



Abstract—The systematic status of North Pacific sand lances (genus *Ammodytes*) was assessed from mitochondrial DNA (cytochrome oxidase c subunit 1) sequence data and morphological data to identify the number of species in the North Pacific Ocean and its fringing seas. Although only 2 species, *Ammodytes hexapterus* and *A. personatus*, have been considered valid in the region, haplotype networks and trees constructed with maximum parsimony and genetic distance (neighbor-joining) methods revealed 4 highly divergent monophyletic clades that clearly represent 4 species of *Ammodytes* in the North Pacific region. On the basis of our material and comparisons with sequence data reported in online databases, *A. personatus* is found throughout the eastern North Pacific Ocean, Gulf of Alaska, Aleutian Islands, and the eastern Bering Sea where it co-occurs with a northwestern Arctic species, *A. hexapterus*, that is found throughout the North American Arctic from Hudson Bay, Canada, in the east, through the Beaufort and Chukchi seas, into the northern and western Bering Sea, and to the southern Sea of Okhotsk in the Soya Strait off Hokkaido, Japan. Two other species reside in waters around Japan: *A. japonicus* throughout the Sea of Japan and the Seto Inland Sea and a new species in the Sea of Japan and the North Pacific Ocean off northern Honshu. We designate neotypes for *A. hexapterus* and *A. personatus* because of the absence of type material and the close similarity of these 2 species. *Ammodytes aleutensis* is a junior synonym of *A. japonicus*, and *A. alascanus* is a junior synonym of *A. personatus*.

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Systematics of North Pacific sand lances of the genus *Ammodytes* based on molecular and morphological evidence, with the description of a new species from Japan

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Sand lances of the genus *Ammodytes* (family Ammodytidae) are small silvery fishes that inhabit marine and adjacent brackish waters of the Northern Hemisphere. They reside primarily over sandy substrates, where they are able to quickly bury themselves to avoid predators, but are found also over bedrock, eelgrass, and kelp. Species of *Ammodytes* are cornerstone prey items for more than 100 species of marine mammals, birds, and other fishes in the region of the North Pacific Ocean (Field, 1988; Willson et al.¹). Despite

their tremendous importance in ecosystems and as targets in fisheries off Japan (Hamada, 1985; Han et al., 2012) and in the North Sea (Sherman et al., 1981; Furness, 2002), little is known about their distribution or life history.

The family Ammodytidae comprises about 31 species in 7 genera and 2 subfamilies found in the Arctic, Atlantic, Indian, and Pacific oceans (Nelson, 2006; Randall and Heemstra, 2008; Shibukawa and Ida, 2013; Randall and Ida, 2014). Placed within the subfamily Ammodytinae,

¹ Willson, M. F., R. H. Armstrong, M. D. Robards, and J. F. Piatt. 1999. Sand lance as cornerstone prey for predator populations. In Sand lance: a review of biology and predator relations and annotated bibliography (M. D. Robards, M. F.

Willson, R. H. Armstrong, and J. F. Piatt, eds.), p. 17–44. Research Paper PNW-RP-521. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland OR. [http://www.fs.fed.us/pnw/pubs/rp_521a.pdf]

which also includes the genera *Gymnammodytes* and *Hyperoplus*, *Ammodytes* is diagnosed by the presence of scales deeply embedded in dermal plicae below the lateral line, a highly protrusible upper jaw (Pietsch, 1984), and non-expanded neural and haemal spines on the caudal vertebrae (Ida et al., 1994). Six species currently are recognized in the genus *Ammodytes*: 2 in the eastern North Atlantic Ocean (*A. tobianus* Linnaeus, 1758, and *A. marinus* Raitt, 1934), 2 in the western North Atlantic Ocean (*A. americanus* DeKay, 1842, and *A. dubius* Reinhardt, 1837), and 2 in the North Pacific Ocean (*A. hexapterus* Pallas, 1814, and *A. personatus* Girard, 1856). All are very similar morphologically, having an elongate body up to 280 mm in total length, scales aligned in dermal plicae for the length of the body, long dorsal and anal fins, and no pelvic fins. Species generally are distinguished by meristic characters and relative body depth. We focus primarily on the sand lances of the North Pacific Ocean and adjacent seas for the purpose of clarifying their systematic status.

