifth gill slit length relatively large 0.6-2.4% TL. Upper jaw moderately well arched, possessing a symphysis; lower jaw convex. Teeth similar in both jaws; teeth unicuspid, with a strong, bluntly pointed posteriorly directed cusp; arranged in longitudinal rows; upper and lower teeth low in number (23-30 and 11-22, respectively).

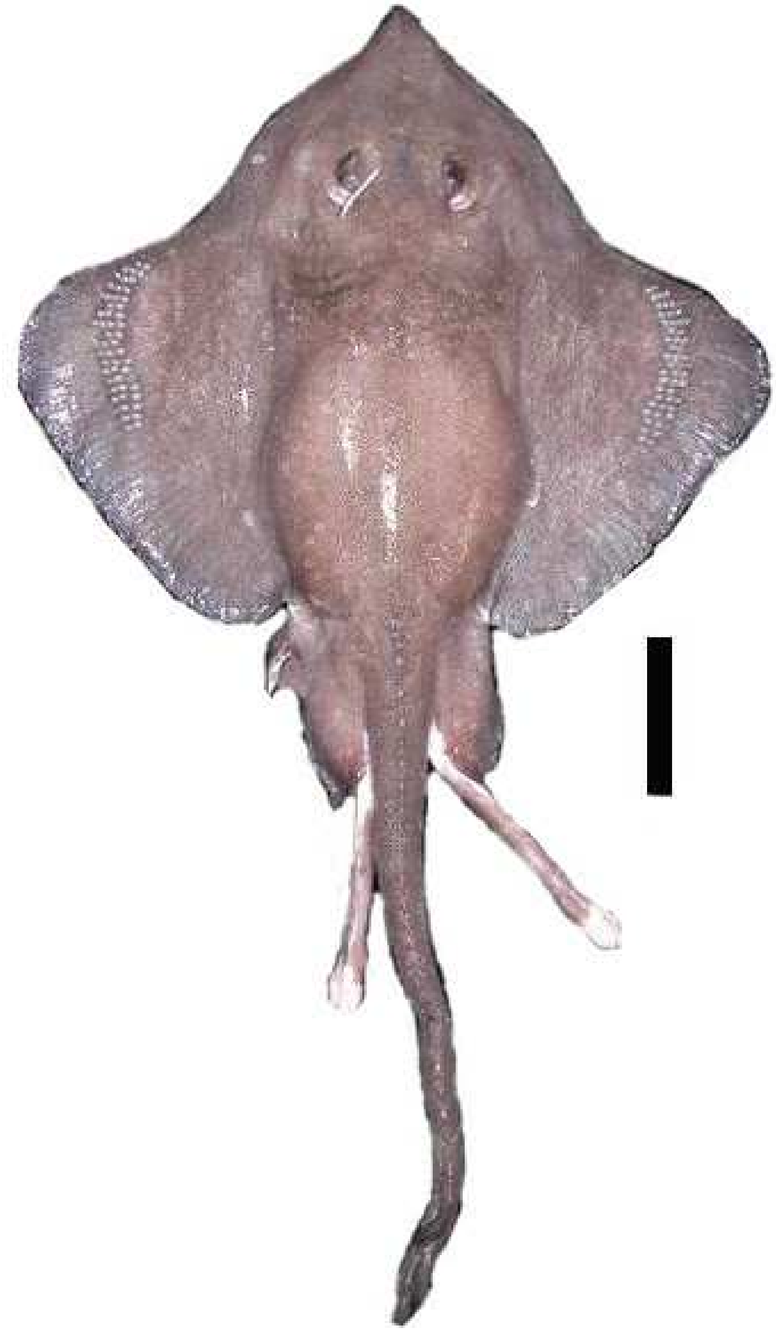

Figure 21. *Bathyraja microtrachys*, mature male, dorsal view, fresh. Photo by D.A. Ebert. Scale bar = 70 mm.

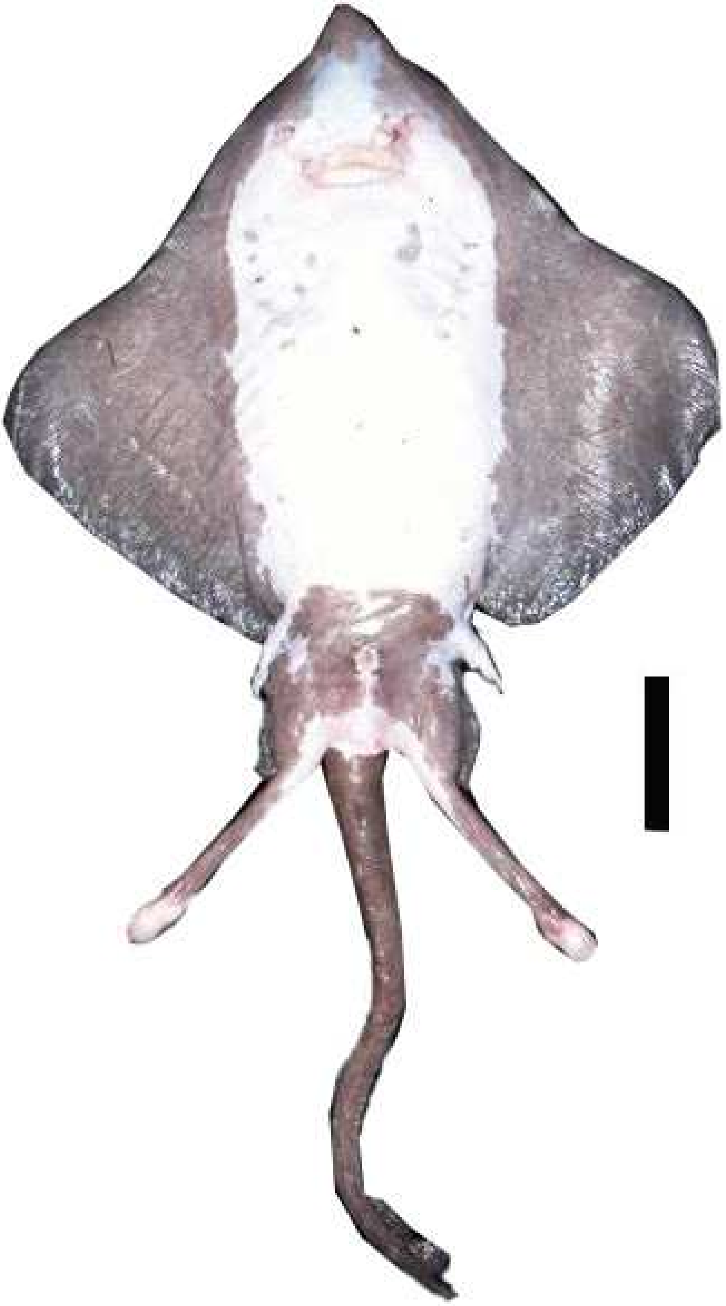

Figure 22. *Bathyraja microtrachys*, mature male, ventral view, fresh. Photo by D.A. Ebert. Scale bar = 70 mm.

Figure 23. Bathyraja microtrachys, holotype, USNM 5198, 737 mm TL, mature female, dorsal view, preserved. Photo by D.A. Ebert. Scale bar = 95 mm.

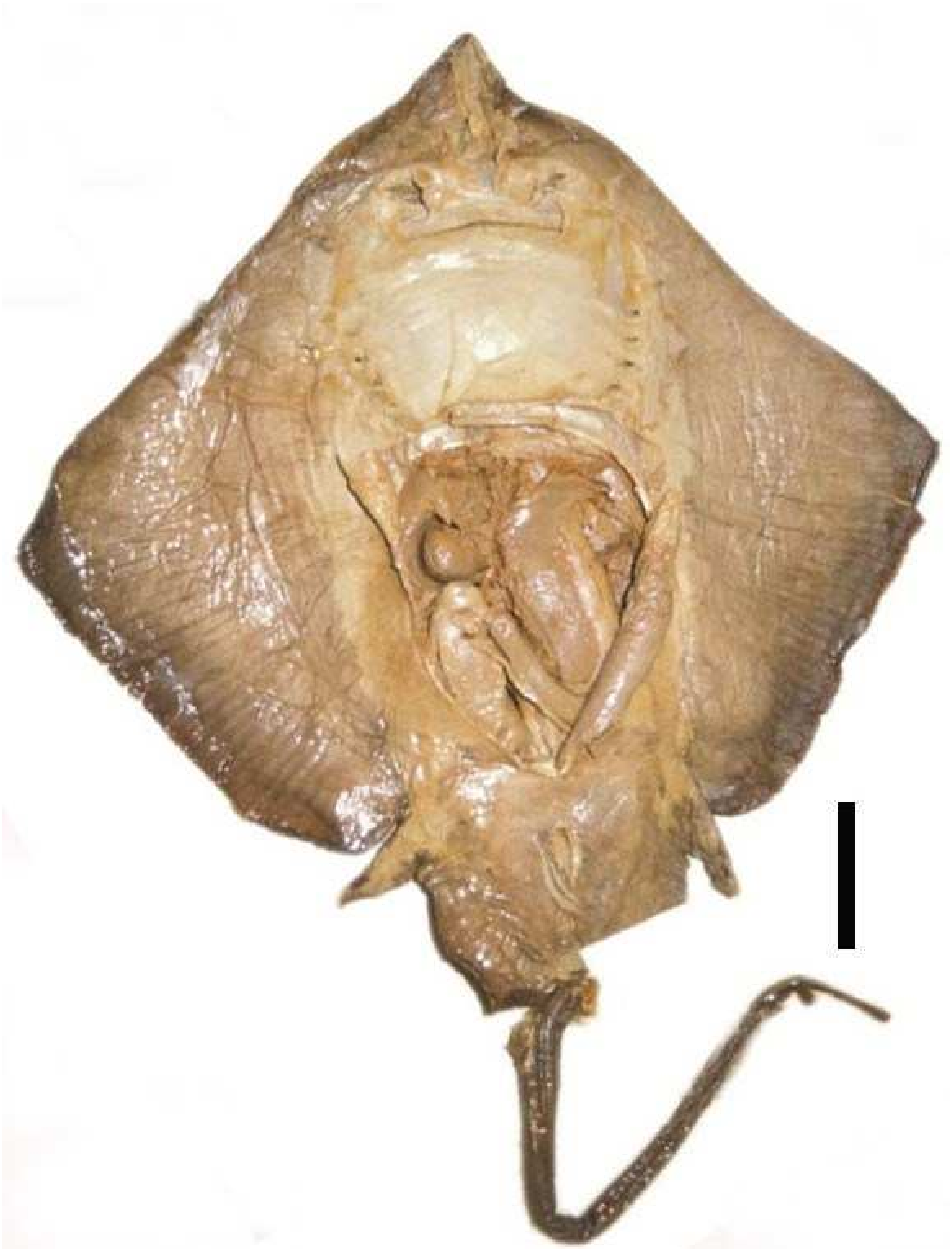

Figure 24. *Bathyraja microtrachys*, holotype, USNM 5198, 737 mm TL, mature female, ventral view, preserved. Photo by D.A. Ebert. Scale bar = 95 mm.

Table 6.

Morphometric and Meristic Data for Bathyraja microtrachys (N = 7) Specimens.

Measurements	**% TL**
Total length (mm)	164 - 754
Disc length	41.5 - 51.1
Disc width	56.4 - 61.5
Anterior disc length	40.2 - 50.2
Posterior disc length	23.2 - 38.8
Inner disc length	4.9 - 5.7
Disc base length	10.4 - 18.8
Snout to maximum disc width	25.9 - 34.7
Head length	18.3 - 21.2
Preorbital snout length	9.8 - 14.3
Eye length	2.9 - 5.5
Interorbital width	3.5 - 8.1
Spiracle length	0.8 - 3.0
Interspiracular width	6.0 - 7.3
D1 origin to tail tip	11.6 - 19.5
D1 base length	2.9 - 5.6
D1 vertical height	1.4 - 2.5
D2 base length	2.7 - 5.2
D2 vertical height	1.6 - 2.8
Interdorsal space	0.0 - 2.4
Caudal base length	2.1 - 6.7
Caudal vertical height	0.3 - 1.1
Lateral tail fold length	18.9 - 46.0
Preoral snout length	9.9 - 13.7
Mouth width	6.3 - 8.2
Prenarial snout length	8.8 - 11.0
Internarial width	7.3 - 8.6
Nasal curtain length	2.0 - 4.0
Nasal curtain width	7.9 - 8.9
Snout to 1st gill slit	15.9 - 20.9
Snout to 5th gill slit	23.8 - 36.7
1st gill slit length	0.6 - 2.4
2nd gill slit length	0.6 - 1.6
3rd gill slit length	0.6 - 1.6

4th gill slit length	0.6 - 1.6
5th gill slit length	0.6 - 2.4
Space between the 1st gill slits	15.9 - 16.5
Space between the 5th gill slits	9.8 - 11.9
Pelvic length	11.6 - 22.7
Pelvic posterior lobe length	7.2 - 15.3
Pelvic anterior lobe length	7.0 - 11.0
Inner anterior lobe length	2.3 - 7.3
Clasper inner length	5.5 - 21.9
Clasper outer length	2.4 - 18.1
Clasper base length	1.2 - 2.6
Precaudal length	48.0 - 101.8
Tail length	45.5 - 67.7
Interdorsal thorn count	0 - 1
Middorsal thorn count	0
Nuchal thorn count	0
Orbital thorn count- right side	0
Orbital thorn count- left side	0
Rostral thorn count	0
Scapular thorn count- right side	0
Scapular thorn count- left side	0
Tail thorn count	19 - 26
Alar thorn count- rows- right side (males only)	3 - 5
Alar thorn count- rows- left side (males only)	3 - 5
Alar thorn count- columns- right side (males only)	19 - 24
Alar thorn count- columns- left side (males only)	19 - 24
Malar thorn count- rows- right side (males only)	0
Malar thorn count- rows- left side (males only)	0
Malar thorn count- columns- right side (males only)	0
Malar thorn count- columns- left side (males only)	0
Upper teeth- total count	23 - 30
Lower teeth- total count	11 - 22
Spiral valve count	6 - 9
Pectoral fin radial count	61 - 74
Pelvic fin radial count	14
Vertebral count	130
Rostral cartilage length	32.8
Prefontanelle rostral length	41.4

Cranial width	87.5
Least interorbital width	24.2
Anterior prefontanelle length	16.4
Posterior prefontanelle length	18.8
Rostral appendices length	14.1

Note: Includes the ranges of the measurements. Total length is the actual measurement in millimeters; all other measurements are expressed as a percentage of total length (% TL).

Pelvic fins small overall; anterior lobe short 4.8-9.7% TL, posterior lobe 7.2-15.3% TL, and inner margin short 2.3-7.3% TL. Tail moderate 45.5-67.7% TL, moderately stout; wider at base, tapering to the first dorsal fin origin, not expanded in the middle. Precaudal length (48.0-101.8% TL) shows significant differences between all of its congeners, with other species having significantly longer or shorter lengths ($F_{6,104} = 10.23$, $p < 0.0001$ (see Statistical Results section for further detail)). Dorsal fins relatively moderate in height and shape, both dorsal fins similar in size and height, 1.4-2.5% TL and 1.6-2.8% TL, respectively; base of the first dorsal fin longer than the second dorsal fin, 4.0-5.6% TL and 2.7-5.2% TL, respectively; anterior margins of both fins concave, apices rounded; free rear tip pointed and overlaps caudal fin; interdorsal space absent to short 0.0-1.6% TL, rear tip of first dorsal fin not overlapping base of second dorsal fin. Caudal fin short and low, height 0.3-1.1% TL; its dorsal margin weakly concave; connected to second dorsal fin by a small membranous ridge.

Dorsal surface covered in uniform, small, fine prickles; ventral surface smooth. Interdorsal and tail thorns present, males with a well-developed set of alar thorns; malar thorns absent; thorns vary slightly in size, from short to moderately well developed. Tail thorns high in number and moderately well developed (19-26); interdorsal thorns very weakly developed, and absent in most specimens (0-1). Alar thorn patches range between 3-5 rows and 19-24 columns on both pectoral fins. No multiple rows of thorns on body.

Mature claspers relatively short and robust, base length 1.3-2.6% TL, inner length 18.4-21.9% TL, tip of clasper rounded and bulbous (Figure 25). Clasper inner length 40.5-44.8% of tail length; very large pseudosiphon present near outer lateral edge of dorsal lobe; the inner surface of the dorsal lobe with very long, slender pseudorhipidion that nearly reaches the tip of the clasper; V-shaped cleft; projection absent.

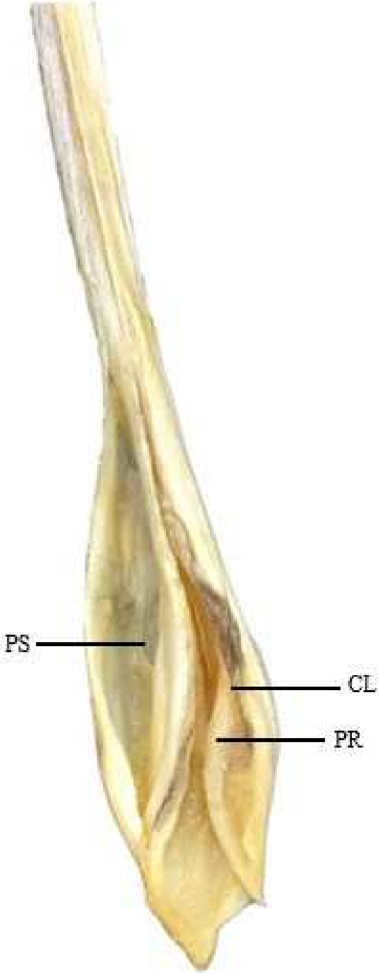

Figure 25. Components of the clasper for *Bathyraja microtrachys*. CL- cleft, PR- pseudorhipidion, PS- pseudosiphon. Photo by J.D.S. Knuckey.

Clasper skeleton consists of 3 dorsal terminal, 1 accessory terminal, ventral terminal and axial cartilages; dorsal terminal 1 very large, rounded, and narrow, curves onto the ventral side and united with ventral terminal; dorsal terminal 1 forms a large pseudosiphon 1 externally, its length 41.8% the length of the clasper; tip of dorsal marginal is pointed, forming a clearly defined pseudorhipidion externally; accessory terminal 1 rod-like and does not form a sentinel externally; tip of ventral marginal sharply pointed that does not form an external projection.

Length of rostral cartilage short, 32.8% of cranial length; prefontanelle rostral length 41.4%; cranial width 87.5%; least interorbital width 24.2%; length of anterior prefontanelle 16.4%; length of posterior prefontanelle long, 18.8% of cranial length; length of rostral appendices 14.1%. Rostral appendices nearly straight; anterior fontanelle rectangular-shaped; posterior fontanelle gourd-shaped and longer than anterior one (Figure 26).

Figure 26. Ventral view X-radiogram of *Bathyraja microtrachys*, CAS 243652, mature female. X-radiogram by Jon Fong (CAS).

Size and sexual maturity. According to material examined, size at maturity for males is at least 64-75 cm TL and 60-70 cm TL for females. Males grow to 75 cm TL. Size at birth is about 17 cm TL (Ebert, 2003).

Coloration. Doral coloration uniformly brown; slightly darker at the disc margins. Ventral coloration white, with the exception of brown pectorals and pelvic fins.

Distribution. *Bathyraja microtrachys* has been verified as occurring in the eastern North Pacific, specifically from Washington, USA, south to San Diego, California (Ebert, 2003). It occurs at depths of 1,995-2,900 m and is fairly common below 2,000 m (Kyne et al., 2012).

Etymology. The species was named after the Latin *micro*, meaning small, and *trachys*, meaning spine, referring to the uniform fine prickles covering the dorsal surface.

Common name. Fine-Spined skate.

Comparisons. *Bathyraja microtrachys* is markedly different from the other ENP bathyrajids that share the same geographic range. *Bathyraja microtrachys* is easily separated from *B. spinosissima*, which is a much larger species with pale dorsal and ventral coloration. *Bathyraja abyssicola* and *B. aleutica* are also larger-bodied species compared to *B. microtrachys*, and both possess middorsal, nuchal, and scapular thorns, traits that *B. microtrachys* lacks.

Bathyraja interrupta and *B. kincaidii* differ from *B. microtrachys* based on multiple character traits. An obvious difference is in the beige dorsal coloration with dark, irregular blotches and pale ventral coloration of *B. interrupta* and *B. kincaidii*, compared to the darker brown dorsal coloration and pale ventral coloration with dark fin edges found in *B. microtrachys*. *Bathyraja microtrachys* is further distinguished from *B. interrupta* and *B. kincaidii* by the fact that it often lacks an interdorsal space. Moreover, *Bathyraja microtrachys* possesses a shorter pelvic fin anterior lobe length (2.3-7.3% TL) than *B. kincaidii* (5.5-8.5% TL). Furthermore, the pelvic fin posterior lobe length of *B. microtrachys* is much smaller (7.2-15.3% TL) than the same measurement in *B. interrupta* (10.4-23.4% TL).

Morphologically, *B. microtrachys* is most closely related to *B. trachura,* but can easily be distinguished from *B. trachura* based on several characters. The coloration of *B. microtrachys* is uniformly brown on the dorsal surface and white on the ventral surface.

Dorsally, *B. trachura* is dark purple to dark grey and possesses a grey ventral surface that is characterized as possessing white blotches on the body, gills, mouth, and cloaca. When it comes to separation based on dermal denticles, *B. microtrachys* has very fine dermal denticles on the dorsal surface and does not possess noticeably larger denticles on the tail region. This is compared to the large, rough dermal denticles found on *B. trachura*, especially for those found on the tail. *Bathyraja microtrachys* possesses a moderately shorter disc size than *B. trachura* does (disc length 41.5-51.1% TL and 28.7-56.7% TL, respectively). The interorbital width is noticeably longer in *B. microtrachys* than it is in *B. trachura* (3.5-8.1% TL and 3.7-5.6% TL, respectively) and is a feature that can be used to distinguish the two species.

Bathyraja spinosissima (Beebe & Tee-Van, 1941)

Description. A very large sized skate with a rhomboidal disc, 1.18-1.25 times as broad as long; the disc length large 44.1-56.9% TL; disc width large 50.6-67.3% TL; straight to moderately convex beside and forward of eyes; apex broadly rounded; posterior margin slightly convex; free rear tip broadly rounded (Figures 27-30; Table 7). Head length moderate 14.0-20.5 % TL, preorbital snout length 6.1-12.8% TL; preoral length 9.1-12.3% TL. Snout tip pointed; possessing no fleshy process at apex. Eye length moderate 2.3-5.0% TL; interorbital width large 4.9-9.5% TL. Spiracles relatively small 1.2-2.3% TL; oval shaped; interspiracular length significantly larger than all of its congeners 9.1-12.2% TL ($F_{6,104} = 4.67$, $p = 0.0003$ (see Statistical Results section for further detail)). Mouth width significantly larger than the other ENP species 6.1-13.0% TL ($F_{6,104} = 9.70$, $p < 0.0001$ (see Statistical Results section for further detail)). Nasal curtain length and width both moderate, 2.4-3.5% TL and 6.1-11.8% TL, respectively, its posterior margin fringed at the corners; anterior margin of curtain lobe-like. Internarial distance significantly longer than all of its conspecific species 7.3-11.3% TL ($F_{6,104} = 21.86$, $p < 0.0001$ (see Statistical Results section for further detail)); first gill slit length 1.2-2.0% TL; fifth gill slit length 0.6-2.0% TL; distance between gill slits large, distance between first gill slits 15.9-24.0% TL, and distance between fifth gill slits 11.0-15.4% TL. Upper jaw moderately well arched, possessing a symphysis; lower jaw convex. Teeth similar in both jaws; teeth unicuspid, with a strong, bluntly pointed posteriorly directed cusp; arranged in longitudinal rows; teeth relatively high in number and similar in number, upper teeth (31-33) and lower teeth (24-31).

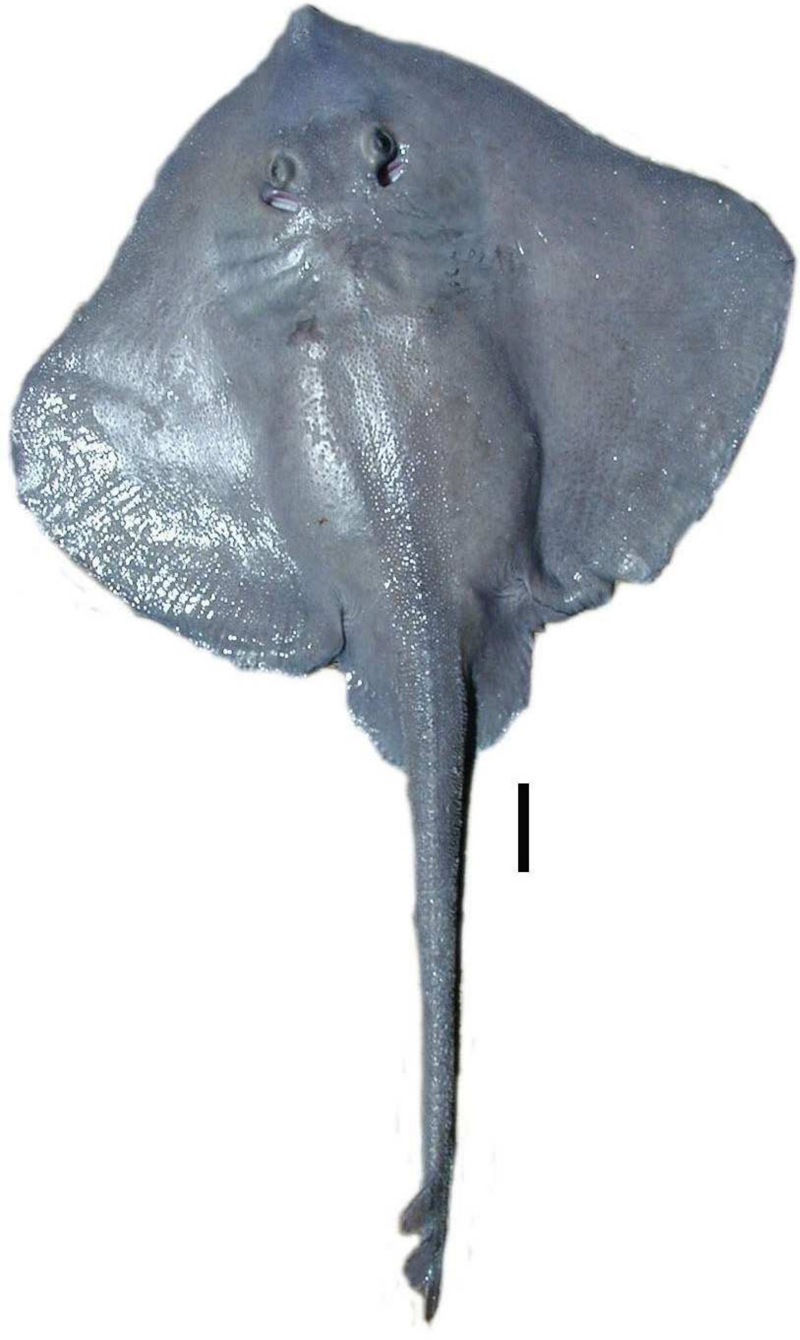

Figure 27. Bathyraja spinosissima, dorsal view, fresh. Photo by Dan Kamikawa (NOAA). Scale bar = 100 mm.

Figure 28. Bathyraja spinosissima, ventral view, fresh. Photo by Dan Kamikawa (NOAA). Scale bar = 100 mm.

Figure 29. *Bathyraja spinosissima*, holotype, CAS 25617, 164 mm TL, prenatal male, dorsal view, preserved. Photo by D.A. Ebert. Scale bar = 50 mm.

Figure 30. Ventral view X-radiogram of *Bathyraja spinosissima*, holotype, CAS 25617, neonate male. X-radiogram by Jon Fong (CAS).

Table 7.

Morphometric and Meristic Data for Bathyraja spinosissima (N = 4) Specimens.

Measurements	**% TL**
Total length (mm)	164 - 1492
Disc length	42.1 - 56.9
Disc width	50.6 - 67.3
Anterior disc length	36.0 - 46.8
Posterior disc length	21.3 - 35.3
Inner disc length	6.0 - 7.6
Disc base length	13.4 - 15.8
Snout to maximum disc width	26.2 - 34.1
Head length	14.0 - 20.5
Preorbital snout length	6.1 - 12.8
Eye length	2.3 - 5.0
Interorbital width	4.9 - 9.5
Spiracle length	1.2 - 2.3
Interspiracular width	9.1 - 12.2
D1 origin to tail tip	4.2 - 13.4
D1 base length	2.4 - 4.3
D1 vertical height	0.9 - 1.8
D2 base length	2.7 - 3.0
D2 vertical height	1.1 - 1.8
Interdorsal space	0.4 - 0.6
Caudal base length	4.4 - 5.5
Caudal vertical height	0.5 - 1.8
Lateral tail fold length	19.5
Preoral snout length	9.1 - 12.3
Mouth width	6.1 - 13.0
Prenarial snout length	6.1 - 9.3
Internarial width	7.3 - 11.3
Nasal curtain length	2.4 - 3.5
Nasal curtain width	6.1 - 11.8
Snout to 1st gill slit	14.6 - 20.6
Snout to 5th gill slit	19.5 - 29.4
1st gill slit length	1.2 - 2.0
2nd gill slit length	1.2 - 2.3
3rd gill slit length	1.2 - 2.4

4th gill slit length	1.2 - 2.4
5th gill slit length	0.6 - 2.0
Space between the 1st gill slits	15.9 - 24.0
Space between the 5th gill slits	11.0 - 15.4
Pelvic length	12.2 - 18.7
Pelvic posterior lobe length	9.0 - 12.2
Pelvic anterior lobe length	4.3 - 7.9
Inner anterior lobe length	3.5 - 7.3
Clasper inner length	4.3
Clasper outer length	2.4
Clasper base length	1.8
Precaudal length	94.5 - 95.7
Tail length	47.3 - 66.5
Interdorsal thorn count	0 - 1
Middorsal thorn count	0
Nuchal thorn count	0
Orbital thorn count- right side	0
Orbital thorn count- left side	0
Rostral thorn count	0
Scapular thorn count- right side	0
Scapular thorn count- left side	0
Tail thorn count	22 - 28
Alar thorn count- rows- right side (males only)	0
Alar thorn count- rows- left side (males only)	0
Alar thorn count- columns- right side (males only)	0
Alar thorn count- columns- left side (males only)	0
Malar thorn count- rows- right side (males only)	0
Malar thorn count- rows- left side (males only)	0
Malar thorn count- columns- right side (males only)	0
Malar thorn count- columns- left side (males only)	0
Upper teeth- total count	31 - 33
Lower teeth- total count	24 - 31
Vertebral count	137

Note: Includes the ranges of the measurements. Total length is the actual measurement in millimeters; all other measurements are expressed as a percentage of total length (% TL).

Pelvic fins moderate; anterior lobe relatively short 4.3-7.9% TL, posterior lobe 9.0-12.2% TL, and similar between sexes and maturities, inner margin incised. Tail relatively moderately sized 47.3-66.5% TL, stout, wider at base, tapering to the first dorsal fin origin, not expanded in the middle. Dorsal fins small in size, second dorsal fin taller than first dorsal fin, 1.1-1.8% TL and 0.9-1.8% TL, respectively; dorsal fin lengths similar, 2.4-4.3% TL and 2.7-3.0% TL, for the first and second dorsal fins, respectively; anterior margins of both fins concave, apices rounded; free rear tip rounded; interdorsal space short 0.4-0.6% TL; rear tip of first dorsal fin not overlapping base of second dorsal fin. Caudal fin relatively long, base length 4.4-5.5% TL; its dorsal margin weakly concave; connected to second dorsal fin by a small membranous ridge.

Dorsal surface covered with prickles and some thorns; ventral surface covered in small prickles. Tail thorns present (22-28) and moderate in size; interdorsal thorns weakly developed and occasionally absent (0-1); middorsal, nuchal, and scapular thorns absent. Thorns in a single, non-continuous row; no multiple rows of thorns on body. As no mature males were included in this study, number of alar or malar thorn counts is unknown. Based on congener species, malar thorns are unlikely to be present in this species.

Mature males were not available during the course of this study, so clasper descriptions are currently unavailable.

Dermal denticles possess 4-5 base points and are well developed on the posterior third of the dorsal surface; denticles on the first dorsal fin thick, straight, posteriorly-oriented; denticles on head stouter than dorsal fin; found in high density patches (Figure 31).

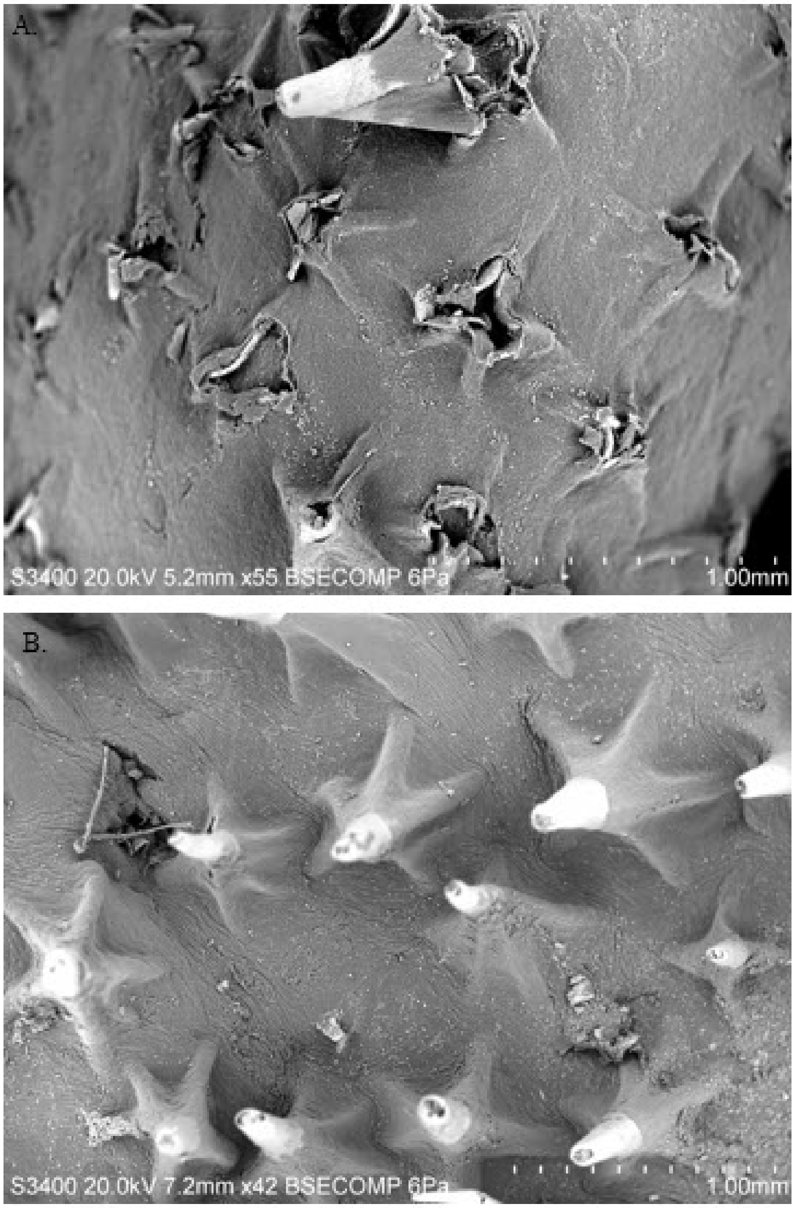

Figure 31. Scanning electron microscope images of the dermal denticles of *Bathyraja spinosissima* from A. the first dorsal fin and B. the head region, behind the eyes. Photos by Justin Cordova (MLML).

Size and sexual maturity. Size at maturity is unknown for males; female specimens in this study were found to be mature at 98 cm TL. Size at birth is 25 cm TL (Ebert, 2003). Maximum size is at least 2 m TL (Ebert, 2003).

Coloration. Dorsal coloration pale white to light grey; outer edges of pectorals slightly darker in coloration. Ventral coloration pale white. Thorns on dorsal surface pale.

Distribution. *Bathyraja spinosissima* is a wide spread species and has been verified as occurring in the North Pacific, specifically from Oregon, south to the Galapagos Islands (Ebert, 2003). It occurs at depths of 800-2,938 m (Ebert, 2003), making it one of the deepest-dwelling species in this study. The species appears to prefer rockier habitat than its congeners, as it has been videoed over rocky substrate (MBARI, unpublished video). The preference for rocky substrate is why no fresh specimens were captured for this study. The study utilized bottom trawl, which does not work on highly rocky surfaces.

Etymology. The species name comes from the Latin *spinosus*, meaning thorny. It was named thus for the prickles on both the ventral and dorsal surface.

Common name. Pacific White skate.

Comparisons. *Bathyraja spinosissima* is the most easily identifiable softnose skate in the ENP, mostly due to its large size and coloration. *Bathyraja interrupta* is a smaller skate that does not share the same geographic range as *B. spinosissima*. Other smaller-bodied skates in the region (e.g., *B. kincaidii*, *B. microtrachys*, and *B. trachura*) lack the pale dorsal surface coloration that *B. spinosissima* possesses.

The two other large-bodied skates in the same geographic range as *B. spinosissima* are investigated and compared. *Bathyraja abyssicola* and *B. aleutica* are easily differentiated by the dark brown dorsal coloration that the two species display and by the fact that both species possess middorsal, nuchal, and scapular thorns, which *B. spinosissima* lacks. Furthermore, *B. spinosissima* has significantly longer internarial and interspiracular widths (7.3-11.3% TL and 9.1-12.2% TL, respectively) than *B. abyssicola* and *B. aleutica* (5.5-8.6% TL and 2.0-6.4% TL; 6.6-7.7 and 4.3-7.0% TL, respectively).

Bathyraja trachura (Gilbert, 1892)

Description. A moderately sized skate with a rhomboidal disc, 1.14-1.95 times as broad as long; anterior margin moderately concave in adult males, straight to moderately convex beside and just forward of eyes; apex broadly rounded; posterior margin slightly convex; free rear tip broadly rounded (Figures 32-34; Table 8). Head length relatively short 14.95-24.1% TL, preorbital snout length significantly shorter than every species but *B. spinosissima* 9.0-13.5% TL ($F_{6,104} = 12.41$, $p < 0.0001$ (see Statistical Results section for further detail)); preoral length short 8.0-13.5% TL. Snout tip pointed; possessing no fleshy process at apex. Eye length moderate 2.5-5.0% TL; interorbital width short 3.7-5.6% TL. Spiracles average 1.5-3.9% TL; oval shaped. Mouth width short 6.7-8.1% TL. Nasal curtain length relatively short 2.1-4.1% TL, width average 5.9-9.7% TL, its posterior margin highly fringed at the corners; anterior margin of curtain lobe-like. Interspiracular space short 4.7-7.9%. Internarial distance relatively long 5.1-8.7% TL; first gill slit length relatively long 1.8-2.7% TL; fifth gill slit length 0.3-2.9% TL; distance between gill slits moderate, distance between first gill slits 12.3-21.2% TL, and distance between fifth gill slits 7.7-13.3% TL. Upper jaw moderately well arched, possessing a symphysis; lower jaw convex. Teeth similar in both jaws; teeth unicuspid, with a strong, bluntly pointed posteriorly directed cusp; arranged in longitudinal rows; teeth relatively high in number and similar in number, upper teeth (27-36) and lower teeth (26-36).

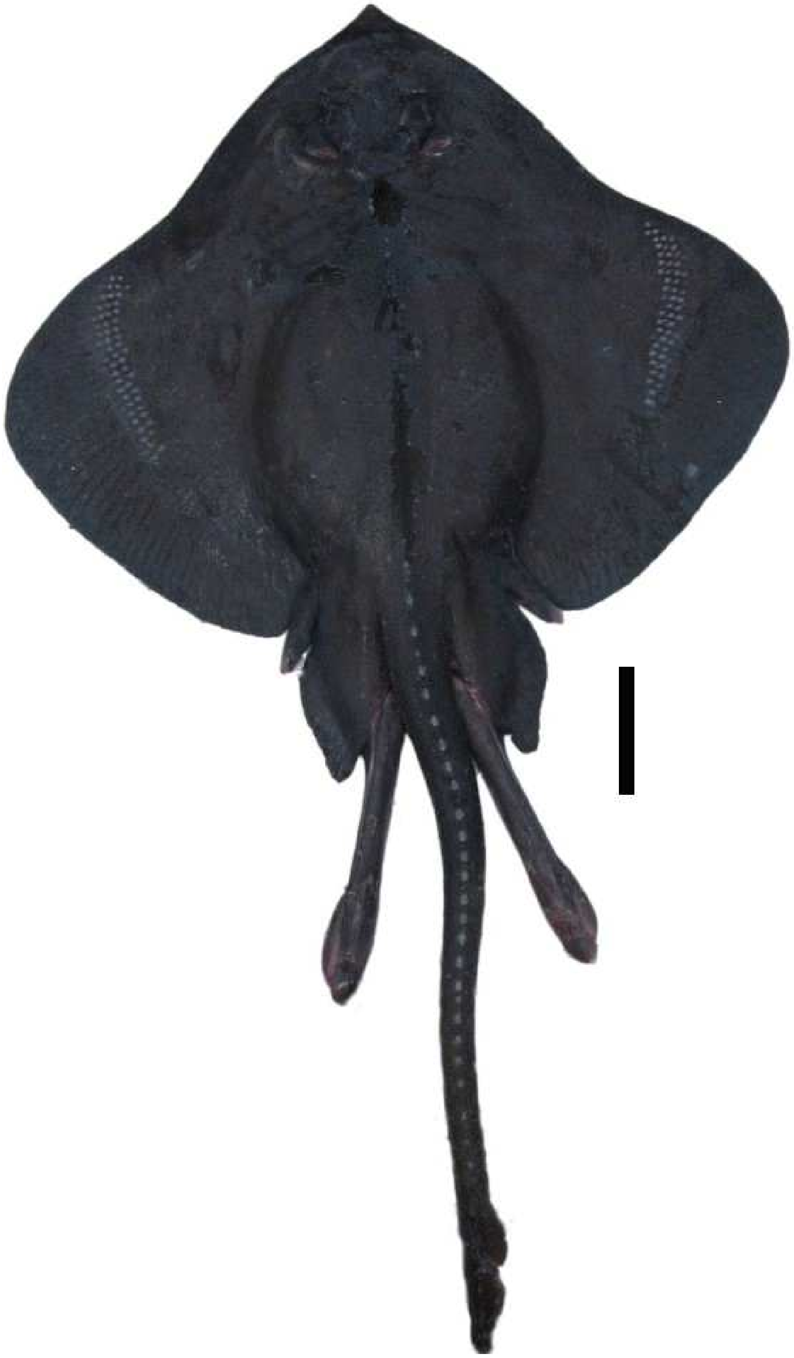

Figure 32. *Bathyraja trachura*, PSRC Btra 062212-2, 805 mm TL, mature male, dorsal view, fresh. Photo by J.D.S. Knuckey. Scale bar = 100 mm.

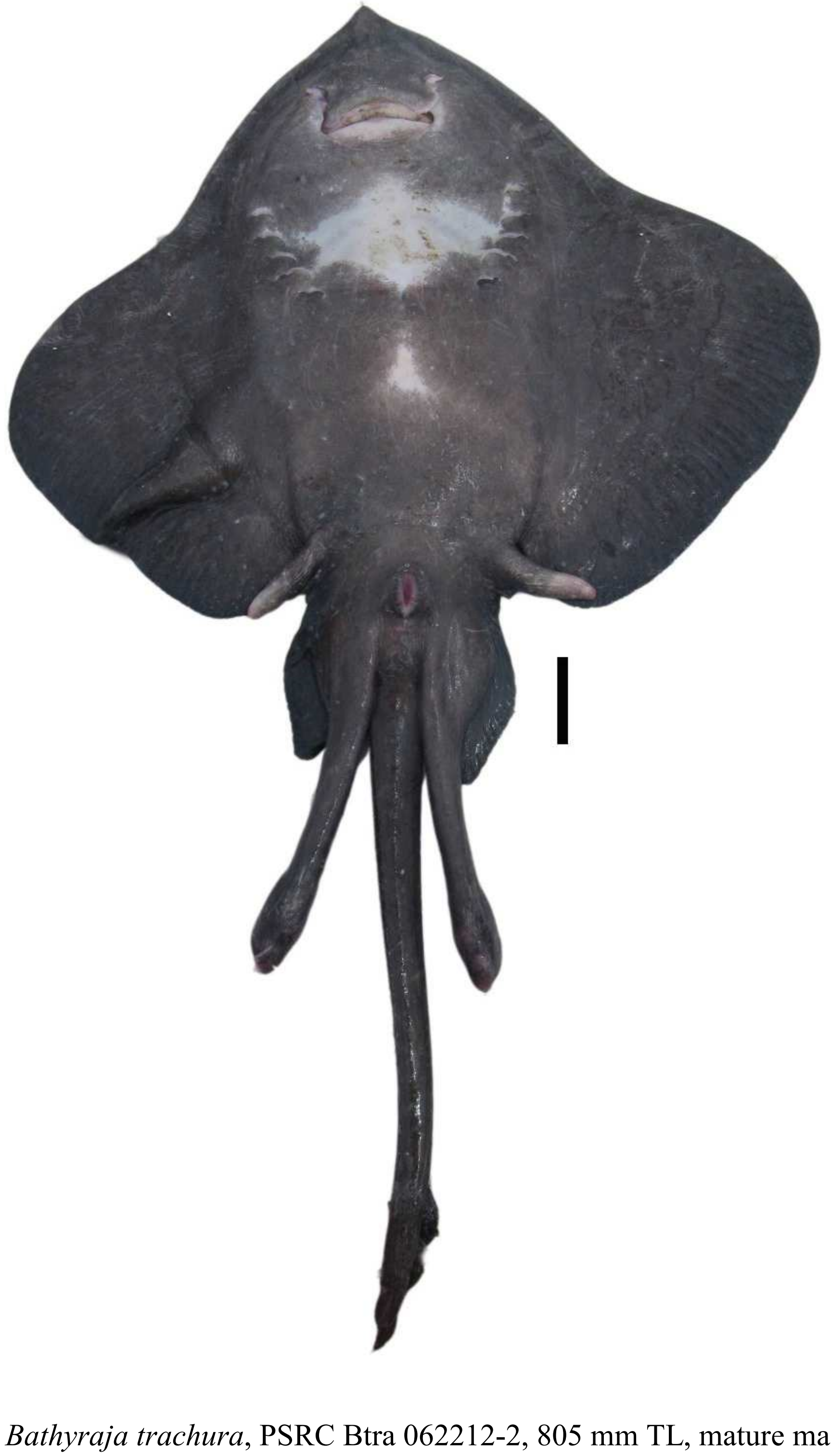

Figure 33. Bathyraja trachura, PSRC Btra 062212-2, 805 mm TL, mature male, ventral view, fresh. Photo by J.D.S. Knuckey. Scale bar = 100 mm.

Figure 34. Bathyraja trachura, holotype, 457 mm TL, female, dorsal view, preserved. Photo by D.A. Ebert. Scale bar = 70 mm.

Table 8.

Morphometric and Meristic Data for Bathyraja trachura (N = 19) Specimens.

Measurements	**% TL**
Total length (mm)	294 - 899
Disc length	28.7 - 56.7
Disc width	47.3 - 68.7
Anterior disc length	32.8 - 49.3
Anterior anterior disc length (males only)	20.0 - 25.3
Anterior posterior disc length (males only)	12.8 - 21.4
Posterior disc length	20.7 - 34.0
Inner disc length	4.9 - 10.4
Disc base length	9.5 - 15.0
Snout to maximum disc width	22.5 - 35.4
Head length	14.9 - 24.1
Preorbital snout length	9.0 - 13.5
Eye length	2.5 - 5.0
Interorbital width	3.7 - 5.6
Spiracle length	1.5 - 3.9
Interspiracular width	4.7 - 7.9
D1 origin to tail tip	7.5 - 13.6
D1 base length	3.0 - 5.0
D1 vertical height	2.0 - 3.0
D2 base length	2.7 - 5.0
D2 vertical height	1.7 - 3.4
Interdorsal space	0.0 - 2.8
Caudal base length	2.3 - 4.5
Caudal vertical height	0.6 - 2.1
Lateral tail fold length	8.6 - 17.4
Preoral snout length	8.0 - 13.5
Mouth width	6.7 - 8.1
Prenarial snout length	6.2 - 12.6
Internarial width	5.1 - 8.7
Nasal curtain length	2.1 - 4.1
Nasal curtain width	5.9 - 9.7
Snout to 1st gill slit	15.2 - 20.7
Snout to 5th gill slit	22.6 - 29.3
1st gill slit length	1.4 - 2.7

2nd gill slit length	1.1 - 3.3
3rd gill slit length	1.1 - 3.3
4th gill slit length	1.1 - 3.3
5th gill slit length	0.3 - 2.5
Space between the 1st gill slits	12.3 - 21.2
Space between the 5th gill slits	7.7 - 13.3
Pelvic length	12.1 - 18.9
Pelvic posterior lobe length	8.3 - 15.2
Pelvic anterior lobe length	7.4 - 10.7
Inner anterior lobe length	4.6 - 10.5
Clasper inner length	4.4 - 28.8
Clasper outer length	3.0 - 17.6
Clasper base length	0.8 - 2.5
Precaudal length	67.6 - 98.4
Tail length	42.7 - 61.2
Interdorsal thorn count	0 - 1
Middorsal thorn count	0 - 2
Nuchal thorn count	0 - 3
Orbital thorn count- right side	0
Orbital thorn count- left side	0
Rostral thorn count	0
Scapular thorn count- right side	0
Scapular thorn count- left side	0
Tail thorn count	21 - 30
Alar thorn count- rows- right side (males only)	4 - 6
Alar thorn count- rows- left side (males only)	4 - 5
Alar thorn count- columns- right side (males only)	20 - 23
Alar thorn count- columns- left side (males only)	20 - 23
Malar thorn count- rows- right side (males only)	0
Malar thorn count- rows- left side (males only)	0
Malar thorn count- columns- right side (males only)	0
Malar thorn count- columns- left side (males only)	0
Upper teeth- total count	27 - 36
Lower teeth- total count	26 - 36
Spiral valve count	7 - 10
Pectoral fin radial count	81
Pelvic fin radial count	23
Vertebral count	109

Rostral cartilage length	41.7 - 47.2
Prefontanelle rostral length	44.9 - 50.4
Cranial width	89.4 - 92.1
Least interorbital width	16.5 - 20.3
Anterior prefontanelle length	17.3
Posterior prefontanelle length	8.7
Rostral appendices length	11.8 - 15.4

Note: Includes the ranges of the measurements. Total length is the actual measurement in millimeters; all other measurements are expressed as a percentage of total length (% TL).