The first species recognized in this genus was collected from Sweden to the Mediterranean and described by Linnaeus (1758) as *A. tobianus*. Of 2 other names published in this genus in the early 1800s, *A. alliciens* Lacepède, 1800, was designated an unneeded replacement name for *A. tobianus*, and *A. cicereus* Rafinesque, 1810, was allocated to *Gymnammodytes* as a valid species (Eschmeyer, 2013). In the North Pacific region, the first species described was *A. hexapterus*, from material collected or observed from off the Kamchatka Peninsula and Kuril Islands in Russia, the islands “between Asia and North America,” and the coast of North America (Pallas, 1814; Lindberg, 1937). Pallas (1814) compared it with the Atlantic species *A. tobianus* as described by Artdedi (1738; Walbaum 1792), noting that *A. hexapterus* had more numerous vertebrae.

In his work on fishes collected during the Pacific railroad surveys of the early 1800s, Girard (1856) described *A. personatus* from Cape Flattery, Washington. In 1873, Cope described *A. alascanus* from Sitka, Alaska, without comparing it with previously described species. Jordan (1906) referred all *Ammodytes* of the North Pacific region to *Ammodytes personatus*, including populations from Alaska to Monterey, California, and from Siberia to the Inland Sea of Japan. He made no comments on *A. hexapterus* and was uncertain about the status of *A. alascanus*, as well as of the northernmost populations of *Ammodytes*, suggesting that they may be referable to a circumboreal *A. tobianus*. Lindberg (1937) recognized differences between *Ammodytes* off the coast of Japan and species from more northern areas, referring these populations in Japan to *A. personatus*, although much later he and Krasnyukova (Lindberg and Krasnyukova, 1975) synonymized all nominal North Pacific species of *Ammodytes* under *A. hexapterus*.

The last 2 species to be described from the North Pacific region were *Ammodytes aleutensis* and *A. ja-*

ponicus of Duncker and Mohr (1939). They recognized *A. aleutensis* to be widely distributed from Unalaska in the eastern Aleutian Islands to Hokkaido in northern Japan and Nagasaki in southern Japan and *A. japonicus* to be only from the type locality of Otaru (=“Otaka”), Hokkaido, that also is included among the type localities of *A. aleutensis*. Duncker and Mohr (1939) distinguished *A. japonicus* from *A. aleutensis* on the basis of its fewer dorsal-fin rays and higher number of dermal plicae. In addition, they observed that, in their specimens of *A. japonicus*, the origin of the dorsal fin was farther posterior (posterior half versus middle of pectoral fin) and the ventrolateral fold was shorter (extending to mid-anal fin versus the posterior third of the anal fin and beyond). Although Andriashev (1954) noted the presence of significant variation among more southern forms and the need for additional taxonomic work, he recognized 2 species of *Ammodytes* across northern seas: *A. tobianus* in the Atlantic Ocean and *A. hexapterus* from the Barents Sea to the Baltic Sea. Within *A. hexapterus*, he recognized the subspecies *A. hexapterus marinus* from the Barents Sea to the Baltic Sea and *A. hexapterus hexapterus* in the North Pacific region.

The number of species of *Ammodytes* in waters off Japan has been in question for the last century. Ohshima (1950) examined the numbers of vertebrae in *Ammodytes* from 7 locations around Japan—in the Seto Inland Sea, southern and northern Japan on the Pacific Ocean side, the northern tip of Honshu, and the northcentral Kuril Islands—and found differences in vertebral numbers. Lindberg and Krasnyukova (1975) noted confusion in use of the names *A. hexapterus* and *A. personatus*, as well as the uncertain status of *A. aleutensis* and *A. japonicus*, and proposed the synonymy of all northern *Ammodytes* within *A. hexapterus*, including those species in the western North Pacific region around Japan. Kitaguchi (1979) also examined meristic data and found that 2 species, which he identified as *A. personatus* and *A. hexapterus*, occurred together in the area around Wakkanai in the Soya Strait off northeastern Hokkaido. In their study of the life history characteristics of *Ammodytes*, Hashimoto and Kawasaki (1981) concluded that 2 populations were included in “*A. personatus*” collected from the Pacific Ocean coast of northern Japan (Tohoku district) on the basis of meristic and allozyme analyses. Later, Hashimoto (1984) expanded his study of meristics within *Ammodytes*, examining material from several localities around Japan, and concluded that 3 genetically independent but geographically overlapping subspecies were likely present around Japan.