Pelvic fins moderate overall; anterior lobe 7.4-10.7% TL, posterior lobe short 8.3-15.2% TL, and similar between sexes and maturities, inner margin deeply incised. Tail relatively moderately sized 42.7-61.2% TL, stout, wider at base, tapering to the first dorsal fin origin, not expanded in the middle. Lateral tail fold short, 8.6-17.9% TL, similar in both sexes; not obviously broader at any point along its length. Dorsal fins moderate in size and shape, first dorsal fin slightly taller than second dorsal fin, 2.0-3.0% TL and 1.7-2.7% TL, respectively; first dorsal fin slightly longer than the second dorsal fin, 3.0-4.0% TL and 2.7-3.9% TL, respectively; anterior margins of both fins concave, apices rounded; free rear tip rounded; interdorsal space absent or short 0.0-1.6% TL; rear tip of first dorsal fin not overlapping base of second dorsal fin. Caudal fin large, low, height 0.6-2.0% TL; its dorsal margin weakly concave; connected to second dorsal fin by a small membranous ridge.

Dorsal surface covered with prickles and some thorns, with the prickles on the tail being larger than elsewhere; ventral surface smooth. Middorsal, nuchal, interdorsal, and tail thorns present, males with a well-developed set of alar thorns; malar thorns absent; thorns vary in size, from very weakly to moderately well developed. Middorsal thorns absent or weakly developed (0-1); nuchal thorns absent or weakly developed (0-3); tail thorns moderate in size (21-30); interdorsal thorns weakly developed and occasionally absent (0-1). Thorns in a single, non-continuous row; no multiple rows of thorns on body. Alar thorn patches possess 4-6 rows and 20-23 columns on both pectoral fins.

Mature claspers short and robust, base length 1.9-2.5% TL, inner length 19.1-25.7% TL, tip of clasper bulbous and relatively rounded (Figure 35). Clasper inner length 41.7-44.7% of tail length; a large pseudosiphon is present near the outer lateral edge of dorsal lobe, its length 33.0% of the length of the clasper; inner surface of dorsal lobe with robust, shortened pseudorhipidion that does not reach the tip of the clasper; V-shaped cleft; projection absent from tip.

Figure 35. Components of the clasper for *Bathyraja trachura*. CL- cleft, PJ- projection, PR- pseudorhipidion, PS- pseudosiphon. Photo by J.D.S. Knuckey.

Clasper skeleton consists of 3 dorsal terminal, 1 accessory terminal, ventral terminal and axial cartilages; dorsal terminal 1 large and rectangular, covering almost the entire dorsal surface, curved around clasper onto the ventral side and united with ventral terminal; dorsal terminal 1 forms the pseudosiphon externally; tip of dorsal marginal is pointed, forming the relatively short pseudorhipidion externally; accessory terminal 1 narrow and does not form a sentinel externally; tip of the ventral marginal is pointed and does not form a projection externally.

Dermal denticles possess 4 points to the base; very well developed on the posterior third of the dorsal surface; denticles on both the first dorsal fin and the head stout, curved towards posterior, found in low densities (Figure 36).

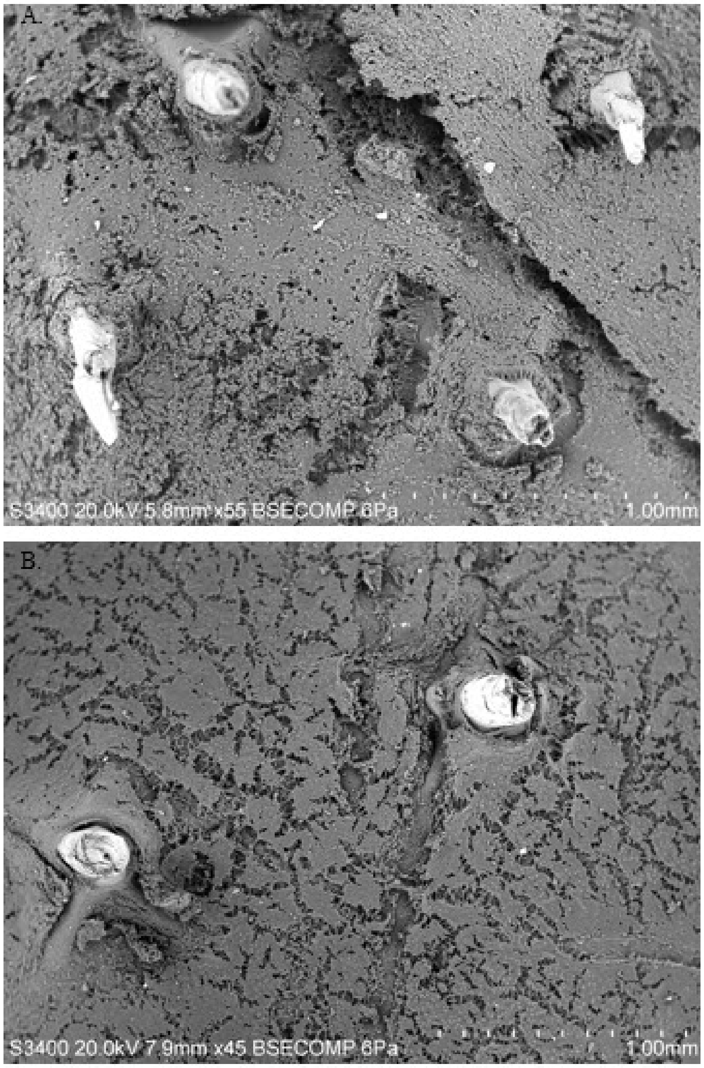

Figure 36. Scanning electron microscope images of the dermal denticles of *Bathyraja trachura* from A. the first dorsal fin and B. the head region, behind the eyes. Photos by Justin Cordova (MLML).

Length of rostral cartilage 41.7-47.2% of cranial length; prefontanelle rostral length 44.9-50.4%; cranial width 89.4-92.1%; least interorbital width 16.5-20.3%; length of anterior prefontanelle 17.3%; length of posterior prefontanelle 8.7%; length of rostral appendices 11.8-15.4%. Rostral appendices nearly straight; anterior fontanelle dagger-shaped; posterior fontanelle gourd-shaped and longer than anterior one (Figure 37).

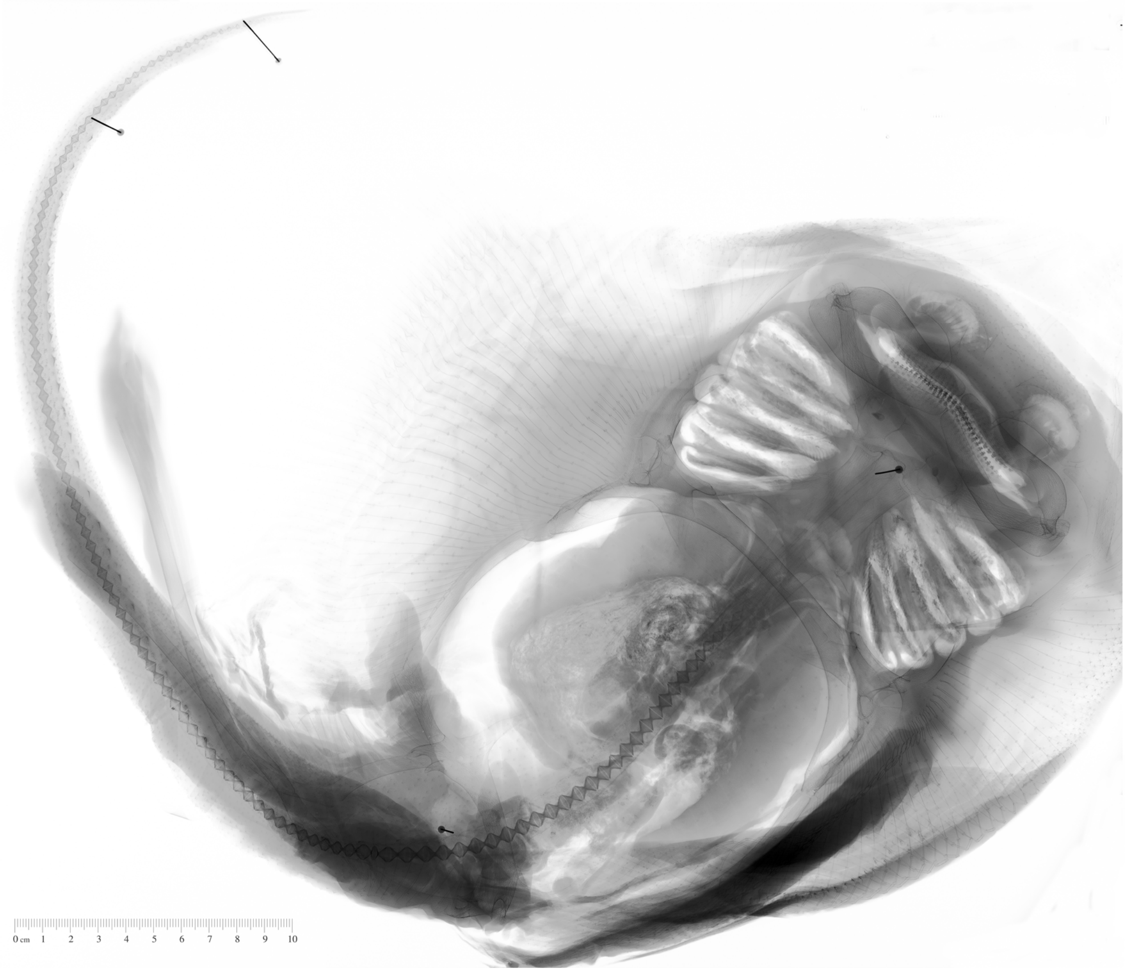

Figure 37. Ventral view X-radiogram of *Bathyraja trachura*, CAS 243650, mature male. X-radiogram by Jon Fong (CAS).

Size and sexual maturity. Size at maturity for males about 75 cm TL; 74 cm TL for females. Males grow to at least 90 cm TL; females grow to at least 89 cm TL. Size at birth is 9-16 cm TL (Ebert, 2003). Maximum size to at least 90 cm TL.

Coloration. Doral coloration dark purple, brown, or dark grey. Spiracles sometimes pale; claspers externally dark, but internally pale; pelvic fins brown-purple. Ventral coloration grey, lighter in color overall than the dorsal surface, often with white blotches around mouth, gill area, cloaca, and scattered across the body; cloaca light pink to brown.

Distribution. *Bathyraja trachura* has been verified as occurring in the eastern North Pacific, specifically from the Bering Sea, south to Baja California, Mexico, and as far west as the Sea of Okhotsk (Ebert, 2003). It is reported to occur at depths of 213-2,550 m, with most specimens coming from below 600 m in California (Ebert, 2003), but from deeper than 500 m in Alaska (Stevenson, 2004).

Etymology. The species was named after the Greek *trachys*, meaning rough, referring to the thorny dorsal surface.

Common name. Roughtail skate.

Comparisons. *Bathyraja trachura* is a wide-ranging, medium-sized skate that can be easily separated from its congeners in the ENP. Large-bodied skates in the region (e.g., *B. abyssicola, B. aleutica*, and *B. spinosissima*) display obvious coloration differences that separate them from *B. trachura*. *Bathyraja interrupta*, a similarly sized species, possesses middorsal, nuchal, and scapular thorns, which *B. trachura* lacks and has a pale ventral side compared to the dark surface of *B. trachura*. *Bathyraja kincaidii*, which also possesses middorsal, nuchal, and scapular thorns, further distinguishes itself from *B.*

trachura in its long interdorsal space (0.6-3.3% TL and 0.0-2.8% TL, respectively). In fact, *B. trachura* often lacks an interdorsal space entirely.

Bathyraja trachura is closely related to *B. microtrachys* morphologically, but can be distinguished from the later species based on several characteristics. Besides the coloration, dermal denticle, and morphological differences listed in the prior *B. microtrachys* comparison, both species possess short and robust mature claspers, but *B. microtrachys* has a very long pseudorhipidion that nearly touches the tip of the clasper. Conversely, *B. trachura* has a short pseudorhipidion that does not approach the tip. Further mature clasper differences exist, in that *B. trachura* possesses an external projection, whereas the structure is absent in *B. microtrachys*. As with other species, the thorn counts can indicate differences between species. *Bathyraja microtrachys* does not possess nuchal thorns, but the thorns are present in *B. trachura*. *Bathyraja trachura* is the only species in the study that possesses nuchal thorns, but lacks middorsal or scapular thorns. Other species either possess thorns in all those locations, or lack them entirely.

Statistical Results

Non-metric multidimensional scaling (nMDS) ordination was performed on the morphometric measurements of all seven skate species studied in order to visualize whether the putative *Bathyraja* species separate out from each other in multivariate space, based on the collection of traits used in the analysis (Figure 38a). Certain measurements were omitted from the dataset for *Bathyraja interrupta*, as they were not collected during the course of the study. Results from an nMDS plot of all skate species showed a large amount of overlap, indicating low levels of dissimilarity between species. It was difficult to identify species clusters when all skates were included in a single ordination, as the species grouped together. The only species to consistently group outside of the main cluster was *B. spinosissima*. In order to clarify the nMDS ordinations, all adult skates, all female skates, and all male skates were compared separately. The analyses showed that separating by life stage and sex allowed for some parsing out of species. In the all-adult nMDS plot, *B. abyssicola* and *B. aleutica* grouped together, *B. interrupta* and *B. kincaidii* formed a cluster, and *B. microtrachys*, *B. spinosissima*, and *B. trachura* all clustered in their own groups (Figure 38b). When all female specimens were compared, there was a lower level of dissimilarity than the all-adult ordination (Figure 39a). Specifically, *B. abyssicola* and *B. aleutica* grouped together as they did in the adult ordination, *B. interrupta* and *B. kincaidii* formed another cluster, this time with the addition of *B. trachura* and the one specimen of *B. microtrachys*. The all-male nMDS ordination showed relatively low levels of dissimilarity as, *B. spinosissima* and *B. microtrachys* were located outside of the cluster that held the other species (Figure 39b).

When all sexes or life stages are run together it is difficult, if not impossible, to find discrete groupings of species; there is a high level of overlap. Later ordinations utilized the approach of separating species apart by grouping sex with a life stage, either juvenile or adult.

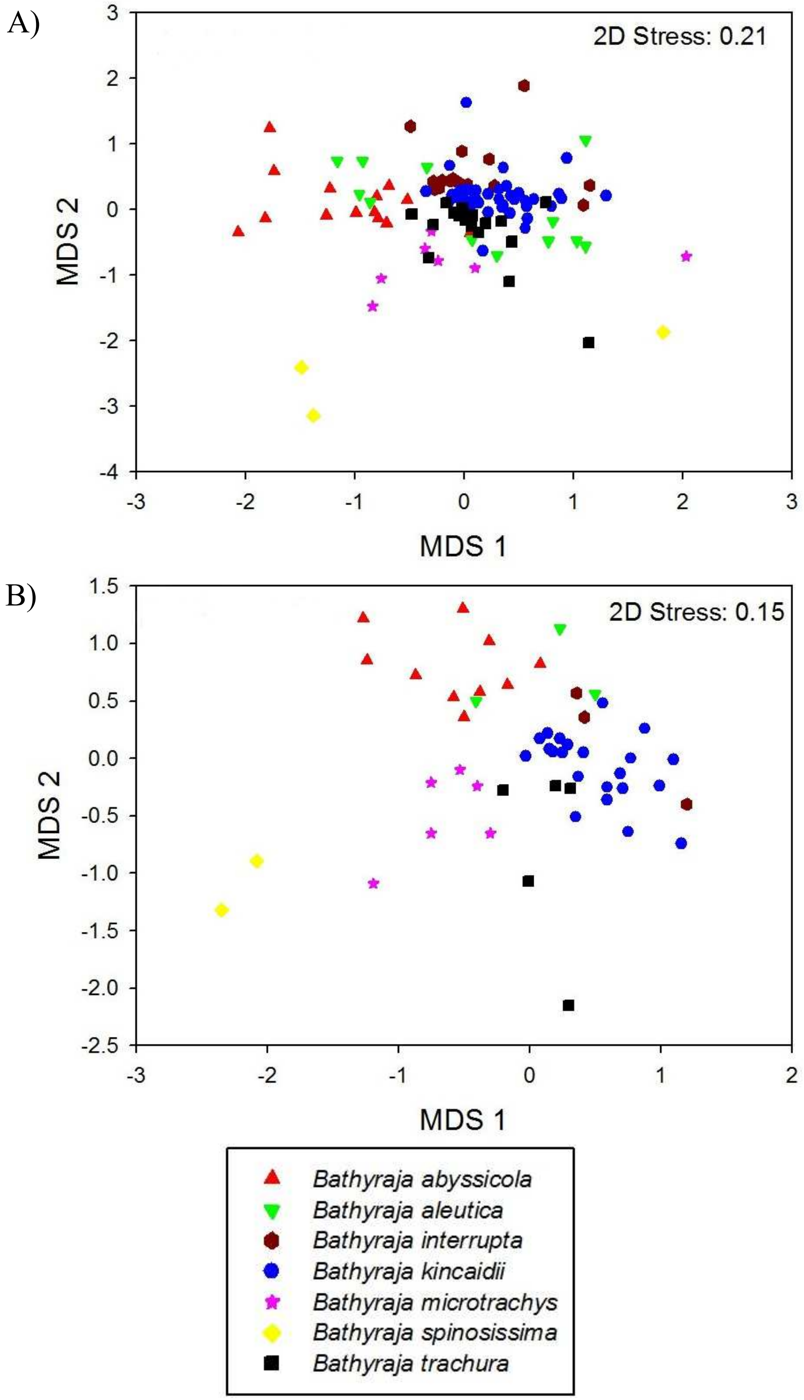

Figure 38. Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of A. all skate specimens included in this study; B. all adults. Species shown by color: *Bathyraja abyssicola* (red triangle), *B. aleutica* (green triangle), *B. interrupta* (maroon hexagon), *B. kincaidii* (blue circle), *B. microtrachys* (pink star), *B. spinosissima* (yellow diamond), and *B. trachura* (black square).

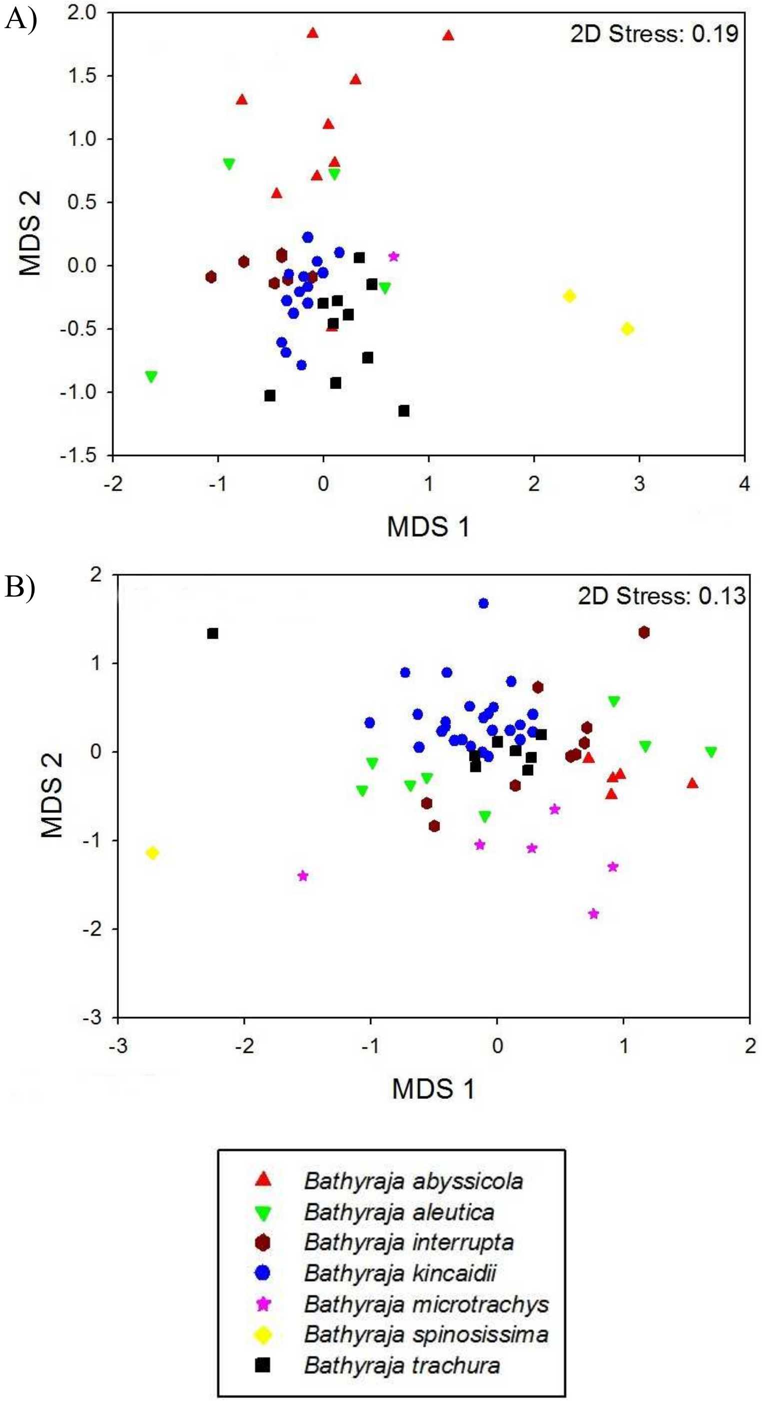

Figure 39. Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of A. all females; B. all males. Species shown by color: *Bathyraja abyssicola* (red triangle), *B. aleutica* (green triangle), *B. interrupta* (maroon hexagon), *B. kincaidii* (blue circle), *B. microtrachys* (pink star), *B. spinosissima* (yellow diamond), and *B. trachura* (black square).

For clarity, nMDS analyses were run individually for adult and juvenile life stages, with sex taken into account, and the results were more descriptive than when all sexes and life stages were combined (Figure 40). Tight species clusters were obvious when sex and life stage were separated, and allowed for the visualization of species separation. Results of the nMDS analysis for adult females of all species revealed the highest levels of dissimilarity found across the ordinations (Figure 40a). Adult female bathyrajids displayed clustering for *B. microtrachys*, *B. spinosissima*, and *B. trachura*, with *B. interrupta* and *B. kincaidii* forming a group, and *B. abyssicola* and *B. aleutica* forming another group. *Bathyraja spinosissima* grouped further away from the other clusters in the ordination, indicating high levels of dissimilarity between it and the other species.

nMDS ordinations were performed on all adult male skates with the intention of visualizing the levels of dissimilarities across species (Figure 40b). As with the adult female ordination, the plot of adult males showed discrete groups, and therefore high levels of dissimilarity across species. Similar to the adult female ordination, *B. aleutica* and *B. abyssicola* formed a distinct cluster, which appears to show low levels of dissimilarity between the two species. *Bathyraja microtrachys* formed another cluster in the ordination and was more informative for the species than in the adult female plot, as more adult male *B. microtrachys* specimens were collected. A further cluster was comprised of *B. kincaidii*, *B. interrupta*, and *B. trachura*, which indicates that the three species may be difficult to tell apart morphologically. *Bathyraja interrupta* and *B. trachura* both had a single outlier that was positioned outside of the rest of the specimens.

Results of the adult ordinations show that the inclusion of sexual maturity with sex allows for the visualization of differences between the species investigated in this study.

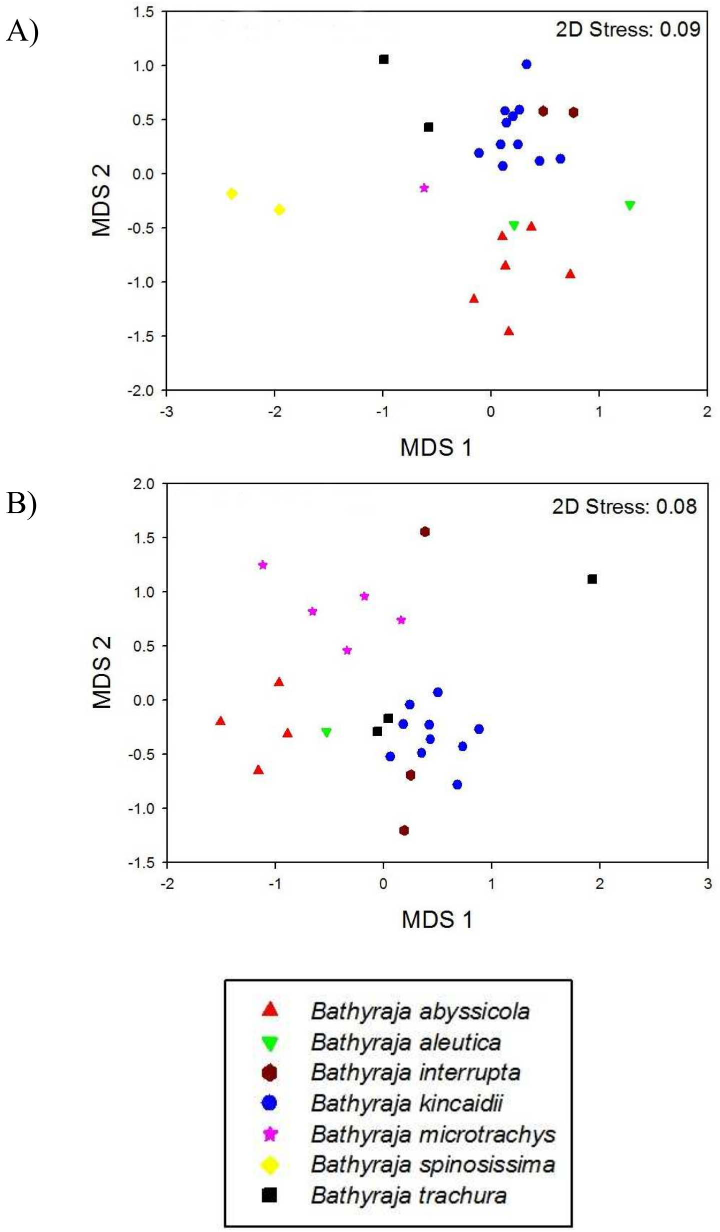

Figure 40. Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of A. adult females; B. adult males. Species shown by color: *Bathyraja abyssicola* (red triangle), *B. aleutica* (green triangle), *B. interrupta* (maroon hexagon), *B. kincaidii* (blue circle), *B. microtrachys* (pink star), *B. spinosissima* (yellow diamond), and *B. trachura* (black square).

Further nMDS ordinations were run on the juvenile the ENP softnose skates for the purposes of visualizing the differences between species (Figure 41). When juveniles, whether male or female, were compared there were relatively low levels of dissimilarity across species. Species-specific clusters were difficult to tell apart as specimens of the same species were found scattered across the ordinations. In general, *B. kincaidii* and *B. trachura* grouped together, with *B. spinosissima* and *B. microtrachys* being located in separate areas of the plot. These groupings were similar to the adult ordinations, but the scattering of specimens in the juvenile plots was greater. Overall, the ordinations for juveniles were uninformative and did not allow for the visualization of morphological differences.

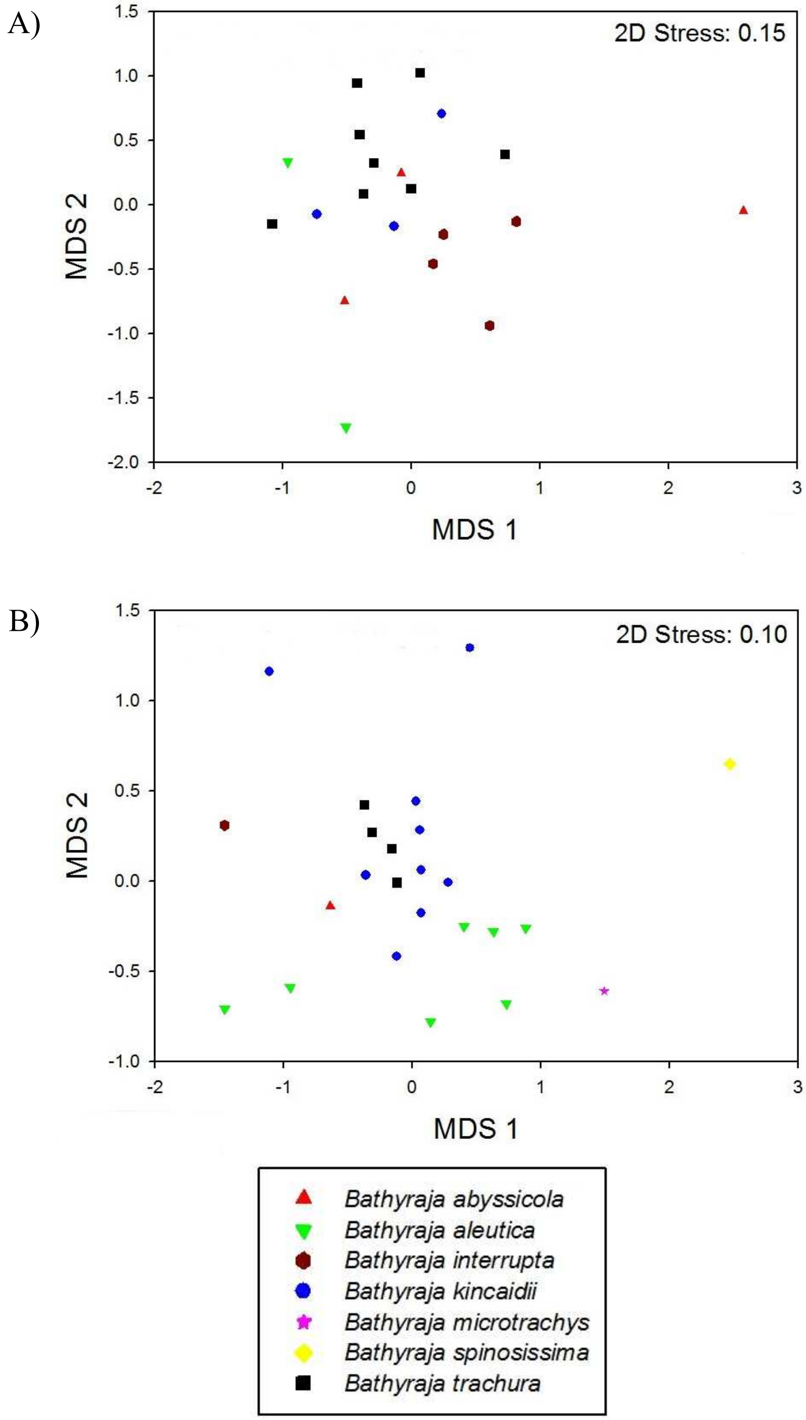

Figure 41. Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of A. juvenile females; B. juvenile males. Species shown by color: *Bathyraja abyssicola* (red triangle), *B. aleutica* (green triangle), *B. interrupta* (maroon hexagon), *B. kincaidii* (blue circle), *B. microtrachys* (pink star), *B. spinosissima* (yellow diamond), and *B. trachura* (black square).

Additional nMDS ordinations were run to visualize the relationship between the closely related species, *B. interrupta* and *B. kincaidii* (Figure 42). The resulting ordinations, which grouped sex by life stage, displayed very high levels of dissimilarity, supporting the hypothesis of the two being separate species. Adults, whether they were female or male, clustered in separate groups and displayed clear differences (Figure 42a-b). Juvenile females and males displayed similar ordinations, with obvious species groupings (Figure 43a-b). The exception to this statement was the ordination for juvenile males, in which one *B. interrupta* grouped closer to *B. kincaidii* than the *B. interrupta* group. Despite this, the ordinations displayed tight clusters, indicating high levels of dissimilarity between the two species.

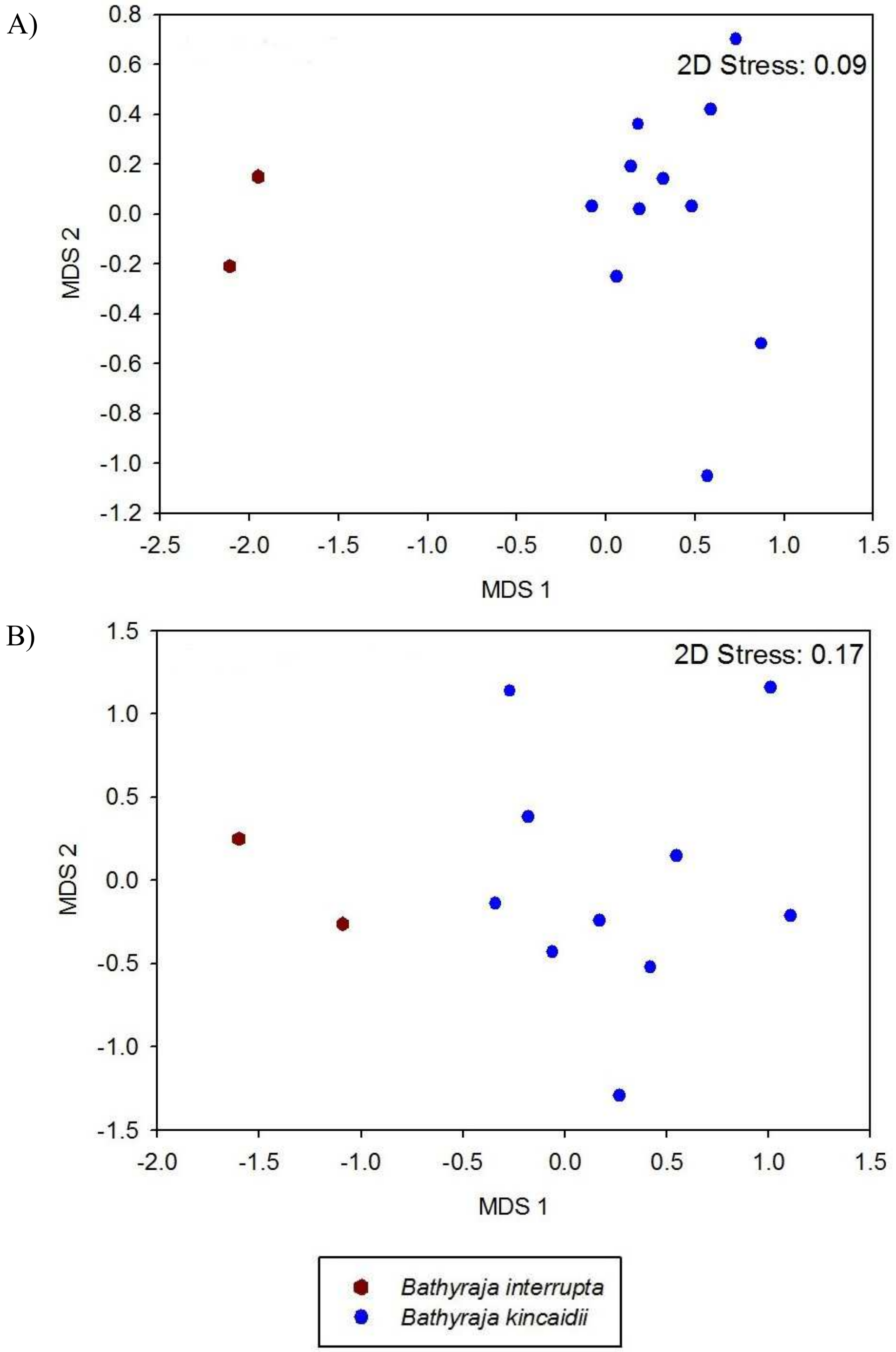

Figure 42. Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of A. adult females; B. adult males. Species shown by color: *Bathyraja interrupta* (maroon hexagon) and *B. kincaidii* (blue circle).

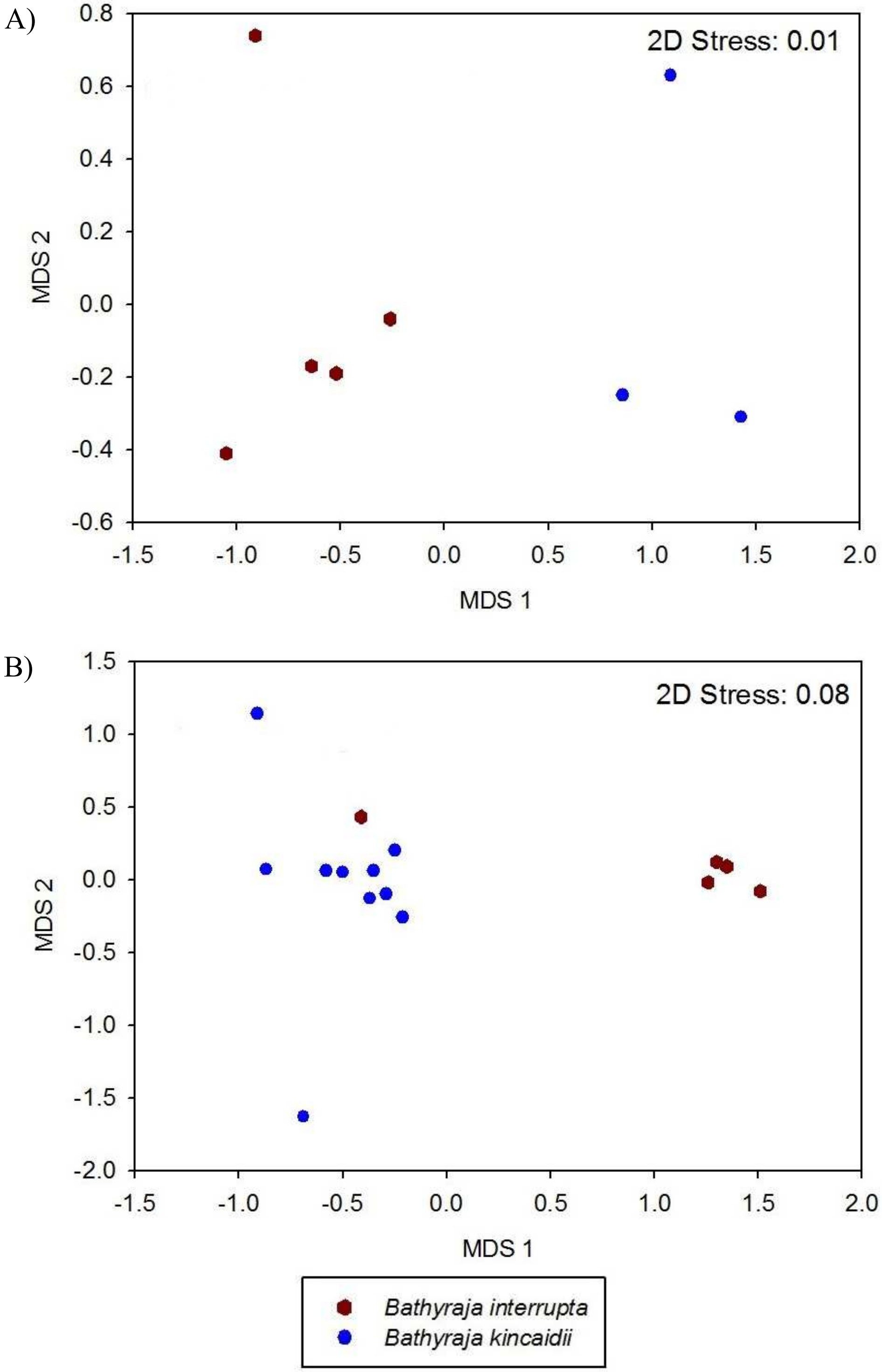

Figure 43. Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of A. juvenile females; B. juvenile males. Species shown by color: *Bathyraja interrupta* (maroon hexagon) and *B. kincaidii* (blue circle).

Further nMDS analyses were conducted to better portray the relationship between another closely related pair of species, *B. microtrachys* and *B. trachura* (Figure 44). Females were omitted from the *B. microtrachys* and *B. trachura* ordinations, as an insufficient number of female samples were collected during the course of the study. As with the *B. interrupta* and *B. kincaidii* plots, the *B. microtrachys* and *B. trachura* ordinations displayed high levels of dissimilarity, pointing to the two species being valid and separate. In the adult male ordination, *B. microtrachys* showed very tight clustering, and while the clustering was not as tight for *B. trachura*, the specimens were located in a distinct area of the ordination than was unoccupied by *B. microtrachys* (Figure 44a). The juvenile male ordination displayed strong levels of dissimilarities between the species, with the single specimen of *B. microtrachys* grouping away from the *B. trachura* specimens (Figure 44b). When sex and life stage are compared between closely related species, obvious differences were displayed, indicating that the species are separate from each other.

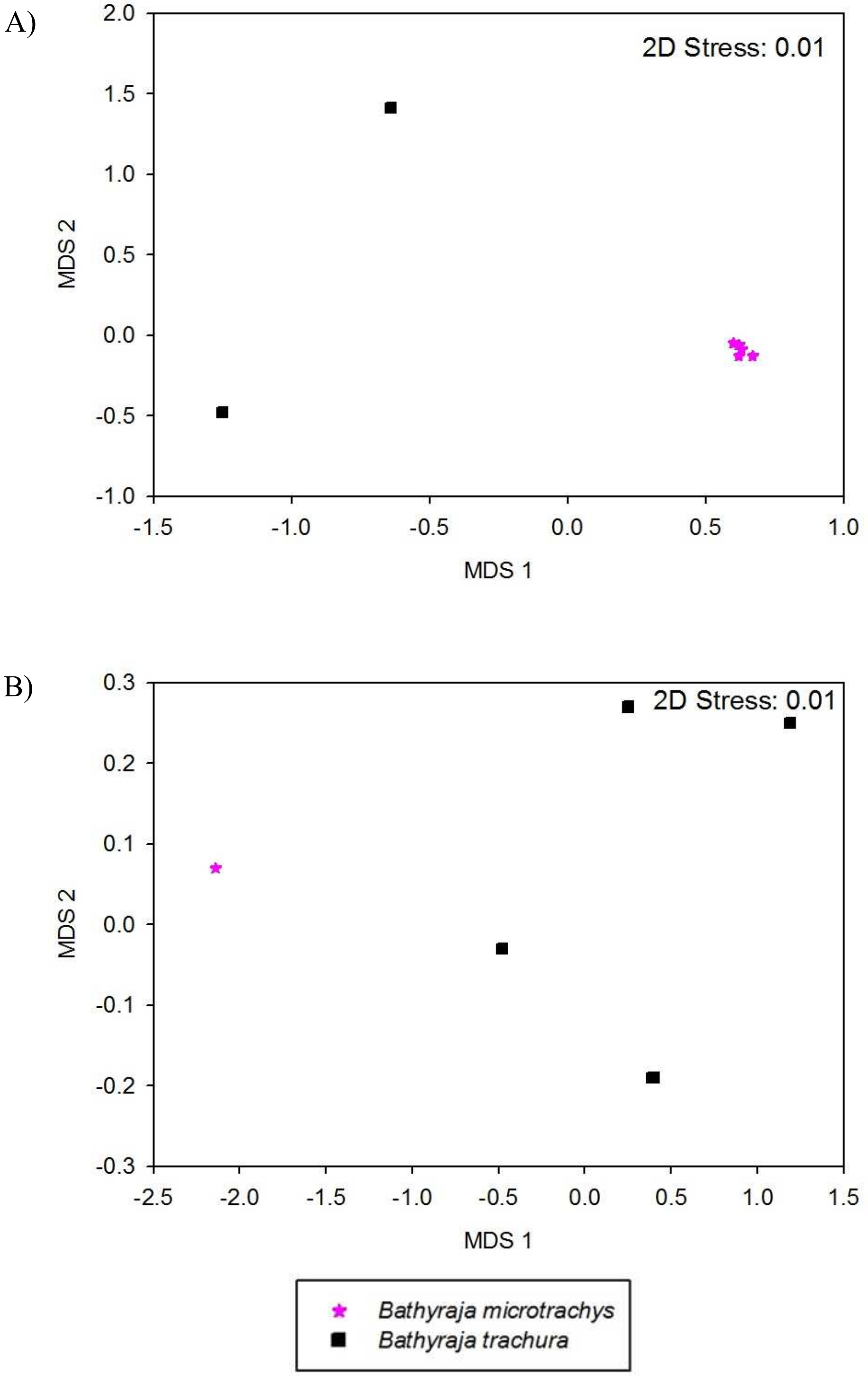

Figure 44. Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of A. adult males; B. juvenile males. Species shown by color: *Bathyraja microtrachys* (pink star) and *B. trachura* (black square).

One-way analyses of variance (ANOVA) tested for significant differences in the morphometric trait values of each species and confirmed that the putative species differed in select traits (Table 9). Sequential Bonferroni adjustments were completed after the ANOVAs were run to correct for any potential type I errors. Clasper measurements were only analyzed for mature males; therefore specimens of *B. spinosissima* were omitted from clasper-specific analyses. The one-way ANOVA revealed statistically significant differences in the means of a majority of the morphological measurements, with p values ranging from < 0.0001-0.0550. Many measurements showed strong differences in the means, including total length, disc width, head length, interdorsal space, and pelvic posterior lobe length. Snout to maximum disc width ($p = 0.0476$) and clasper outer length ($p = 0.0413$) displayed p values that were close to alpha, and were therefore unlikely to be useful for identifying species. Three measurements, specifically the anterior disc length ($p = 0.055$), posterior disc length ($p = 0.0543$), and pelvic fin length ($p = 0.0520$) had p values greater than the significance level. Means were not significant for these measurements and were not considered in future analyses. The measurements included in the ANOVAs that met test assumptions were then subjected to Tukey-Kramer HSD *post hoc* tests to compare species. The results of the Tukey-Kramer HSD tests showed significant differences for various measurements amongst all of the species and are included in the species descriptions found earlier in the study.

Table 9.

One-Way Analyses of Variance (ANOVAs) for Morphological Measurements by Species.

Measurement	Degrees of Freedom	Mean Square	F	P
Total length	6, 104	617508.00	12.772	<0.0001
Disc length	6, 104	81.00	2.943	0.0208
Disc width	6, 104	193.03	16.615	<0.0001
Anterior disc length	6, 104	21.07	4.709	0.0550
Posterior disc length	6, 104	33.20	4.138	0.0543
Inner disc length	6, 104	8.95	5.268	0.0021
Disc base length	6, 104	17.52	4.935	0.0038
Snout to maximum disc width	6, 104	10.68	1.739	0.0476
Head length	6, 104	35.36	10.225	<0.0001
Preorbital length	6, 104	25.73	12.414	<0.0001
Eye length	6, 104	2.20	4.024	0.0156
Interorbital width	6, 104	8.47	16.428	<0.0001
Spiracle length	6, 104	1.22	4.669	0.0054
Interspiracular width	6, 104	13.15	32.374	<0.0001
First dorsal fin total length	6, 104	11.28	3.999	0.0168
First dorsal fin base length	6, 104	1.49	5.429	<0.0001
First dorsal fin height	6, 104	1.72	11.989	<0.0001
Second dorsal fin base length	6, 104	1.02	3.183	0.0096
Second dorsal fin height	6, 104	0.62	3.541	0.0288
Interdorsal space	6, 104	5.42	15.274	<0.0001
Caudal fin base length	6, 104	2.44	3.938	0.0154
Caudal fin height	6, 104	0.38	4.264	0.0105
Preoral length	6, 104	23.23	12.013	<0.0001
Mouth width	6, 104	9.13	9.700	<0.0001
Prenarial length	6, 104	24.55	16.239	<0.0001
Internarial width	6, 104	13.35	21.856	<0.0001
Nasal curtain width	6, 104	4.87	4.678	0.0068
Snout to first gill slits	6, 104	24.37	10.976	<0.0001
Snout to fifth gills slits	6, 104	16.67	3.253	0.0378
First gill slit length	6, 104	0.43	3.752	0.0230
Second gill slit length	6, 104	1.02	8.712	<0.0001

Third gill slit length	6, 104	1.10	7.612	<0.0001
Fourth gill slit length	6, 104	1.22	8.435	<0.0001
Fifth gill slit length	6, 104	0.88	5.195	0.0020
Space between the first gill slits	6, 104	39.16	7.929	<0.0001
Space between the fifth gill slits	6, 104	24.86	11.550	<0.0001
Clasper inner length	5, 55	19.16	2.884	0.0390
Clasper outer length	5, 55	6.87	4.533	0.0413
Pelvic fin length	6, 104	10.85	2.539	0.0520
Pelvic fin posterior lobe length	6, 104	128.92	25.455	<0.0001
Pelvic fin anterior lobe length	6, 104	20.77	17.654	<0.0001
Pelvic fin anterior inner lobe length	6, 104	17.52	5.436	<0.0001
Precaudal length	6, 104	5131.64	86.701	<0.0001
Tail length	6, 104	64.26	2.861	0.0156

Note: Alpha = 0.05. P-values were corrected for multiple comparisons using the sequential Bonferroni correction.

Means and standard errors of key morphological and meristic measurements showed clear differences between species, with certain measurements showing strong differentiation. Standard errors for *B. spinosissima* were often larger than the other species. This is due to *B. spinosissima* representing the lowest sample size (N = 4), which drove the larger standard errors displayed by the species. Overall, morphological variations were easily identifiable and can be used for species identification. Despite several morphological characters being valuable for species-specific identification, disc measurements were shown to be relatively similar across all species (Figure 45). Measurements such as disc length, anterior disc length, and posterior disc length did not show significant differences in means. Other measurements, including total length and disc base length, were more informative and showed differences between species.

Bathyraja abyssicola was found to be significantly different from most species, based on length and disc measurements. *Bathyraja abyssicola* was significantly larger than *B. kincaidii*, which represents the smallest species included in the study. The only species investigated that was similar in size to *B. abyssicola* is *B. spinosissima*. Disc width was informative, as significant differences in the means were found for *B. abyssicola* and *B. aleutica*. The two species were also significantly different in disc width from *B. interrupta* and *B. kincaidii*, which showed similar widths to each other.