No comprehensive genetic studies of sand lances of the North Pacific Ocean and surrounding seas have been conducted; however, several regional studies have been published. An allozyme study compared populations around Japan with one sample from Kodiak Island, Alaska, and described 3 non-interbreeding groups that were living sympatrically around Japan;

none of these groups were genetically similar to the Kodiak population (Okamoto, 1989). In recent studies where the mitochondrial DNA (mtDNA) control region and 16s ribosomal RNA (rRNA) were examined (Kim et al., 2006) and where mtDNA cytochrome oxidase c subunit 1 (COI) was used to identify larvae, Kim et al. (2006, 2008, 2010) proposed that at least 2 species of sand lances were present in material from around Korea and Japan. Han et al. (2012) examined the population structure of *Ammodytes* in waters off Japan and determined that 2 lineages resulted from the past isolation of the Sea of Japan from neighboring seas—a separation that was facilitated by current flows and temperature barriers. Mecklenburg et al. (2011) used evidence from COI to suggest that 2 species were among specimens collected in Alaska: 1 species (*A. hexapterus*) in the Bering and Chukchi seas and 1 species in the Gulf of Alaska (“likely ... *A. personatus*”). Most recently, Turanov and Kartavtsev (2014) combined sequence data from 7 specimens collected in the Bering and Okhotsk seas with 34 samples taken from the online data source GenBank (www.ncbi.nlm.nih.gov) and concluded that 4 species are present in the North Pacific region.

Two names are now considered valid in the region of the North Pacific Ocean, with *A. hexapterus* applied to populations in the eastern North Pacific Ocean, Bering Sea, Chukchi Sea, Sea of Okhotsk, and Sea of Japan (Miller and Lea, 1972; Hart, 1973; Mecklenburg et al., 2002; Hatooka, 2013) and *A. personatus* recognized in the western North Pacific Ocean, southern Sea of Okhotsk, and Sea of Japan (e.g. Ida, 1984; Hatooka, 2000, 2002, 2013). As a result of this study, we revise the genus *Ammodytes* in the North Pacific region, on the basis of an examination of genetic variation at the COI gene and morphological variation in specimens collected throughout nearly the entire range of the genus in the North Pacific region: from California to Puget Sound, the Gulf of Alaska, the Bering and Chukchi seas, Sea of Okhotsk, Sea of Japan, Seto Inland Sea, and the Pacific coast of Japan.

Materials and methods

Whole samples of *Ammodytes* were obtained from archival collections and collected over the 13 years from 2000 to 2013, from the eastern and western coastlines of the North Pacific Ocean and its fringing seas from latitudes of 40°N to 70°N (Table 1; Fig. 1; Appdx. 1). Additional samples of Atlantic species were obtained from the eastern and western North Atlantic Ocean for comparison. Specimens with known preservation histories from archival collections had been fixed in 10% formalin and preserved in 70% ethanol or 45% isopropanol. For freshly collected specimens obtained for genetic analyses, tissues were fixed and preserved in 95% ethanol, and whole specimens were then fixed in 10% formalin and preserved in 70% ethanol. Institutional abbreviations are listed in Leviton et al. (1985).

Genetics

DNA was extracted and purified from more than 498 tissue samples with a Qiagen² (Valencia, CA) DNeasy Blood & Tissue Kit. Primers were developed for the flanking regions of the COI gene of the mitochondrial DNA from a consensus of 21 DNA sequences obtained from GenBank (FJ666901–FJ666921). Primers used to sequence DNA were F: 5'CTCCTGCAGGGTCAAAGAAG and R: 5'GGCACCCCTTTATCTAGTATT, resulting in a 638 base-pair (bp) fragment of the COI region. The fragment was amplified by polymerase chain reaction (PCR) in a 50- μ L reaction volume containing 1X GoTaq Buffer (Promega Corp., Madison, WI), 2.5 mM MgCl₂, 0.2 mM of each dNTP, 0.2 μ M each of forward and reverse primer, 1 unit of GoTaq, 10 ng DNA, and deionized water. Thermal cycling conditions were as follows: 95°C for 2 min; 30 cycles of 95°C for 40 s, 55°C for 40 s, and 72°C for 1 min; 72°C for 7 min; and 4°C indefinitely. Forward sequences were obtained from the PCR product by the Sanger sequencing method. Sequences were aligned and edited with the software program CodonCode Aligner, vers. 3.7.1 (CodonCode Corp., Dedham, MA). Ambiguous end regions, particularly on the 3' end of the sequences, were aggressively trimmed to 560 bp in length to achieve the maximum number of high-quality sequences.