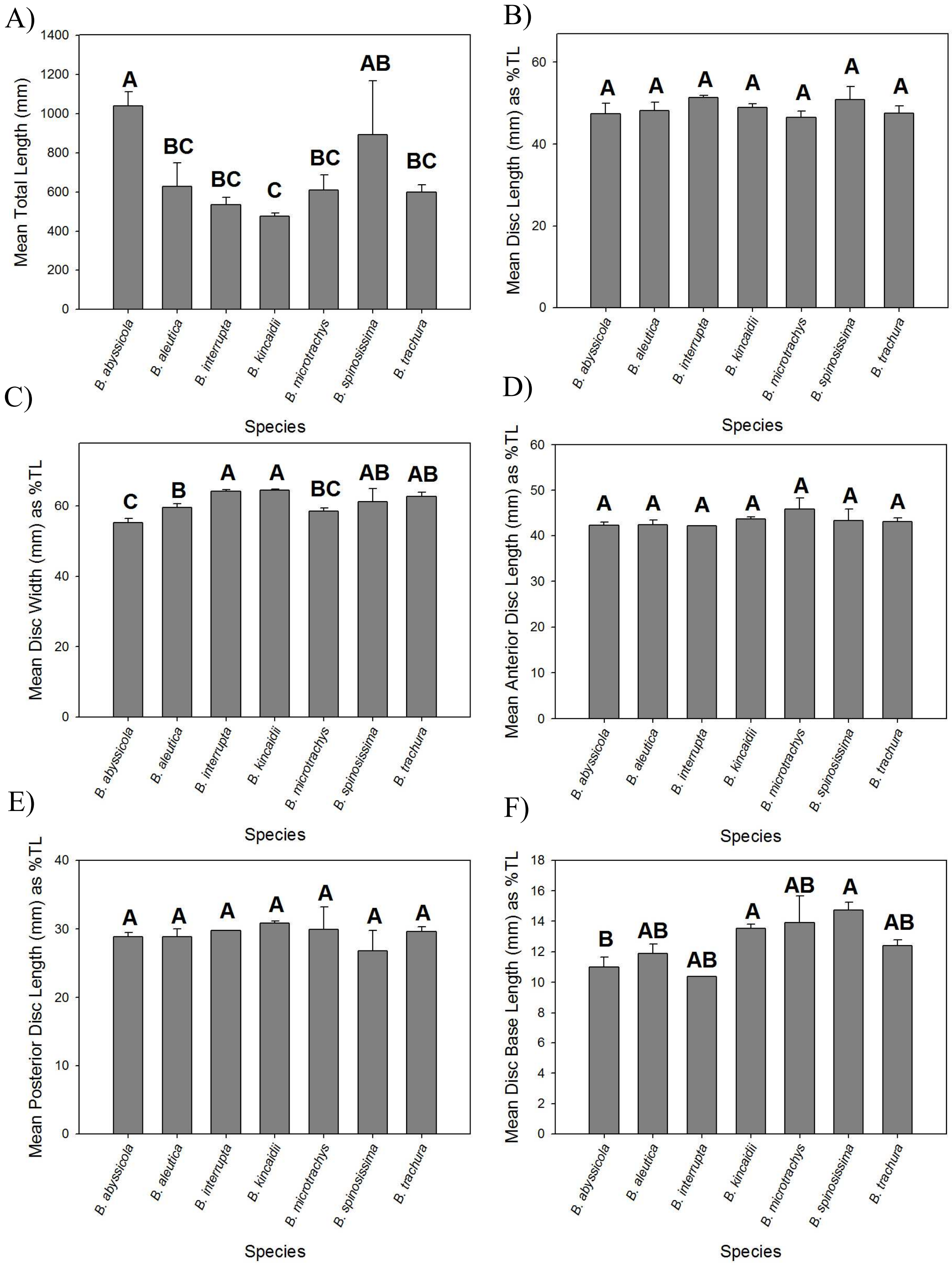

Figure 45. Mean total length and disc measurements by species in millimeters. Other than total length, all other measurements are taken as a percentage of total length (% TL). Bars indicate the standard error from the mean. Letters show whether means are significantly different across species; A. total length; B. disc length; C. disc width; D. anterior disc length; E. posterior disc length; F. disc base length.

Means and standard errors of morphological head and interdorsal measurements showed significant differences between species, with specific measurements showing strong differentiation (Figure 46). *Bathyraja aleutica* possessed a significantly larger interdorsal space than the other species investigated in this study. Another species, *B. abyssicola*, was shown to possess a significantly larger prenarial length than other species, especially when compared to *B. spinosissima* and *B. trachura*. Conversely, the mean measurement of mouth width for *B. spinosissima* was shown to be significantly larger than any other species investigated in this study. Moreover, *B. spinosissima* had significantly larger nasal curtain widths than the means for *B. interrupta* and *B. kincaidii*. Internarial width displayed the widest range in significant means for any measurement included in the study. As with other measurements of the head, the internarial width was shown to be significantly larger in *B. spinosissima* and significant differences in the means were found for *B. interrupta*, *B. kincaidii*, and *B. microtrachys*.

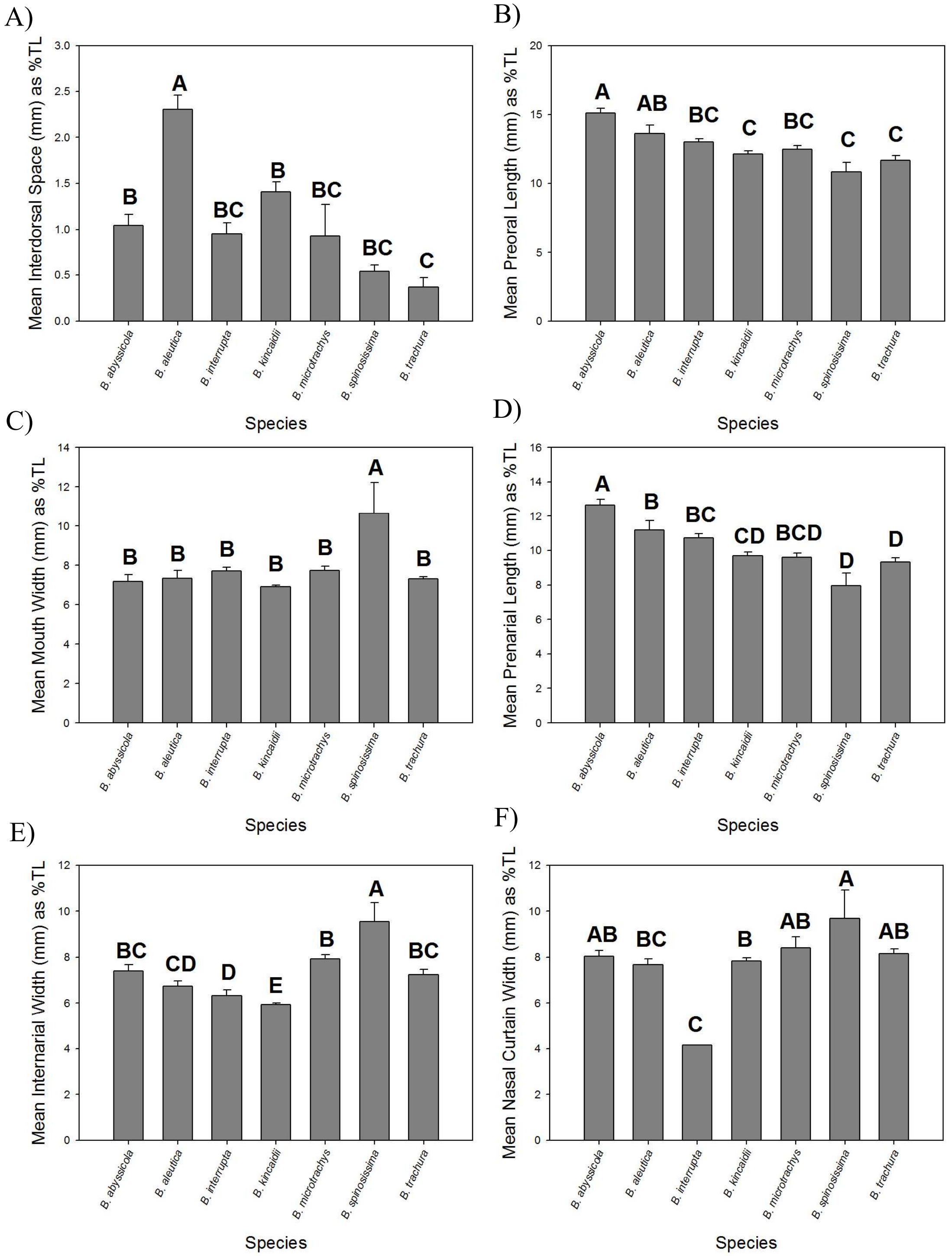

Figure 46. Mean body measurements by species in millimeters, measurements are taken as a percentage of total length (% TL). Bars indicate the standard error from the mean. Letters show whether means are significantly different across species; A. interdorsal space; B. preoral length; C. mouth width; D. prenarial length; E. internarial width; F. nasal curtain width.

Bar plots of mean head measurements showed significant differences between species, with specific measurements showing clear dissimilarities (Figure 47). *Bathyraja abyssicola* displayed significantly larger average head lengths and preorbital lengths than any other species included in the study. The results of this comparison supports the previously reported statement that *B. abyssicola* displayed the largest head length and snout length measurements of any species investigated in the study. *Bathyraja spinosissima* also showed significant dissimilarities for mean interspiracular length measurements, with the species having a longer length than any other species. Significant differences in the mean interspiracular lengths were shown to exist between *B. abyssicola* and *B. microtrachys*, which was in turn similar to *B. trachura*. The measurement for preorbital length showed a high degree of diversity, and points to the measurement being useful for identification of species. Significant differences were also found in the mean spiracle lengths for *B. trachura* and *B. microtrachys*, with *B. trachura* possessing a longer length.

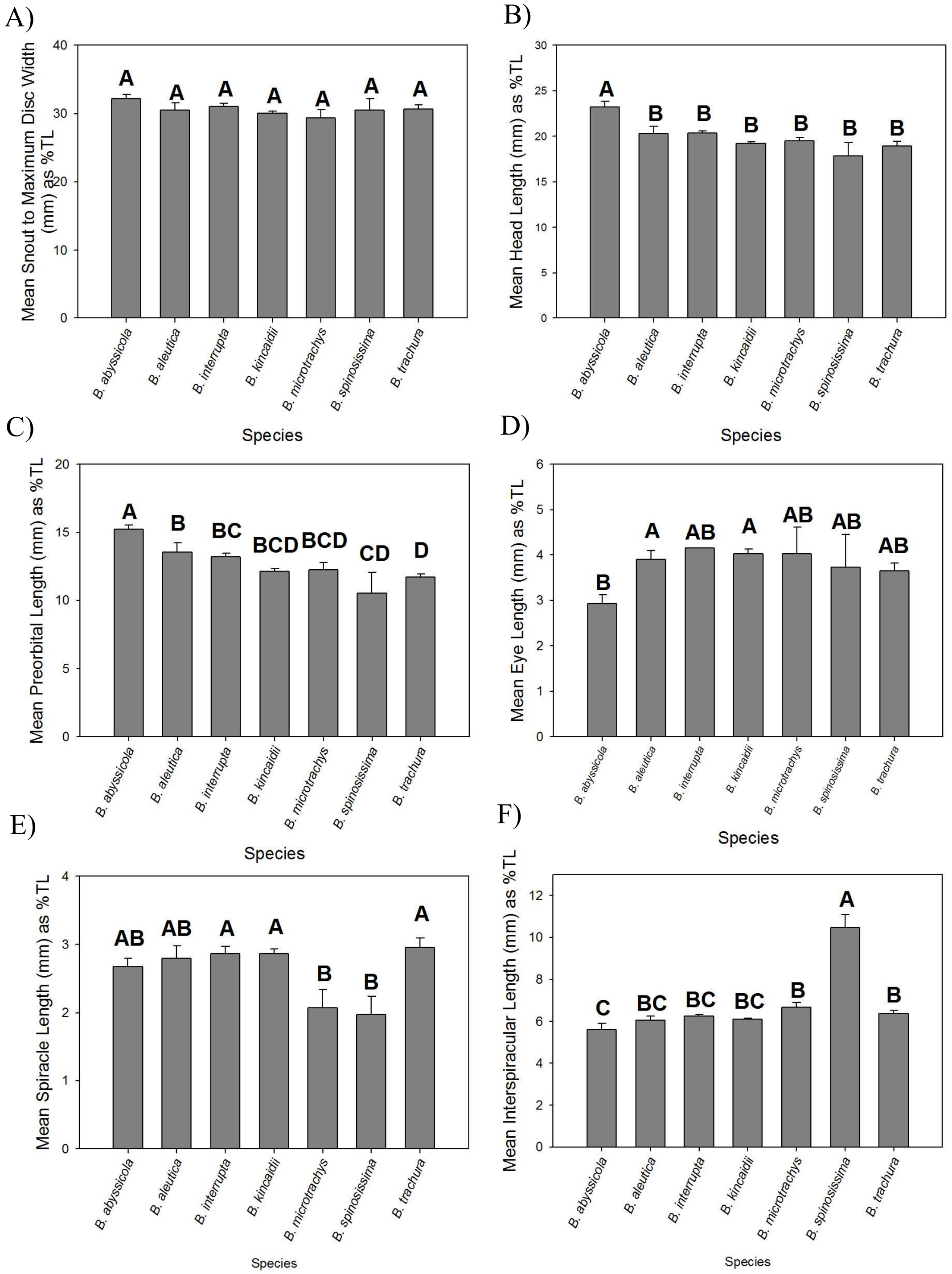

Figure 47. Mean body measurements by species in millimeters, measurements are taken as a percentage of total length (% TL). Bars indicate the standard error from the mean. Letters show whether means are significantly different across species; A. snout to max disc width; B. head length; C. preorbital length; D. eye length; E. spiracle length; F. interspiracular length.

Means and standard errors of morphological tail fin measurements displayed significant differences, with certain measurements showing obvious differentiation between species (Figure 48). *Bathyraja spinosissima* had a significantly larger caudal base length than all the species investigated in this study, with the exception of *B. microtrachys*. Significant differences existed between *B. interrupta* and *B. kincaidii* when comparing second dorsal fin base lengths, with *B. interrupta* possessing a larger base length. Moreover, *B. kincaidii* had a significantly larger first dorsal fin height than *B. abyssicola*, *B. microtrachys*, and *B. spinosissima*. In fact, *B. spinosissima* had a significantly smaller first dorsal fin height measurement than every other species and possessed one of the smallest second dorsal fin heights of the species investigated. Despite several significant differences in the means being portrayed by the bar plots, fin measurements were not as informative differentiators as other morphological measurements taken in this study.

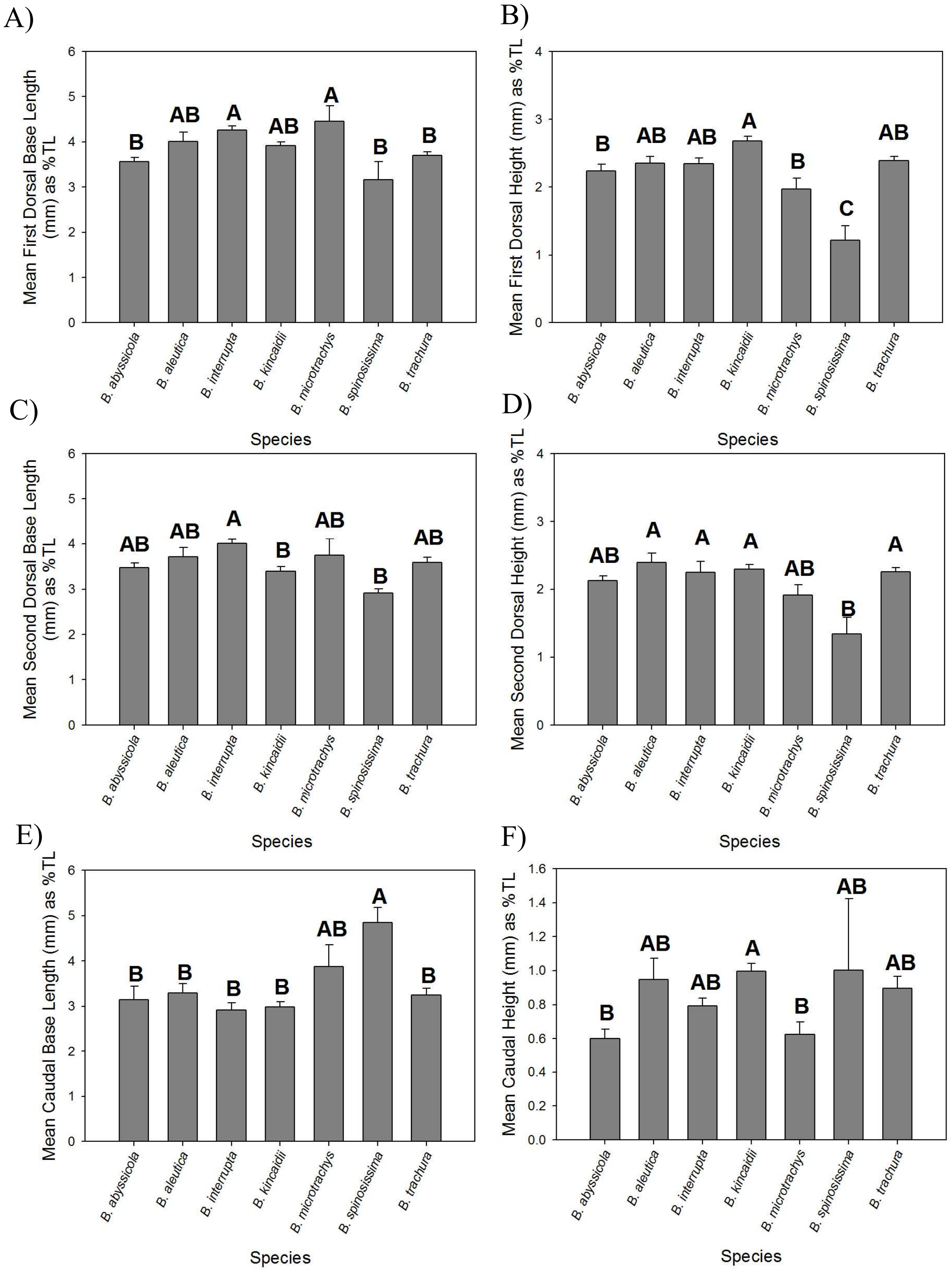

Figure 48. Mean fin measurements by species in millimeters, measurements are taken as a percentage of total length (% TL). Bars indicate the standard error from the mean. Letters show whether means are significantly different across species; A. first dorsal fin base length; B. first dorsal fin height; C. second dorsal fin base length; D. second dorsal fin height; E. caudal fin base length; F. caudal fin height.

Means and standard errors of pelvic fin and tail length measurements showed significant dissimilarities between species, with specific measurements displaying strong differentiation for the species investigated (Figure 49). Specifically, *B. interrupta* had a much longer pelvic fin posterior lobe than all other species of ENP bathyrajids, pointing to its usefulness when identifying species, especially against the closely related *B. kincaidii*. The precaudal length also proved useful for identification, as significant differences were displayed for *B. interrupta* and *B. microtrachys*, with *B. interrupta* possessing the shortest length of any ENP bathyrajid species. Pelvic length was found to be uninformative, as no significant differences were found in the means. The pelvic fin anterior lobe length did display obvious differences and had a high diversity of significance. *Bathyraja kincaidii* possessed a longer pelvic anterior lobe length than all species, except for the closely related *B. interrupta*. Similarly, the pelvic fin anterior lobe inner length showed a wide range of differences and can be useful for species identification.

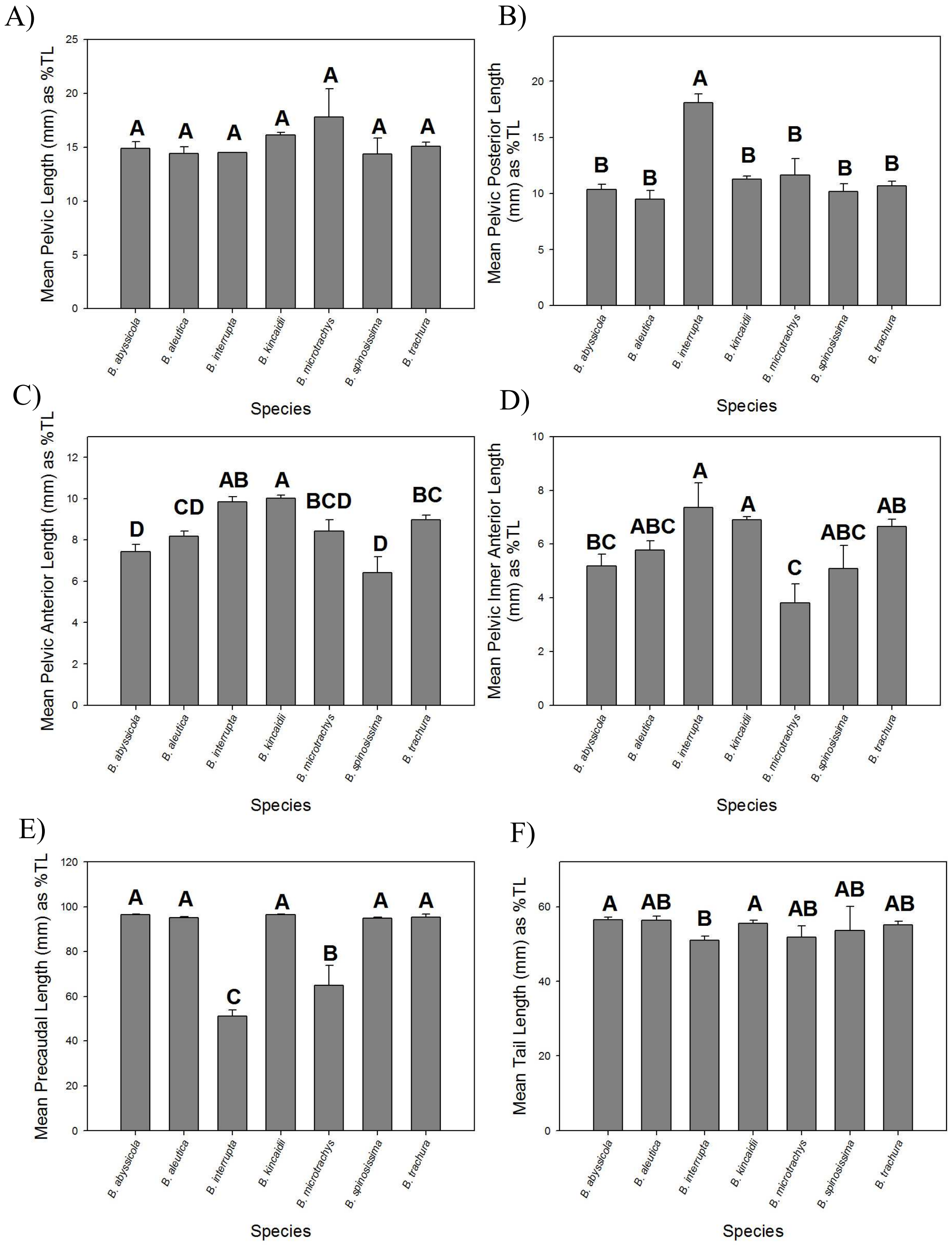

Figure 49. Mean pelvic fin and tail measurements by species in millimeters, measurements are taken as a percentage of total length (% TL). Bars indicate the standard error from the mean. Letters show whether means are significantly different across species; A. pelvic fin length; B. pelvic fin posterior lobe length; C. pelvic fin anterior lobe length; D. pelvic fin anterior lobe inner length; E. precaudal length; F. tail length.

Thorn counts have been known to be important in the identification of skates and bar plots showed significant differences between the means of thorn counts for the species investigated in this study (Figure 50). Middorsal thorn counts were shown to be the most significant, with *B. aleutica* having the largest mean thorn count and *B. abyssicola* possessing the smallest count. Scapular thorns on the left side of the disc showed no significant differences, but *B. abyssicola* had a significantly higher count on the right side when compared to *B. kincaidii*. Additionally, *B. kincaidii* displayed a significantly smaller tail thorn count when compared to all other ENP bathyrajids. Moreover, *B. trachura* had the largest tail thorn count and was significantly larger than *B. interrupta*. It should be noted that thorns do not exist in the middorsal, nuchal, and scapular regions in *B. microtrachys* and *B. spinosissima*. *Bathyraja trachura* possesses nuchal thorns, but lacks them in the middorsal and scapular regions. The results of the bar plots and the significance attached to them support the importance of thorn counts in skate species identification.

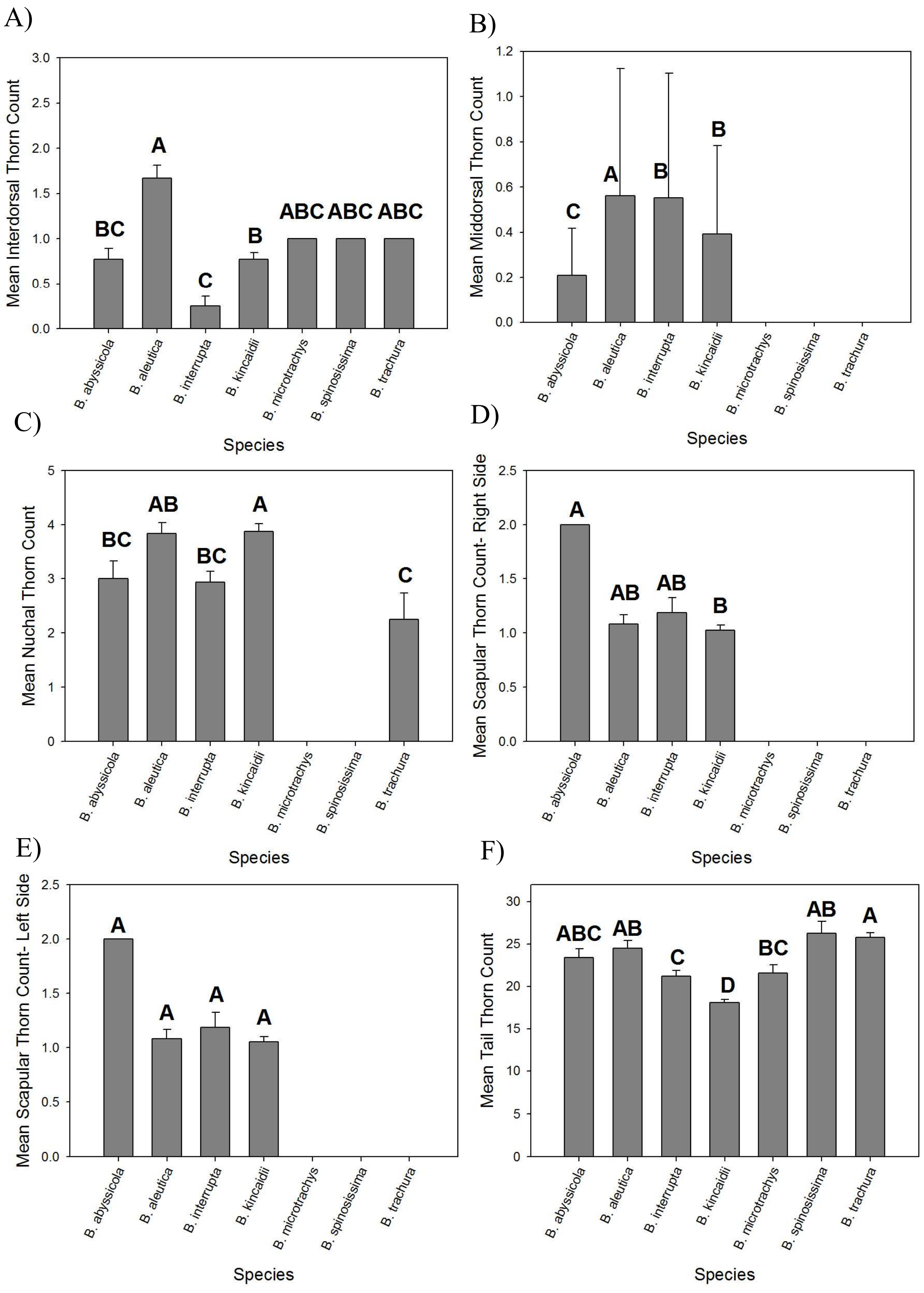

Figure 50. Mean thorn counts by species by species, bars indicate the standard error from the mean. Letters show whether means are significantly different across species; A. interdorsal thorns; B. middorsal thorns; C. nuchal thorns; D. scapular thorns- right side; E. scapular thorns- left side; F. tail thorns.

ANOSIM tests detected fairly strong separations among species groupings (Global R = 0.578, p = 0.1) (Table 10). Results of the pairwise comparisons between species indicate that there is significant separation of species, with *B. kincaidii* and *B. spinosissima* displaying the most significant separation (R = 0.988, p = 0.1). Other pairwise comparisons that showed significant separation of species were *B. abyssicola* and *B. spinosissima* (R = 0.911, p = 0.1) and *B. interrupta* and *B. spinosissima* (R = 0.976, p = 0.1). Some pairwise comparisons showed less significant separation of species, such as *B. abyssicola* and *B. aleutica* (R = 0.223, p = 0.4) and *B. aleutica* and *B. microtrachys* (R = 0.305, p = 0.6). Despite the relatively few species comparisons that had weaker separation, the results of the ANOSIM tests suggest that species can be separated based on their morphological traits, as is visually demonstrated in the nMDS ordinations. Additional techniques may be required to separate some of the closely related species in these tests.

Table 10.

ANOSIM Values for the Seven Species of Bathyraja Included in this Study.

Species Comparisons	**R**	**p**
B. abyssicola and *B. aleutica*	0.223	0.4
B. abyssicola and *B. interrupta*	0.619	0.1
B. abyssicola and *B. kincaidii*	0.770	0.1
B. abyssicola and *B. microtrachys*	0.505	0.2
B. abyssicola and *B. spinosissima*	0.911	0.1
B. abyssicola and *B. trachura*	0.553	0.1
B. aleutica and *B. interrupta*	0.569	0.1
B. aleutica and *B. kincaidii*	0.657	0.1
B. aleutica and *B. microtrachys*	0.305	0.6
B. aleutica and *B. spinosissima*	0.852	0.2
B. aleutica and *B. trachura*	0.477	0.1
B. interrupta and *B. kincaidii*	0.427	0.1
B. interrupta and *B. microtrachys*	0.753	0.1
B. interrupta and *B. spinosissima*	0.976	0.1
B. interrupta and *B. trachura*	0.455	0.1
B. kincaidii and *B. microtrachys*	0.854	0.1
B. kincaidii and *B. spinosissima*	0.988	0.1
B. kincaidii and *B. trachura*	0.344	0.1
B. microtrachys and *B. spinosissima*	0.560	2.5
B. microtrachys and *B. trachura*	0.497	0.2
B. spinosissima and *B. trachura*	0.787	0.2
Global	0.568	0.1

Percent contributions of characteristics to the difference between species were determined via the utilization of a SIMPER analysis (Table 11). The SIMPER analysis selected five characteristics per species that contributed 4.34-16.78% of the differences between species with multiple measurements reoccurring as differentiating characteristics in multiple species. The traits that appear to be driving most of the speciation across all species are the interdorsal space, pelvic fin posterior lobe length, disc length, and interspiracular width. There are a couple species that have consistent measurements driving a majority of the differences. *Bathyraja aleutica* is differentiated from its congeners based on its interdorsal space. *Bathyraja interrupta* has a strong differentiation in its pelvic fin posterior lobe length from all of its conspecifics. Similarly, the interspiracular width appears to be driving the differences between *B. spinosissima* and the other species investigated. As with *B. aleutica*, differences between *B. trachura* and its congeners are consistently driven by the interdorsal space. Results of the SIMPER analysis point towards certain morphological measurements being important for separating certain species. Not every species shares the same measurements as being important for speciation, but when taken as a whole, each putative species displays strong differences from each other.

Table 11.

SIMPER Pairwise Comparison of Morphological Measurements.

Species Comparisons	**Measurement**	**Contributing Percent (%)**	**Cumulative Percent (%)**
B. abyssicola and *B. aleutica*	Disc length	9.35	
	Interdorsal space	7.44	
	Head length	6.10	
	Disc width	5.96	
	Pelvic posterior lobe length	5.46	34.31
B. abyssicola and *B. interrupta*	Pelvic posterior lobe length	14.04	
	Disc width	8.00	
	Pelvic anterior lobe inner length	7.45	
	Disc length	6.17	
	Pelvic anterior lobe length	5.91	41.57
B. abyssicola and *B. kincaidii*	Disc width	8.37	
	Disc length	7.34	
	Pelvic anterior lobe length	6.30	
	Prenarial length	6.21	
	Pelvic anterior lobe inner length	6.11	34.33
B. abyssicola and *B. microtrachys*	Disc length	7.61	
	Pelvic anterior lobe inner length	6.85	
	Pelvic posterior lobe length	6.73	
	Interdorsal space	6.34	
	Prenarial length	5.99	33.52
B. abyssicola and *B. spinosissima*	Interspiracular width	7.62	
	Preorbital length	7.16	
	Prenarial length	7.09	
	Head length	6.9	
	Preoral length	6.17	34.94
B. abyssicola and *B. trachura*	Interdorsal space	8.30	
	Disc length	8.25	
	Disc width	7.55	
	Prenarial length	6.74	
	Head length	6.51	

	Preorbital length	6.44	43.79
B. aleutica and *B. interrupta*	Pelvic posterior lobe length	16.78	
	Interdorsal space	8.04	
	Pelvic anterior lobe length	6.07	
	Disc length	5.97	
	Disc width	4.75	41.61
B. aleutica and *B. kincaidii*	Disc length	7.62	
	Pelvic posterior lobe length	7.42	
	Interdorsal space	6.75	
	Disc width	5.49	
	Preorbital length	5.22	32.50
B. aleutica and *B. microtrachys*	Interdorsal space	9.80	
	Pelvic posterior lobe length	7.94	
	Pelvic anterior lobe inner length	7.85	
	Disc length	6.20	
	Snout to maximum disc width	4.76	31.79
B. aleutica and *B. spinosissima*	Interdorsal space	7.65	
	Interspiracular width	6.73	
	Preorbital length	5.92	
	Mouth width	5.76	
	Interorbital width	5.53	31.59
B. aleutica and *B. trachura*	Interdorsal space	15.64	
	Disc length	8.05	
	Pelvic posterior lobe length	6.01	
	First dorsal fin total length	5.26	
	Disc width	5.10	40.06
B. interrupta and *B. kincaidii*	Pelvic posterior lobe length	16.57	
	Interdorsal space	6.88	
	Pelvic anterior lobe inner length	6.08	
	Disc length	4.85	
	Prenarial length	4.34	38.72
B. interrupta and *B. microtrachys*	Pelvic posterior lobe length	12.43	
	Pelvic anterior lobe inner length	11.10	
	Interdorsal space	6.70	
	Disc length	5.02	

	Disc width	5.01	40.26
B. interrupta and *B. spinosissima*	Pelvic posterior lobe length	10.76	
	Pelvic anterior lobe length	6.01	
	Interspiracular width	5.99	
	Interorbital width	5.92	
	Pelvic anterior lobe inner length	5.64	34.32
B. interrupta and *B. trachura*	Pelvic posterior lobe length	15.65	
	Interdorsal space	9.35	
	Disc length	6.28	
	Pelvic anterior lobe inner length	5.82	
	First dorsal fin total length	4.38	41.48
B. kincaidii and *B. microtrachys*	Pelvic anterior lobe inner length	10.47	
	Interdorsal space	7.92	
	Pelvic posterior lobe length	6.84	
	Disc length	5.58	
	Disc width	5.42	36.23
B. kincaidii and *B. spinosissima*	Interspiracular width	6.96	
	Pelvic anterior lobe inner length	6.96	
	Mouth width	6.30	
	Interorbital width	5.83	
	Internarial width	5.68	31.73
B. kincaidii and *B. trachura*	Interdorsal space	13.70	
	Disc length	8.27	
	Pelvic posterior lobe length	5.40	
	Prenarial length	4.92	
	First dorsal fin total length	4.51	36.80
B. microtrachys and *B. spinosissima*	Interspiracular width	6.38	
	Mouth width	6.35	
	Pelvic anterior lobe inner length	6.00	
	Pelvic posterior lobe length	5.90	
	Interdorsal space	5.55	30.18
B. microtrachys and *B. trachura*	Pelvic anterior lobe inner length	10.34	
	Interdorsal space	9.14	

	Pelvic posterior lobe length	7.37	
	Disc length	7.08	
	Disc width	5.46	39.39
B. spinosissima and *B. trachura*	Interspiracular width	6.96	
	Mouth width	6.50	
	Disc length	5.82	
	Pelvic anterior lobe length	5.62	
	Pelvic anterior lobe inner length	5.45	30.35

Note: Displayed are the top five ranked morphometric measurements for each species comparison; the contributing and cumulative percents are expressed as %.

Principal component analyses (PCAs) were performed to visualize the characters that drive the species separation displayed in the nMDS ordinations (Figure 51). Traits were selected to be analyzed based on the multivariate analyses and *post hoc* tests performed earlier in the study. Characters that appeared to be driving species differentiation were selected and morphological differences in species were shown to be well described by the loadings of with the two principal components (PC1 and PC2) in multivariate space. Specimens with long disc lengths showed a positive correlation with disc width and the snout to maximum disc width, with PC1 and PC2 explaining 83.7% of the variability (Figure 51a). *Bathyraja abyssicola* had small disc width, but a long snout to maximum disc width. PC1 described large disc measurements and PC2 described species with long snout to maximum disc widths and short disc widths. Disc length was non-informative when described byPC2. As would be expected, specimens with long snout to maximum disc widths possessed longer head lengths and snout lengths, with PC1 and PC2 explaining 90.0% of the combined variability (Figure 51b). As was demonstrated in prior analyses, *B. abyssicola* possesses the longest head length of any species investigated and this was shown by its positive correlation with head length and lengths of the snout.

Bathyraja spinosissima showed an opposite trend, as it possesses a smaller head than *B. abyssicola* when compared to its total length. PC1 described species with long head measurements; PC2 described species with long snout to maximum disc widths and short snout lengths. The PCA plot of dorsal and caudal fin measurements showed a positive correlation as specimens possessing long fin heights had large fin base lengths (Figure 52a). PC1 and PC2 explained 58.1% of the variability in fin measurements and PC1 described the fins in a positive fashion, with PC2 describing species with large fin heights and short fins bases. *Bathyraja spinosissima* displayed a very large caudal base length, but relatively short fin heights. The rest of the species tended to group together and were not as correlated as *B. spinosissima*. Additionally, the relationship between pelvic measurements was positive, as specimens with long anterior lobe lengths had longer pelvic fin and posterior lobes (Figure 52b). PC1 was shown to describe species with long pelvic measurements. Conversely, PC2 generally described species with long anterior lobe lengths and shorter posterior lobe lengths. Combined, PC1 and PC2 explained 79.8% of the variability in the plot. *Bathyraja interrupta* had long pelvic lobe lengths, as compared to the shorter lengths found in *B. spinosissima*, *B. microtrachys*, *B. abyssicola*, and *B. aleutica*. As shown in the plot, tail length was negatively correlated with disc length and width; specimens with short tails had long disc measurements (Figure 53a). Tail length was shown to have a correlation with total length and interdorsal space. PC1 generally described species with long disc measurements and short tail, interdorsal, and total lengths. PC2 explained species with long tail lengths and interdorsal spaces, but with shorter total lengths. Overall, PC1 and PC2 explained 56.9% of the total variability for disc and tail measurements. The two largest species in the study, *B. abyssicola* and *B. spinosissima*, had short tails compared to other species in the study, such as *B. kincaidii*. *Bathyraja aleutica* had a long tail length and a shorter disc length and width. Unexpectedly, specimens with shorter spiracle lengths were found to have long interorbital and interspiracular widths, with PC1 and PC2 explaining 88.3% of the total variability (Figure 53b). PC1 tended to describe species with short spiracle lengths and long interspiracular and interorbital widths, whereas PC2 generally described species with large spiracles and widths. *Bathyraja spinosissima* was located in a distinct area of the plot due to its significantly larger interorbital and interspiracular widths, when compared to other species. All other species clustered around the center of the plot, so the correlation was not as informative for those species.

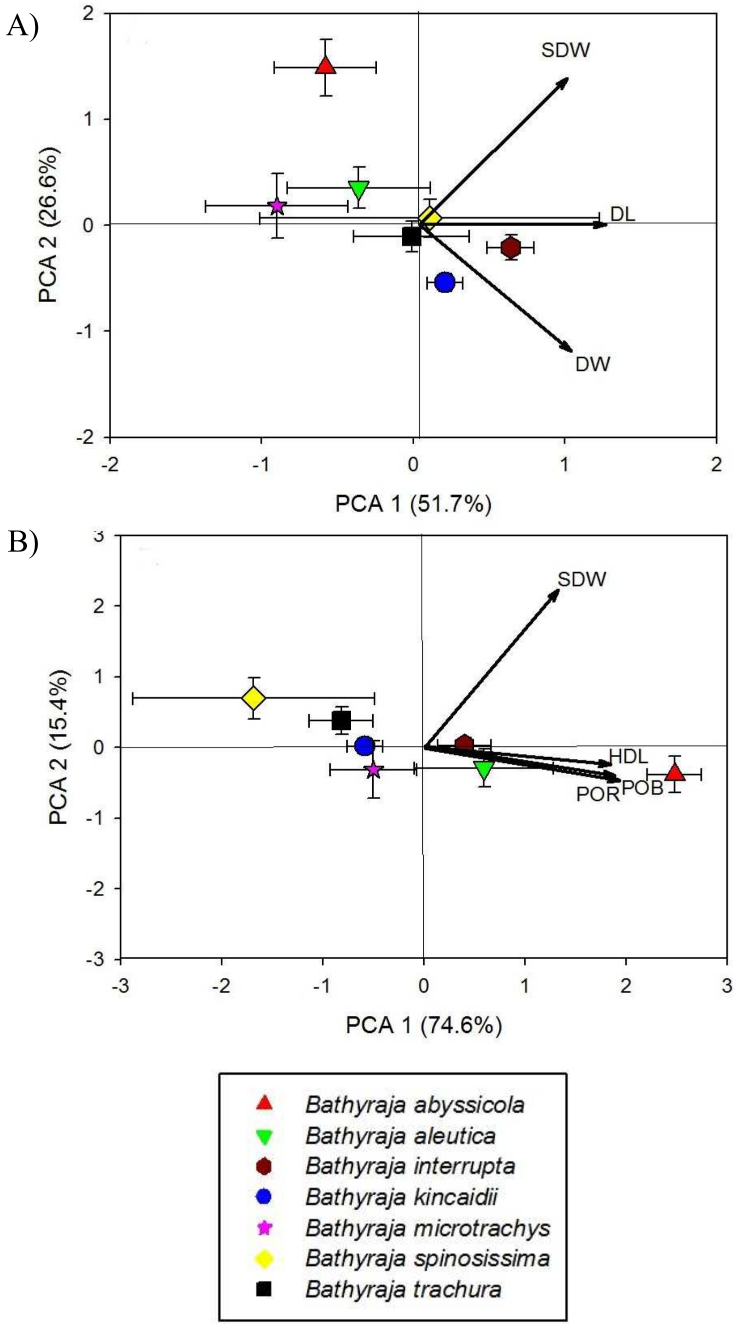

Figure 51. PCA plots of measurements relative to total length and their relationships to each other. Points indicate the average principal component (PC) scores with standard error bars. Lines indicate the eigenvector scores for each measurement. A. Disc length (DL), disc width (DW), and snout to maximum disc width (SDW); B. snout to maximum disc width, head length (HDL), preorbital length (POB), and preoral length (POR); Species shown by color: *Bathyraja abyssicola* (red triangle), *B. aleutica* (green triangle), *B. interrupta* (maroon hexagon), *B. kincaidii* (blue circle), *B. microtrachys* (pink star), *B. spinosissima* (yellow diamond), and *B. trachura* (black square).

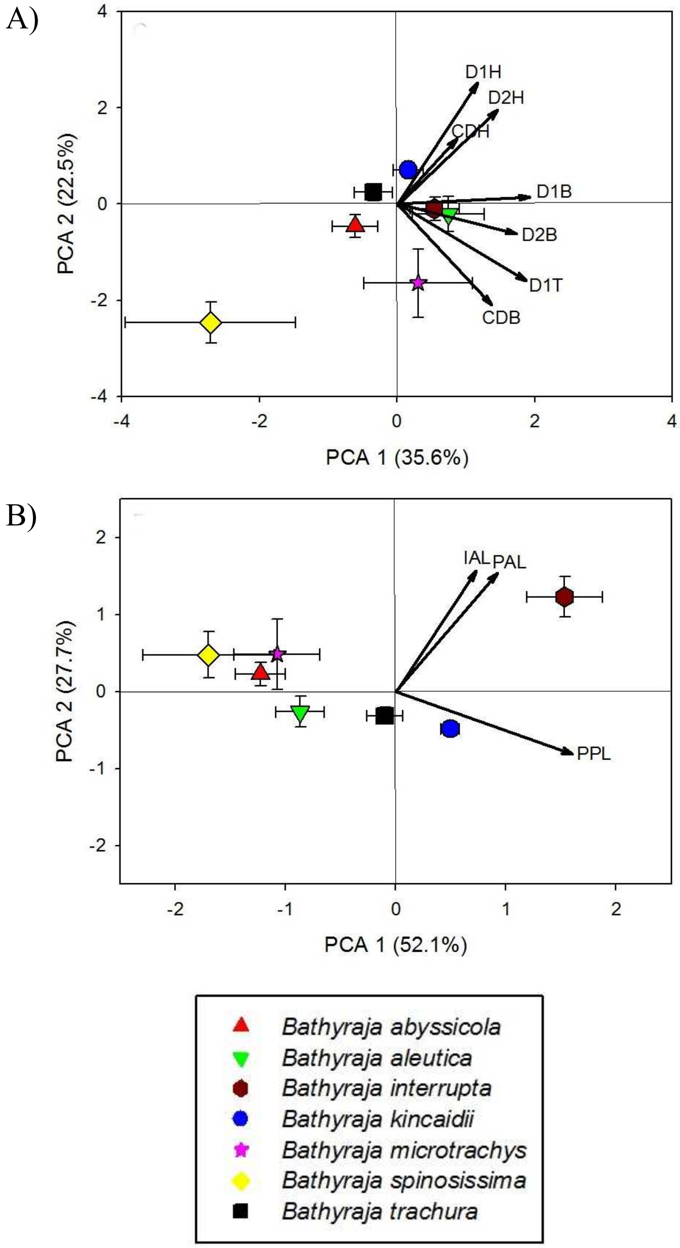

Figure 52. PCA plots of measurements relative to total length and their relationships to each other. Points indicate the average principal component (PC) scores with standard error bars. Lines indicate the eigenvector scores for each measurement. A. First dorsal fin total length (DIT), first dorsal fin height (D1H), first dorsal fin base length (D1B), second dorsal fin height (D2H), second dorsal fin base length (D2B), caudal fin height (CDH), and caudal fin base length (CDB); B. pelvic fin anterior lobe length (PPL), pelvic fin anterior lobe inner length (PAL), and pelvic fin posterior lobe length (IAL). Species shown by color: *Bathyraja abyssicola* (red triangle), *B. aleutica* (green triangle), *B. interrupta* (maroon hexagon), *B. kincaidii* (blue circle), *B. microtrachys* (pink star), *B. spinosissima* (yellow diamond), and *B. trachura* (black square).

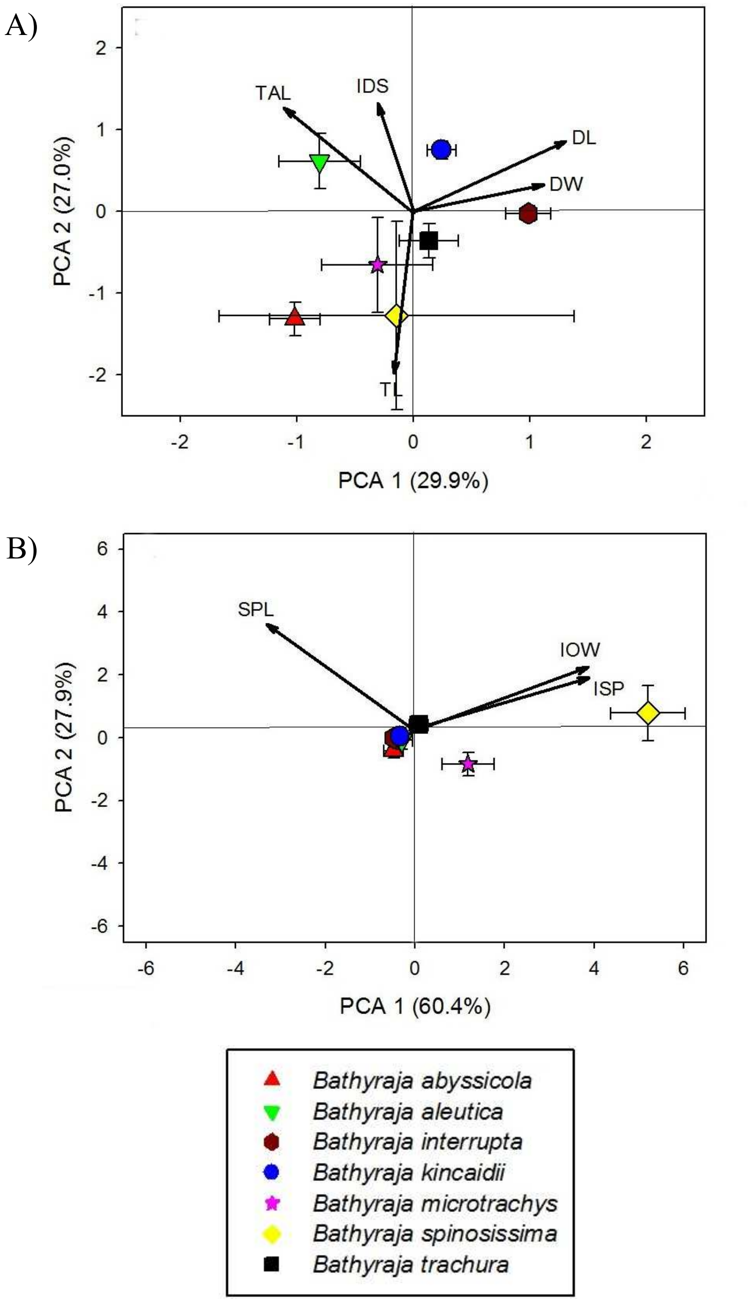

Figure 53. PCA plots of measurements relative to total length and their relationships to each other. Points indicate the average principal component (PC) scores with standard error bars. Lines indicate the eigenvector scores for each measurement. A. Total length (TL), disc length, disc width, interdorsal space (IDS), and tail length (TAL); B. spiracle length (SPL), interspiracular space (ISP), and interorbital width (IOW). Species shown by color: *Bathyraja abyssicola* (red triangle), *B. aleutica* (green triangle), *B. interrupta* (maroon hexagon), *B. kincaidii* (blue circle), *B. microtrachys* (pink star), *B. spinosissima* (yellow diamond), and *B. trachura* (black square).

Three equally parsimonious trees were created to show the phylogenetic relationships between the seven study species, in addition to an outgroup, *Beringraja inornata* (Figure 54, Tables 12-13). The resolved trees show three likely phylogenetic relationships and all three took 152 steps to complete. The three trees are similar, but some differences exist between them. In all trees *B. interrupta* and *B. kincaidii*, the two species who are the closest morphologically, are located near each other and are the most basal bathyrajids in the ENP. *Bathyraja interrupta* and *B. kincaidii* therefore appear to be the closest softnose skate relatives to *Beringraja* in the ENP. Based on morphological and meristic data, *B. spinosissima* and *B. microtrachys* group together in two of the three trees and appear to be closely related. *Bathyraja trachura* is consistently located on other branches from *B. microtrachys*, a species that it is similar to in size and coloration. *Bathyraja abyssicola* and *B. aleutica* appear to be the most derived of the species examined in the tree and are found on separate branches from the other species in all three parsimonious trees. *Bathyraja abyssicola* and *B. aleutica* appear to be the closest related species, despite obvious morphological differences.

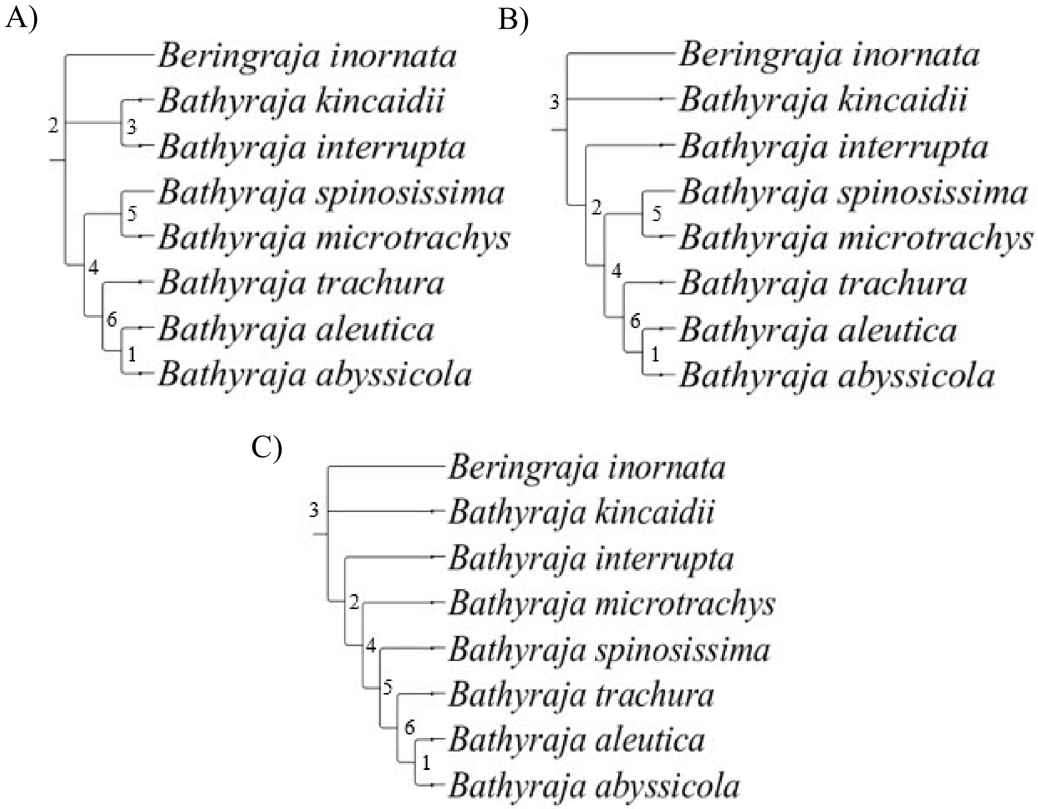

Figure 54. Three equally parsimonious trees of the seven study species, plus a rooted outgroup species, *Beringraja inornata*. A. Maximum parsimony tree displaying a branch that is comprised of *Bathyraja interrupta* and *B. kincaidii*; B. Maximum parsimony tree with *B. kincaidii* and *B. interrupta* on separate branches; C. Maximum parsimony tree displaying all species as being on separate branches, except *B. abyssicola* and *B. aleutica*. The numbers on the branches indicate the number of changes between character states.

Table 12.

Data Matrix of the Characters States Used to Generate the Three Equally Parsimonious Trees for Bathyraja abyssicola, B. aleutica, B. interrupta, and B. kincaidii.

Measurement	***Bathyraja abyssicola***	***Bathyraja aleutica***	***Bathyraja interrupta***	***Bathyraja kincaidii***
Dorsal coloration	1	1	2	2
Ventral coloration	2	1	1	1
Total Length	1	2	2	3
Disc length	1	2	2	3
Disc width	1	2	2	3
Anterior disc length	1	1	3	1
Anterior anterior disc length	1	1	3	1
Posterior anterior disc length	1	1	3	1
Posterior disc length	3	3	3	2
Inner disk length	2	2		1
Disk base length	2	2	3	2
Snout to maximum disk width	1	1		2
Head length	1	1	2	2
Preorbital length	1	2	2	3
Eye length	1	2		3
Interorbital width	1	3	3	3
Spiracle length	2	1	2	2
Interspiracular width	1	2	3	3
First dorsal fin origin to tail tip	1	1	2	2
First dorsal fin base length	1	1	2	2
First dorsal fin vertical height	1	2	1	2
Second dorsal fin base length	1	1	2	2
Second dorsal fin vertical height	1	1	2	2
Interdorsal space	1	1	2	2
Caudal fin base length	1	2	3	3
Caudal fin height	3	1	2	1
Preoral snout length	1	1	3	3
Prenarial snout length	1	1	3	3
Internarial width	2	3	3	3
Nasal curtain length	2	3	1	1
Nasal curtain width	2	3		3

Mouth width	2	3	3	3
Snout to first gill slit	2	2	2	2
Snout to fifth gill slit	1	1		3
First gill slit length	2	2		2
Pelvic fin posterior lobe length	1	2	1	3
Pelvic fin anterior lobe length	1	3	2	3
Pelvic fin anterior lobe inner length	1	2	2	3
Clasper length (mature)	1	3	1	1
Clasper width (mature)	3	1	1	3
Cleft shape	1	2	2	1
Projection	1	2	1	1
Pseudosiphon	1	1	2	2
Pseudorhipidion	2	3	1	2
Sentina	2	2	1	1
Precaudal length	2	2	2	2
Tail length	1	2	3	3
Interdorsal thorn count	3	2	3	2
Middorsal thorns	1	1	1	1
Nuchal thorns	1	1	1	1
Scapular thorns	1	1	1	1
Tail thorn count	1	1	3	3
Alar thorn count- rows	2	1	2	3
Alar thorn count- columns	2	2	2	2
Vertebral count	2	1	2	2
Upper tooth count	1	1	2	2
Lower tooth count	2	2	2	2
Pectoral fin radial count	2	1		3
Pelvic fin radial count	2	2		3
Calcified rostrum	2	2	2	2

Table 13.

Data Matrix of the Characters States Used to Generate the Three Equally Parsimonious Trees for Bathyraja microtrachys, B. spinosissima, B. trachura, and Beringraja inornata.

Measurement	***Bathyraja microtrachys***	***Bathyraja spinosissima***	***Bathyraja trachura***	***Beringraja inornata***
Dorsal coloration	1	3	1	2
Ventral coloration	1	1	2	1
Total Length	2	1	2	2
Disc length	2	1	2	3
Disc width	2	1	2	3
Anterior disc length	2	3	3	3
Anterior anterior disc length	2	3	3	3
Posterior anterior disc length	2	3	3	3
Posterior disc length	1	2	3	3
Inner disk length	3	3	2	2
Disk base length	1	2	2	1
Snout to maximum disk width	2	2	1	3
Head length	3	3	1	3
Preorbital length	2	2	2	3
Eye length	2	1	2	
Interorbital width	3	1	3	2
Spiracle length	2	3	1	2
Interspiracular width	2	1	3	2
First dorsal fin origin to tail tip	1	2	2	2
First dorsal fin base length	1	2	2	1
First dorsal fin vertical height	2	3	2	2
Second dorsal fin base length	2	3	2	3
Second dorsal fin vertical height	2	3	1	1
Interdorsal space	2	2	3	2
Caudal fin base length	1	1	2	2
Caudal fin height	2	1	1	2
Preoral snout length	3	2	2	2
Prenarial snout length	3	3	2	3
Internarial width	2	1	2	3
Nasal curtain length	3	1	3	1
Nasal curtain width	3	1	2	3
Mouth width	3	1	3	3

Snout to first gill slit	2	2	2	1
Snout to fifth gill slit	3	3	3	3
First gill slit length	3	2	2	2
Pelvic fin posterior lobe length	2	2	3	1
Pelvic fin anterior lobe length	3	2	2	2
Pelvic fin anterior lobe inner length	3	2	2	3
Clasper length (mature)	3		3	3
Clasper width (mature)	1		1	3
Cleft shape	2		2	
Projection	2		2	
Pseudosiphon	1		1	
Pseudorhipidion	1		3	
Sentina	2	2	2	
Precaudal length	1	2	2	3
Tail length	1	1	2	3
Interdorsal thorn count	3	3	3	1
Middorsal thorns	2	2	2	1
Nuchal thorns	2	2	1	1
Scapular thorns	2	2	2	2
Tail thorn count	2	2	1	1
Alar thorn count- rows	2		2	3
Alar thorn count- columns	2		2	3
Vertebral count	2	2	3	
Upper tooth count	2	2	2	1
Lower tooth count	3	2	2	1
Pectoral fin radial count	3		2	3
Pelvic fin radial count	3		2	1
Calcified rostrum	2	2	2	1

Discussion

Skates are a morphologically conservative clade and it is often difficult to identify species based on body measurements (McEachran & Dunn, 1998). Due to the morphological conservatism of skates, it is challenging to describe new species with confidence (McEachran & Dunn, 1998). Characteristics that separate species are often subtle, maybe internal, or may require knowledge of the genera's taxonomy in order to accurately identify to the species level. For example, a well-known and frequently studied European species, common skate, *Dipturus batis*, was shown to be a species complex based mostly on size at maturity (Iglésias, Toulhoat & Sellos, 2009). The species that form this complex are nearly identical in coloration and morphologies and share similar habitats, but are in fact separate species, as determined by morphology, genetics, and life histories (Iglésias et al., 2009). The smaller species, which reaches maturity at a younger age, is almost certainly more productive than the larger species (Iglésias et al., 2009), which has important implications for how the common skate bycatch fishery is managed. Similar to *Dipturus batis*, many of the species in the genus *Bathyraja* have overlapping morphometric characteristics and may involve complexes. It is the lack of obvious differences, combined with the inadequate original descriptions of the species, which compounds the problem of species-specific identification. It is not until the full suite of morphometric and meristic differences are taken into account that species may be separated with confidence.

Systematics underpins our understanding of life histories and those life histories lose value if the species they are describing are incorrectly synonymized and treated as a wide-ranging species (Mayr, 1996). These life history studies are valuable as they have been shown to be important to the effective management of bycatch (Ainsley, 2009). In the example of the *Dipturus batis* species complex above, the taxonomic combination of the larger maturing species with similar smaller species led to the mismanagement of the European skate fishery and the possible local extirpation of some species (Dulvy & Reynolds, 2009; Iglésias et al., 2009). With chondrichthyans, an enormous amount of biodiversity remains to be discovered, especially amongst batoids.

The eastern North Pacific genus *Bathyraja* has several species that have been synonymized due to confusion with overlapping morphological characteristics and a lack of available material to adequately describe them when they were initially defined (Ishihara & Ishiyama, 1985; Miller & Lea, 1972). In the present study, one of the more problematic species relationships is between *B. interrupta* and *B. kincaidii*, which have been synonymized by some authors (Coulson et al., 2011; Ishihara & Ishiyama, 1985) and considered separate species by others (Ebert, 2003; Kyne et al. 2012; Last et al., 2016). These two species are very similar in appearance and most likely form a species complex, especially in Alaska and the Bering Sea, where differences between specimens of *B. interrupta* have been reported (Kyne et al., 2012). The results of this study show that despite their similarities, these two skates are in fact separate species, as some previous life history studies have reported (Ainsley, 2009; Brown, 2010; Kemper, 2012; Perez, 2005). This separation of species is upheld by morphometric, meristic, and significant multivariate statistical differences. Specifically, *B. interrupta* differs from *B. kincaidii* in overall size, pelvic fin measurements, interdorsal distance, clasper morphology, denticle shape, and thorn counts. *Bathyraja interrupta* is a larger species than *B. kincaidii* and attains a larger total length than *B. kincaidii*. While size is a difficult character to use in field identification, as a small specimen could be either species, this study shows that there are other differences that separate the species. Differences in the size, shape, and internal structure of claspers have been shown to be very useful for the identification of skates (Ishihara & Ishiyama, 1985; Ishiyama, 1952). As with other skate species, *B. interrupta* and *B. kincaidii* possessed multiple differences in their claspers, notably in the shape of the projection, the size of the sentina, and the shape of the cleft.

In addition to clasper morphology, the best indicators for species identification in skates are often thorn counts (Ishihara & Ishiyama, 1985; Ishiyama, 1952). Marked differences between the thorn counts were found for *B. kincaidii* and *B. interrupta* in the present study. In *B. kincaidii* the higher numbers of middorsal and nuchal thorns were likely due to the single, uninterrupted row of thorns down the midline of the dorsal surface. *Bathyraja interrupta*, by comparison has an interrupted row of thorns with a gap between the middorsal and tail thorns. The interruption in the midline of the thorns is a highly useful characteristic for field identification. Even with the thorn count, *B. interrupta* and *B. kincaidii* are difficult to tell apart. This difficulty in telling the two species apart in the field has led to some issues in establishing their geographical distributions (Kyne et al., 2012). The possible species complex formed by *B. interrupta* and *B. kincaidii* is problematic when it comes to predicting population trends and setting management strategies.

Morphological and meristic differences between *B. microtrachys* and *B. trachura* were investigated to determine if these two species are the same or represent distinctly different species. *Bathyraja microtrachys* and *B. trachura* have been synonymized by some authors, and appear in some publications as a single species. This confusion arose when Miller and Lea (1972) synonymized *B. microtrachys* with *B. trachura*; based on Carl L. Hubbs' suggestion that *B. microtrachys* was a junior synonym. While recent systematic and life history studies have distinguished *B. microtrachys* as being separate from *B. trachura* (Boyle, 2010; Davis, 2006; Ebert, 2003; Last et al., 2016; Winton, 2011), there are still some authors that regard the two as a single species (Ishihara & Ishiyama, 1985). As this study shows, the two species are morphologically distinct. This is supported by differences in their morphometrics, meristics, and by significant statistical dissimilarities. *Bathyraja microtrachys* differs from *B. trachura* in coloration, dermal denticle size, disc size, pelvic fin measurements, clasper morphology, and nuchal thorn counts. Besides coloration, arguably the best diagnostic characteristic for the separation of these species are the dermal denticles. *Bathyraja microtrachys* has very fine dermal denticles on the dorsal surface and does not possess the noticeably larger and rougher denticles on the tail region that are found in *B. trachura*. As with other skate species, the mature claspers are highly indicative of speciation. Both species possess short and robust mature claspers, but differences in the length of the pseudorhipidion and the presence or absence of a projection can be used for identification purposes. Additionally, the presence of nuchal thorns in *B. trachura* and lack of them in *B. microtrachys* is a useful trait for identification purposes. It should be noted that this study describes the largest known adult male specimen of *B. microtrachys* and is the first time that claspers have been described for the species.

Multivariate statistical tests were run to determine whether there are significant morphological and meristic differences between the study species in a suite of traits. The results of the analyses, and their subsequent *post hoc* tests, showed that there were multiple characters that can be used to accurately identify the species examined this study. For the most part species clustered together in the nMDS ordinations when sex and maturity class were taken into account. Those ordinations in which sex and maturity were not considered showed significant overlap and low levels of dissimilarity between species. It is not until life stage and sex are considered that differences can be visualized. The analysis for adult females showed the species grouping into tight clusters, with *B. aleutica* grouping with *B. abyssicola* and *B. interrupta* and *B. kincaidii* forming a cluster. The other three species showed distinct grouping for adult females. The overlap of *B. abyssicola* and *B. aleutica*, as well as *B. interrupta* and *B. kincaidii*, was true for the adult male ordination as well. Morphological differences are nuanced when viewed from the perspective of the nMDS ordinations. *Bathyraja abyssicola* and *B. aleutica* are morphologically very similar, but significant statistical differences exist between them. The same statement holds true for *B. interrupta* and *B. kincaidii*. Overall, some putative species can be distinguished by the morphometric patterns, while other species cannot be readily distinguished based on their measurements, unless examined in a closer manner.

In order to investigate the relationship between species that had been previously synonymized, nMDS ordinations were ran to compare *B. interrupta* with *B. kincaidii* and

B. microtrachys with *B. trachura*. *Bathyraja interrupta* and *B. kincaidii*, no matter the sex or life stage, all displayed compact groupings, indicating high levels of dissimilarity, and therefore differentiation, between species. All but one juvenile specimen of *B. interrupta* grouped into clusters that were located in different areas of the plots. The visualization of the relationship between *B. microtrachys* and *B. trachura* showed similar levels of dissimilarity, supporting the hypothesis that the species are separate. This is especially true for adult males of the species. Due to the insufficient sampling of females for the two species, further investigations into the relationships are warranted. Overall, the results of the non-parametric tests for adult skates indicate that the specimens are morphologically distinct, which supports the hypothesis of the species status being valid for all species investigated in the study.

Non-parametric tests were run to for juvenile skates to determine whether there are morphological differences between the study species. The results of the nMDS ordinations for juveniles showed weaker dissimilarities than the adults. The species clustered together, but the groups were not as tight as they were in the adult ordinations. When two species were compared, as in the *B. interrupta* and *B. kincaidii* relationship, visualization of obvious differences became apparent. It is when all seven species are compared that morphological differences are more problematic to tease apart. Juveniles are often difficult to separate based solely on morphological characters. Meristics, such as thorn counts, and coloration play a large part in the identification of juvenile bathyrajids in the ENP.

Further analyses were run to determine if the hypotheses of speciation between the ENP bathyrajids could be supported. Analyses from the Tukey-Kramer HSD *post hoc* tests resulted in significant traits that drive differentiation and validated that there was separation amongst species. Not every measurement showed significant differences in the means, but every species displayed certain measurements that could be used to positively identify them. Additionally, ANOSIM and SIMPER analyses pointed to significant differences between species and the traits that drive those differences. PCA results supported the significant differences between species and identified correlations such as species with shorter tails tended to have the larger disc, long fins equated to tall fins, and that species with small spiracles had larger interspiracular and interorbital distances. All of these characters can be used to help positively separate species of bathyrajids from the ENP.

Phylogenetic relationships were investigated during the course of this study through the construction of three equally parsimonious trees and phylogenetic relationships that can be inferred from the trees. *Beringraja* was assigned as a rooted outgroup based on the presence of calcified rostral elements. The presence of a heavily calcified rostrum is considered a primitive state for the skates of the ENP (Ishiyama, 1952). According to the parsimony trees, *B. abyssicola* and *B. aleutica* are the most derived of the species studied. They are also the only two species that consistently grouped together on a branch across all trees. Conversely, *B. interrupta* and *B. kincaidii* are the most phylogenetically primitive and closest to *Beringraja*. While *B. kincaidii* and *B. interrupta* are located near each other in the parsimonious trees, they are not as closely related to each other as some species in this study. This is unexpected, as *B. interrupta* and *B. kincaidii* are the most morphologically conservative species in this study. *Bathyraja spinosissima* appears to be closer related to *B. microtrachys*, than *B. trachura* is to *B. microtrachys*, despite the latter two being closer in size and coloration. Additionally, *B. trachura* is consistently closer to the *B. abyssicola* and *B. aleutica* branch. This is a relatively surprising discovery, as *B. microtrachys* and *B. trachura* have historically been considered to be one species. Further investigations into the relationships between these species are warranted, as obvious statistical differences point to the species being morphologically closer to each other.

A comparison of the various statistical analyses utilized throughout this study points to some patterns that prove useful for species identification. Results of the nMDS analyses show that *B. abyssicola* and *B. aleutica* are morphologically similar, which is supported by their locations on the parsimonious tress. Additionally, *B. interrupta*, *B. kincaidii*, and *B. trachura* cluster together on the nMDS ordinations, and are therefore similar. *Bathyraja spinosissima* and *B. microtrachys* are obviously different from the other species investigated. ANOVAs found differences in means between the species, with pelvic fin length, anterior disc length, and posterior disc length not possessing differences in their means. *Post hoc* tests of the revealed some measurements that are significantly different for various species (e.g., head length, interspiracular width, interdorsal space, precaudal length, and middorsal thorn count), but also showed measurements in which significant differences were not found (e.g., anterior disc length, posterior disc length, and snout to maximum disc width). These results support the previous ANOVAs that were performed. ANOSIM analysis displayed significant differences between all species investigated, with *B. spinosissima* being the most different to its congeners. Results of the SIMPER analysis showed which characters were driving the differences between species, with interdorsal space, pelvic fin posterior lobe, interspiracular width, and disc length describing the biggest differences. The character traits that drove differentiation in the SIMPER analysis were some of the most significant in the *post hoc* tests of the means and back the hypothesis that seven valid species exist in the ENP. PCA analyses supported the results of prior multivariate tests and displayed similar trends that could be used to identify individuals to the species level. The phylogenetic trees showed that *B. kincaidii* and *B. interrupta* were basal and *B. abyssicola* and *B. aleutica* were the most derived. According to the parsimonious trees, *B. microtrachys* may be closer related to *B. spinosissima* than *B. trachura*. This is despite the two species being so similar in size and shape that they have been synonymized in prior studies. Taken as a whole, the results of multiple multivariate tests and morphological differences point to the support of the hypothesis that all the species investigated in this study are valid.

Conservation and Fisheries Management

Results from this study will hopefully assist fisheries managers in developing improved management policy by providing enhanced species-specific identification of ENP softnose skates. To date there has been relatively little research done on the complex systematics of the species included in this study. In California waters, skates are commonly taken as bycatch in commercial trawl and recreational fisheries, as well as directed fisheries. Catch statistics from the California Department of Fish and Game indicate that landings of skates increased between 1995 and 2001 (Zorzi, Martin & Ugoretz, 2001), due to an increase in demand for their “wings.” Previously, skates have been viewed as relatively unprofitable target species; however new directed fisheries have recently emerged to help supplement local economies (Ainsley, Ebert & Cailliet, 2011). Skates are sold fresh, frozen, salted, or dried, mostly to Asian markets in southern California, and are often used as a substitute for scallops (Martin and Zorzi, 1993). The market value of skates increased in the early 1990’s, as a result of a reduction in traditional groundfish quotas (Zorzi et al., 2001). In local fisheries most species of skates are lumped into one fishery category called “unspecified skates.” This lack of species-specific identification leads to problems when it comes to setting priorities for the protection of softnose skates.

Multiple international organizations exist with goals to globally protect chondrichthyan fishes. Organizations such as the Food and Agriculture Organization (FAO) and the International Union for Conservation of Nature (IUCN) have undertaken initiatives to set catch limits and implement much-needed management plans. In 1999 the FAO put in place an International Plan of Action (IPOA). This IPOA directed various international communities to assemble plans to research and protect species of sharks from around the globe (Fowler & Cavanagh, 2005). The IUCN puts together a Red List of Threatened Species in which they provide a comprehensive approach to evaluating conservation strategies for organisms. The IUCN Red List of Threatened Species publishes assessments of plants and animals with the intention of setting guidelines and conservation priorities for both government and non-governmental organizations. Recent studies have suggested that a quarter of all known chondrichthyans species are threatened worldwide (Dulvy et al., 2014). Chondrichthyans possess the lowest percentage of species listed as Least Concern in the IUCN Red List, compared to all vertebrate groups (Dulvy et al., 2014). Most species of softnose skates included in this study are listed as Least Concern due to their deepsea habitats being largely outside of major fishery impacts. Other species in the study are listed as Data Deficient, and are likely to experience low threat levels, but the paucity of life history information for those species hinders their assessment.

Researchers and policy-makers encounter significant problems when they attempt to develop fishery management policies for skates, set conservation measures, and identify individual species, due in large part to the lack of knowledge about the skate species composition in the ENP. Improvements in the identification of species have broad, real-world implications, as life history studies lose value if the species they are investigating are incorrectly identified. These life history studies form the basis for fisheries management decisions and the correct identification of skates is crucial for developing refined policies for this group, as well as maintaining the sustainable use of local, natural resources. The inherent difficulty of obtaining specimens of ENP bathyrajids, combined with outdated descriptions, has led to the need for a simple taxonomic key (Appendix A). That key has been provided at the end of this study in the form of an appendix. This key can help to drive improvements to fisheries statistics, generate enhanced baseline catch data for the species, and potentially alleviate any impacts of future expansions into deepsea fishing.

The research presented in this study will be provided to governmental and non-governmental agencies that regulate fisheries and set catch limits. The dichotomous key will be useful for fisheries observers, based both on land and at sea, to correctly identify the species of softnose skates found in the ENP. The key provides a simple, easy to use tool that can be added to any agency checklist. Baseline data for the skate bycatch fishery is currently lacking. As species are presently combined into one category, the first step that fishery agencies should take is to correctly separate the species out. There are no species found in the geographical range considered in this study that are currently listed as Threatened or Vulnerable, but some are Data Deficient due to a lack of life history material. Part of the paucity of life history information comes from the difficulty in positively identifying species. This research will hopefully alleviate those identification issues and lead to advancements in our knowledge of the histories of bathyrajids in the ENP. The Data Deficient species are of some concern, as fisheries may expand out into deeper water, where the Data Deficient species reside. The deepwater species may be vulnerable to human impacts, but we cannot set management priorities until more is known about their life histories and that cannot be known until skate specimens can be identified to the species level.

Future Research

The results of this study provide valuable taxonomic information for use in future fishery management decisions; however there is still considerable work to be done before the systematic relationships of these skates can be fully defined. There are several suggested improvements that could be made for future research into the taxonomy of ENP bathyrajids.

Classical taxonomic revisions based on morphometrics and meristics are important, but the data would be greatly improved by combing it with molecular techniques. This study included parsimonious trees based on morphological and meristic character states, but they may very well be weaker than a tree built on molecular characters. At the onset of this study polymerase chain reactions (PCR) primers based on the NADH dehydrogenase subunit 2 (NADH2) gene were used, but attempts at PCR failed. Other studies have successfully utilized the NADH2 gene for skates from different geographic ranges and helped resolve phylogenies for those species (Naylor et al., 2012) and suggest that further optimization or redesign of primers might contribute to future studies of *Bathyraja*.

Molecular-based trees would assist with defining species, but they would remain unresolved and/or skewed without a wider sampling of the study species. Species such as *B. aleutica*, *B. microtrachys*, and *B. spinosissima* were under sampled in this study due to multiple factors, such as: the use of otter trawls for primary collection, the catch locations, and the catch depths. Otter trawls would have limited the collection of *B. spinosissima*, as unpublished MBARI video shows that they prefer rocky substrates, where otter trawls are impossible or difficult to use. The utilization of long lines across the study range would probably have solved this issue. Additionally, the trawls were done at the upper edge of the depth ranges for several of these species (Appendix B). Sampling from deeper waters would likely give a larger sample size. Furthermore, the sampling should be widened to include waters north and south of this study. This is especially true for extending the sampling locations north. Bathyrajid species are increasingly diverse in the northern Pacific, with some species in this study being more abundant in northern latitudes.

Conclusions

Overall, this study concluded that the seven species examined are distinctly different and represent valid species. The validation of the seven species and their redescriptions will hopefully prove useful for fisheries biologists and managers. The novel descriptions of claspers and neurocrania for these species will help with improving the unstable phylogeny that surrounds *Bathyraja*. Through the application of meristics, morphometrics, and multivariate statistical analyses, speciation was shown to exist between the closely related species *B. interrupta* and *B. kincaidii*, as well as between *B. microtrachys* and *B. trachura*, which some authors had synonymized. The parsimonious trees presented in this study allow for some visualization of the relationships between the species, including that *B. abyssicola* and *B. aleutica* represent the biggest departure from the rajid body plan. The dichotomous key generated from the data will hopefully be used in the field to correctly identify bycatch down to the species level and will remove the current practice of combining all skates into one fishery category. Accurate knowledge of phylogenies is vital for setting appropriate conservation measurements and for determining which species are most vulnerable to human impacts. The systematics presented in this study will support past and future life history studies and provide insight into the complex relationships between members of the genus *Bathyraja*.

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Appendices

Appendix A: Key to the *Bathyraja* Species in the Eastern North Pacific off of the Continental United States

1a. Middorsal thorns absent …………………………………………….……………….. 2

1b. Middorsal thorns present …….…………………………………………………...…. 4

2a. Nuchal thorns present; dorsal coloration dark grey to purple; white blotches ventrally; large, rough thorns on dorsal surface, especially on the tail; interdorsal distance very short or absent; short, robust claspers on mature males; pseudosiphon present………… ………………….…………………………………………………….…… *B. trachura*

2b. Nuchal thorns absent…………………………………………………………………. 3

3a. Dorsal coloration grey; pale both dorsally and ventrally; large interspiracular width; large interorbital width; wide mouth…………………………...….…….. *B. spinosissima*

3b. Dorsal coloration dark brown; ventral coloration pale with dark edges to the fins; fine spines on dorsal surface; short, robust claspers on mature males; pseudosiphon present… …………………………………….………………….…..………... *B. microtrachys*

4a. Ventral coloration pale …………..…………………………………………………. 5

4b. Ventral coloration dark; large snout to maximum disc width length; large preorbital length; long, thin claspers on mature males; pseudosiphon present……..... *B. abyssicola*

5a. Thorns in a non-continuous, single row on the back; long, robust claspers on mature males; projection conspicuously protrudes; U-shaped cleft........................... *B. interrupta*

5b. Thorns in a continuous, single row on the back …………………………………….. 6

6a. Dorsal coloration dark brown; large interdorsal space; short, stubby claspers on mature males, pseudosiphon present…………..……………………………..… *B. aleutica*

6b. Dorsal coloration light brown with dark blotching across surface; long, thin claspers on mature males; projection does not conspicuously protrude; V-shaped cleft…………… ……………………………..……………………………………………….….. *B. kincaidii*

Appendix B: List of Material Examined

Bathyraja abyssicola. 14 specimens- Comparative material: PSRC Baby 062612-1, 544 mm TL, female, *R/V Ms. Julie*, Haul 171, San Diego, California, USA, 32.598909N, -118.607885W, 1118.8 m, 13 July 2011; PSRC Baby 062812-1, 1087 mm TL, mature male, *R/V Raven*, Haul 181, Tijuana, Mexico, 32.092243N, -118.686307W, 968 m, 15 October 2011; PSRC Baby 020513-1, 498 mm TL, female, *R/V Ms. Julie*, Haul 15, Flattery Rocks National Wildlife Refuge, Washington, USA, 47.607135N, -125.586053W, 1212.3 m, 25 May 2012; PSRC Baby 022813-1, 897 mm TL, female, Monterey, California, USA; PSRC Baby 022813-2, 1241 mm TL, female, Monterey, California, USA; PSRC Baby 022813-3, 1340 mm TL, female, Monterey, California, USA; PSRC Baby 110813-1, 1125 mm TL, female, *R/V Noah's Ark*, Haul 333, Pismo Beach, California, USA, 35.159721N, -121.666863W, 1139.2 m, 29 September 2012; PSRC Baby 121016-1, 1079 mm TL, mature male, Haul 129, Monterey, California, USA, 36.641215N, -122.148045W, 30 June 2016; PSRC Baby 121016-2, 1386 mm TL, mature female, *R/V Noah's Ark*, Haul 89, King Range National Conservation Area, California, USA, 40.135833N, -125.048889, 1203.6335 m, 18 September 2015; PSRC Baby 121016-3, 1331 mm TL, mature female, *R/V Excalibur*, Haul 137, Morro Bay, California, USA, 35.3861111N, -121.6700000W, 1229.2872 m, 14 July 2015; PSRC Baby 121816-1, 1013 mm TL, female, Haul 129, Cambria, California, USA, 35.807680N, -121.970027W, 30 September 2016; PSRC Baby 121816-2, 930 mm TL, immature male, *F/V Last Straw,* Haul 112, Elk, California, USA, 39.127778N, -124.204167W, 1160.0372 m, 24 June 2015; PSRC Baby 121816-3, 1038 mm TL, mature male, *F/V Last Straw,* Haul 179, San Diego, California, USA, 32.469167N, -118.5450000W, 1072.9041 m, 17 July 2015; PSRC Baby 121816-4, 1056 mm TL, mature male, *F/V Last Straw,* Haul 179, San Diego, California, USA, 32.469167N, -118.5450000W, 1072.9041 m, 17 July 2015.

Bathyraja aleutica. 12 specimens- Comparative material: PSRC Bale 011212-1, 436 mm TL, female, *R/V Pandalus*, Haul 25, Prince William Sound, Alaska, USA, 60.162667N, -147.09W, 220.2 m, 26 July 2007; PSRC Bale 062812-1, 1198 mm TL, female, *R/V Excalibur*, Haul 47, Lincoln City, Oregon, USA, 45.027584N, -124.50973W, 379 m, 6 September 2011; PSRC Bale 070313-1, 908 mm TL, immature male, *R/V Noah's Ark*, Haul 108, Eureka, California, USA, 40.253407N, -124.60897W, 427.5 m, 23 July 2012; PSRC Bale 090913-1, 1191 mm TL, mature male, *R/V Noah's Ark*, Haul 108, Eureka, California, USA, 40.253407N, -124.60897W, 427.5 m, 23 July 2012; PSRC Bale 110813-1, 900 mm TL, immature male, *R/V Noah's Ark*, Haul 40, Long Beach, Washington, USA, 46.298489N, -124.662618W, 494 m, 29 May 2012; UW046435-1, 267 mm TL, immature male, Haul 46, Bering Sea, Alaska, USA, 57.77930N, -173.88879W, 665 m, 16 June 2002; UW046435-2, 280 mm TL, immature male, Haul 46, Bering Sea, Alaska, USA, 57.77930N, -173.88879W, 665 m, 16 June 2002; UW046435-3, 275 mm TL, immature male, Haul 46, Bering Sea, Alaska, USA, 57.77930N, -173.88879W, 665 m, 16 June 2002; CAS 232270, 360 mm TL, immature male, *Yakushi Maru*, Haul 38, Southeast Bering Sea, Alaska, USA, 59.9600N, -167.4325W, 620 m, 15 June 1979; CAS 232256-1, 258 mm TL, immature male, *Yakushi Maru*, Pribilof Island, Alaska, USA, 58.3233N, -174.4148W, 725-730 m, 22 June 1979; CAS 232256-2, 306 mm TL, immature female, *Yakushi Maru*, Pribilof Island, Alaska, USA, 58.3233N, -174.4148W, 725-730 m, 22 June 1979; PSRC Bale 121016-1, 1179 mm TL, mature female, *R/V Ms. Julie,* Haul 72, Port Orford, Oregon, USA, 42.7703N, -124.7597W, 13 September 2015.

Bathyraja interrupta. 16 specimens- Comparative material: UW 46479, 417 mm TL, male, Haul 48, Bering Sea, Alaska, USA, 57.8372N, -173.892W; 497 m, 20 June 2002; UW 46452-10, 454 mm TL, female, Haul 67, Bering Sea, Alaska, USA, 59.3654N, -177.6026W, 246 m, 25 June 2002; UW 46452-11, 463 mm TL, female, Haul 67, Bering Sea, Alaska, USA, 59.3654N, -177.6026W, 246 m, 25 June 2002; UW 46452-14, 544 mm TL, male, Haul 67, Bering Sea, Alaska, USA, 59.3654N, -177.6026W, 246 m, 25 June 2002; UW 46452-15, 370 mm TL, female, Haul 67, Bering Sea, Alaska, USA, 59.3654N, -177.6026W, 246 m, 25 June 2002; UW 46452-16, 511 mm TL, female, Haul 67, Bering Sea, Alaska, USA, 59.3654N, -177.6026W, 246 m, 25 June 2002; UW 46452-17, 625 mm TL, female, Haul 67, Bering Sea, Alaska, USA, 59.3654N, -177.6026W, 246 m, 25 June 2002; UW 46452-21, 482 mm TL, male, Haul 67, Bering Sea, Alaska, USA, 59.3654N, -177.6026W, 246 m, 25 June 2002; UW 46458, 752 mm TL, female, Haul 84, Bering Sea, Alaska, USA, 60.5989N, -178.8197W, 2002; UW 46464, 410 mm TL, male, Haul 65, Bering Sea, Alaska, USA, 59.3972N, -177.8658W, 443 m, 24 June 2002; UW 46442-1, 663 mm TL, female, Haul 38, St. George Island, Bering Sea, Alaska, USA, 56.4639N, -171.8309W, 327 m, 18 June 2002; UW 46442-2, 717 mm TL, mature male, Haul 38, St. George Island, Bering Sea, Alaska, USA, 56.4639N, -171.8309W, 327 m, 18 June 2002; UW 46447, 435 mm TL, male, Haul 79, Bering Sea, Alaska, USA, 59.9462N,

-178.9305W, 284 m, 27 June 2002; UW 46450-1, 672 mm TL, male, Haul 56, Bering Sea, Alaska, USA, 58.5699N, -176.6988W, 464 m, 22 June 2002; UW 46450-2, 768 mm TL, mature male, Haul 67, Bering Sea, Alaska, USA, 58.5699N, -176.6988W, 464 m, 22 June 2002; CAS 232254, 289 mm TL, immature male, *Yakushi Maru*, Unalaska Island, Alaska, USA, 54.3912N, -167.2012W, 485-520 m, 10 June 1979.

Bathyraja kincaidii. 39 specimens- Comparative material: PSRC Bkin 012312-1, 531 mm TL, mature male, *R/V Noah's Ark*, Haul 96, Fort Bragg, California, USA, 39.410919N, -123.974946W, 235.6 m, 21 June 2011; PSRC Bkin 012312-2, 475 mm TL, female, *R/V Noah's Ark*, Haul 96, Fort Bragg, California, USA, 39.410919N, -123.974946W, 235.6 m, 21 June 2011; PSRC Bkin 013012-1, 545 mm TL, male, *R/V Noah's Ark*, Haul 96, Fort Bragg, California, USA, 39.410919N, -123.974946W, 235.6 m, 21 June 2011; PSRC Bkin 013012-2, 533 mm TL, mature male, *R/V Noah's Ark*, Haul 96, Fort Bragg, California, USA, 39.410919N, -123.974946W, 235.6 m, 21 June 2011; PSRC Bkin 020612-1, 575 mm TL, mature male, *R/V Noah's Ark*, Haul 67, North Bend, Oregon, USA, 43.543611N, -124.690059W, 458.3 m, 7 June 2011; PSRC Bkin 020612-2, 544 mm TL, female, *R/V Noah's Ark*, Haul 48, Tillamook, Oregon, USA, 45.362077N, -124.654244W, 430 m, 3 June 2011; PSRC Bkin 0201412-1, 542 mm TL, female, *R/V Noah's Ark*, Haul 48, Tillamook, Oregon, USA, 45.362077N, -124.654244W, 430 m, 3 June 2011; PSRC Bkin 021412-2, 448 mm TL, male, *R/V Noah's Ark*, Haul 48, Tillamook, Oregon, USA, 45.362077N, -124.654244W, 430 m, 3 June 2011; PSRC Bkin 061212-1, 535 mm TL, female, *R/V Excalibur*, Haul 31, Long Beach, Washington, USA, 46.402376N, -124.666273W, 1050.4 m, 26 August 2011; PSRC Bkin 061212-2, 522 mm

TL, male, *R/V Excalibur*, Haul 31, Long Beach, Washington, USA, 46.402376N, -124.666273W, 1050.4 m, 26 August 2011; PSRC Bkin 061512-1, 535 mm TL, male, *R/V Excalibur,* Haul 31, Long Beach, Washington, USA, 46.402376N, -124.666273W, 1050.4 m, 26 August 2011; PSRC Bkin 061512-2, 553 mm TL, female, *R/V Noah's Ark*, Haul 54, Newport, Oregon, USA, 44.636403N, -124.632914W, 252.5 m, 5 June 2011; PSRC Bkin 061512-3, 338 mm TL, male, *R/V Noah's Ark*, Haul 46, Tillamook, Oregon, USA, 45.406623N, -124.576685W, 389.6 m, 3 June 2011; PSRC Bkin 061512-4, 415 mm TL, male, *R/V Noah's Ark*, Haul 46, Tillamook, Oregon, USA, 45.406623N, -124.576685W, 389.6 m, 3 June 2011; PSRC Bkin 061812-1, 542 mm TL, female, *R/V Noah's Ark*, Haul 50, Lincoln City, Oregon, USA, 44.995374N, -124.5752W, 441.9 m, 4 June 2011; PSRC Bkin 061812-2, 616 mm TL, mature male, *R/V Noah's Ark*, Haul 50, Lincoln City, Oregon, USA, 44.995374N, -124.5752W, 441.9 m, 4 June 2011; PSRC Bkin 061812-3, 356 mm TL, male, *R/V Noah's Ark*, Haul 50, Lincoln City, Oregon, USA, 44.995374N, -124.5752W, 441.9 m, 4 June 2011; PSRC Bkin 062112-1, 250 mm TL, male, *R/V Noah's Ark*, Haul 56, Newport, Oregon, USA, 44.595353N, -124.53477W, 142.9 m, 5 June 2011; PSRC Bkin 062112-2, 478 mm TL, female, *R/V Noah's Ark*, Haul 56, Newport, Oregon, USA, 44.595353N, -124.53477W, 142.9 m, 5 June 2011; PSRC Bkin 062112-3, 276 mm TL, male, *R/V Noah's Ark*, Haul 56, Newport, Oregon, USA, 44.595353N, -124.53477W, 142.9 m, 5 June 2011; PSRC Bkin 062112-4, 210 mm TL, male, *R/V Noah's Ark*, Haul 56, Newport, Oregon, USA, 44.595353N, -124.53477W, 142.9 m, 5 June 2011; PSRC Bkin 062112-5, 435 mm TL, female, *R/V Noah's Ark*, Haul 48, Tillamook, Oregon, USA, 45.362077N, -124.654244W, 430 m, 3 June 2011; PSRC

Bkin 062612-1, 576 mm TL, female, *R/V Excalibur*, Haul 26, Ocean Shores, Washington, USA, 46.996986N, -124.707605W, 119 m, 25 August 2011; PSRC Bkin 062612-2, 510 mm TL, male, *R/V Excalibur*, Haul 26, Ocean Shores, Washington, USA, 46.996986N, -124.707605W, 119 m, 25 August 2011; PSRC Bkin 062612-3, 485 mm TL, female, *R/V Excalibur*, Haul 26, Ocean Shores, Washington, USA, 46.996986N, -124.707605W, 119 m, 25 August 2011; PSRC Bkin 020113-1, 591 mm TL, mature male, *R/V Noah's Ark*, Haul 47, Tillamook, Oregon, USA, 45.539539N, -124.536993W, 451.6 m, 3 June 2011; PSRC Bkin 020513-1, 551 mm TL, female, *R/V Noah's Ark*, Haul 47, Tillamook, Oregon, USA, 45.539539N, -124.536993W, 451.6 m, 3 June 2011; PSRC Bkin 030613-1, 525 mm TL, female, *R/V Ms. Julie*, Haul 41, Manzanita, Oregon, USA, 45.76475N, -124.40875W, 151.8 m, 3 June 2012; PSRC Bkin 030613-2, 536 mm TL, mature male, *R/V Ms. Julie*, Haul 41, Manzanita, Oregon, USA, 45.76.475N, -124.40875W, 151.8 m, 3 June 2012; PSRC Bkin 080813-1, 563 mm TL, mature male, *R/V Ms. Julie*, Haul 41, Manzanita, Oregon, USA, 45.76475N, -124.40875W, 151.8 m, 3 June 2012; PSRC Bkin 080813-2, 430 mm TL, female, *R/V Noah's Ark*, Haul 193, Santa Catalina Island, California, USA, 33.514113N, -118.702399W, 323.7 m, 18 July 2012; PSRC Bkin 080813-3, 478 mm TL, mature male, *R/V Noah's Ark*, Haul 193, Santa Catalina Island, California, USA, 33.514113N, -118.702399W, 323.7 m, 18 July 2012; PSRC Bkin 110713-1, 260 mm TL, immature male, *R/V Noah's Ark*, Haul 11, Flattery Rocks, Washington, USA, 48.128192N, -125.663567W, 209.4 m, 24 May 2012; PSRC Bkin 110713-2, 521 mm TL, mature male, *R/V Noah's Ark*, Haul 11, Flattery Rocks, Washington, USA, 48.128192N, -125.663567W, 209.4 m, 24 May 2012; PSRC Bkin

110813-1, 511 mm TL, mature male, *R/V Noah's Ark*, Haul 132, Moss Beach, California, USA, 37.537123N, -123.017422W, 372.9 m, 30 June 2012; PSRC Bkin 110813-2, 491 mm TL, mature male, *R/V Noah's Ark*, Haul 132, Moss Beach, California, USA, 37.537123N, -123.017422W, 372.9 m, 30 June 2012; PSRC Bkin 110813-3, 405 mm TL, mature male, *R/V Ms. Julie*, Haul 113, Sonoma Coast State Park, California, USA, 38.382510N, -123.580247W, 351.4 m, 25 June 2012; PSRC Bkin 111113-1, 504 mm TL, mature male, *R/V Ms. Julie*, Haul 113, Sonoma Coast State Park, California, USA, 38.382510N, -123.580247W, 351.4 m, 25 June 2012; PSRC Bkin 111113-2, 372 mm TL, female, *R/V Ms. Julie*, Haul 113, Sonoma Coast State Park, California, USA, 38.382510N, -123.580247W, 351.4 m, 25 June 2012.

Bathyraja microtrachys. 7 Specimens- Comparative material: Bmicro 10.30.09-1, 695 mm TL, mature male, Haul 2000-1, Monterey, California, USA, 36.45281N, -122.27742W, 2250 m, 10 April 2009; Bmicro 10.30.09-2, 675 mm TL, mature male, Haul 2000-2, Monterey, California, USA, 36.37902N, -122.23083W, 2080 m, 9 October 2009; Bmicro 10.30.09-3, 754 mm TL, mature male, Haul 2000-3, Monterey, California, USA, 36.39689N, -122.27504W, 2150 m, 9 October 2009; Bmicro 10.30.09-4, 640 mm TL, mature male, Haul 2000-3, Monterey, California, USA, 36.39689N, -122.27504W, 2150 m, 9 October 2009; Bmicro 10.30.09-5, 715 mm TL, mature male, Haul 2000-4, Monterey, California, USA, 36.35564N, -122.09995W, 2350 m, 10 October 2009; PSRC Bmic 101016-1 630 mm TL, female, 37.700121N, -123.046982W, Farallon Islands, California, USA, 2680-2900 m, 1 March 1991; CAS 80848, 164 mm TL, immature male, *R/V Wecoma,* Farallon Islands, California, USA, 37.3853N, -123.2610W, 2635-2470 m, 29 July 1991.

Bathyraja spinosissima. 4 specimens- Holotype: CAS 25617, 164 mm TL, immature male, *Arcturus,* Station 72, Cocos Island, 4.833333N, -87.00W, 1399 m, 3 June 1925. Comparative material: OSUO 1863 017, 1492 mm TL, female, Cannon Beach, Oregon, USA, 45.84833N, -125.575W, 2121 m, 7 June 1969; OSUO 1885, 984 mm TL, female, Pacific City, Oregon, USA, 45.28N, -125.85333W, 2605 m, 19 March 1970; OSUO 1893 030, 935 mm TL, female; Lincoln City, Oregon, USA, 44.953333N, -125.591667W, 2700 m, 6 July 1969.

Bathyraja trachura. 19 specimens- Comparative material: PSRC Btra 011212-1, 490 mm TL, female, *R/V Excalibur*, Haul 93, Redwood National Park, California, USA, 41.39515N, -124.760808W, 1079.3 m, 20 September 2011; PSRC Btra 062112-1, 647 mm TL, male, *R/V Noah's Ark*, Haul 65, Reedsport, Oregon, USA, 43.79441N, -124.981551W, 1233.6 m, 7 June 2011; PSRC Btra 062212-1, 598 mm TL, female, *R/V Noah's Ark*, Haul 65, Reedsport, Oregon, USA, 43.79441N, -124.981551W, 1233.6 m, 7 June 2011; PSRC Btra 062212-2, 805 mm TL, mature male, *R/V Noah's Ark*, Haul 65, Reedsport, Oregon, USA, 43.79441N, -124.981551W, 1233.6 m, 7 June 2011; PSRC Btra 062212-3, 746 mm TL, female, *R/V Noah's Ark*, Haul 61, Waldport, Oregon, USA, 44.307933N, -124.985313W, 648.1 m, 6 June 2011; PSRC Btra 021513-1, 516 mm TL, female, *R/V Ms. Julie*, Haul 15, Flattery Rocks National Wildlife Refuge, Washington, USA, 47.607135N, -125.586053W, 1212.3 m, 25 May 2012; PSRC Btra 0320613-1, 381 mm TL, female, *R/V Noah's Ark*, Haul 190, San Clemente Island, California, USA

32.711826N, -118.6717W, 102.3 m, 17 July 2012; PSRC Btra 0320613-2, 899 mm TL, mature male, *R/V Noah's Ark*, Haul 190, San Clemente Island, California, USA 32.711826N, -118.6717W, 102.3 m, 17 July 2012; PSRC Btra 080913-1, 649 mm TL, male, *R/V Noah's Ark*, Haul 175, Santa Rosa Island, California, USA, 33.449459N, -120.600798W, 1155.6 m, 13 July 2012; PSRC Btra 080913-2, 404 mm TL, female, *R/V Noah's Ark*, Haul 175, Santa Rosa Island, California, USA, 33449459N, -120.600798W, 1155.6 m, 13 July 2012; PSRC Btra 080913-3, 580 mm TL, female, *R/V Noah's Ark*, Haul 70, Newport, Oregon, USA, 44.384536N, -124.981356W, 638.9 m, 8 June 2012; PSRC Btra 080913-4, 568 mm TL, female, *R/V Noah's Ark*, Haul 70, Newport, Oregon, USA, 44.384536N, -124.981356W, 638.9 m, 8 June 2012; PSRC Btra 080913-5, 495 mm TL, male, *R/V Noah's Ark*, Haul 70, Newport, Oregon, USA, 44.384536N, -124.981356W, 638.9 m, 8 June 2012; PSRC Btra 080913-6, 511 mm TL, male, *R/V Noah's Ark*, Haul 70, Newport, Oregon, USA, 44.384536N, -124.981356W, 638.9 m, 8 June 2012; PSRC Btra 111113-1, 575 mm TL, immature male, *R/V Noah's Ark*, Haul 70, San Simeon, California, USA, 35.647268N, -121.891564W, 1058.6 m, 4 July 2012; PSRC Btra 111113-2, 744 mm TL, mature male, *R/V Noah's Ark*, Haul 70, San Simeon, California, USA, 35.647268N, -121.891564W, 1058.6 m, 4 July 2012; PSRC Btra 120813-1, 735 mm TL, mature male, *R/V Ms. Julie*, Haul 70, Del Norte Coast Redwoods State Park, California, USA, 41.53146N, -124.712003W, 909.5 m, 22 June 2012; CAS 66872, 294 mm TL, female, *Yakushi Maru*, Haul 37, Southeast Bering Sea, Alaska, USA, 1 June 1979.