The following genetic indices were calculated in Arlequin, vers. 3.5 (Excoffier and Lischer, 2010): number of haplotypes (H), number of polymorphic sites (S), haplotype diversity (h), and average nucleotide diversity (π). For the purpose of examining phylogenetic relationships within the genus *Ammodytes*, the data were supplemented with 15 samples representing 4 species of *Ammodytes* from the Atlantic Ocean and a DNA sequence from *Uranoscopus oligolepis* from GenBank (FJ237962) to use as an out-group for phylogenetic analysis.

The number of nucleotide differences between sequences was visually represented by a haplotype network (minimum spanning tree) created with the program Sneath, vers. 2 (Wooding, 2004; <http://user.xmission.com/~wooding/Sneath/>). Phylogenetic relationships among unique mtDNA haplotypes were evaluated with the program MEGA 6 (Tamura et al., 2013), wherein trees were constructed with maximum parsimony (MP) (Nei and Kumar, 2000), maximum likelihood (ML) (Tamura and Nei, 1993), and neighbor-joining (NJ) methods (Saitou and Nei, 1987; by using the distance algorithm of Tamura and Nei, 1993). Support for nodes of the 3 trees was evaluated with 1000 bootstrap replicates (Felsenstein, 1985). Branches with >95% bootstrap support were collapsed into consensus sequences, which were used to create summary trees.

Analyses of the number of substitutions per site between all unique sequences were examined with the

² Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Geographic area of collections and other details about the collections of tissues that were used in molecular analysis of species of *Ammodytes* in the region of the North Pacific Ocean. per=*A. personatus*; hex=*A. hexapterus*; ja=*A. japonicus*; and hn=*A. heian* new species. uncat.=uncataloged.

Area of collection	Latitude	Longitude	Number	Species	Catalog number
Eastern North Pacific Ocean					
Humboldt Bay, CA	40.75	-124.23	10	per	UW 152676
San Juan Islands, WA	48.69	-123.02	9	per	UW 116044-45, 116047-53
San Juan Islands, WA	48.57	-123.05	12	per	UW 116055-60, 116066-71
Gulf of Alaska					
Red Bluff Bay	56.51	-134.45	10	per	ABL 13-0001
Gastineau Channel, off Juneau	58.22	-134.35	10	per	ABL 13-0002
Yakutat Bay	60.02	-142.26	9	per	ABL 13-0003
Prince William Sound	60.51	-147.62	9	per	ABL 13-0004
Resurrection Bay, Kenai Peninsula	59.97	-149.38	10	per	ABL 13-0005
Deadman Bay	57.02	-153.59	9	per	UW 152349
Eastern Bering Sea					
Cold Bay (haul 4)	55.51	-163.02	6	per	ABL uncat.
Bristol Bay	56.6	-159.7	1	per	UW 116220
Bristol Bay	58.29	-160.8	1	per	UW 116219
Bristol Bay	58.6	-163.3	1	per	UW 116221
Kuskokwim Bay (haul 33)	58.99	-165.06	48	per=43, hex=5	ABL uncat.
Kuskokwim Bay (hauls 15, 16, 18, 19, 41)	58.67	-165.02	52	per=50, hex=2	ABL uncat.
Kuskokwim Bay	59.3	-166.6	2	hex	UW 116222-23
Nunivak Island (haul 64)	59.49	-166.96	10	per	ABL uncat.
Norton Sound (haul 58)	64.2	-165.14	14	per=1, hex=13	ABL uncat.
Norton Sound	64.02	-164.01	1	hex	UW 150610
Aleutian Islands					
Unalaska, Summer Bay	53.54	-166.28	10	per	ABL uncat.
Attu Island	53	174	18	per	UW 116092-99, 116200-207
Eastern Chukchi Sea					
Chukchi Sea	70.05	-167.81	44	hex	UW 150610
Chukchi Sea	70.05	-167.81	8	hex	UW 150611
Chukchi Sea	67.404	-173.604	19	hex	UAM 1255, 2813
Chukchi Sea	70.049	-167.861	16	hex	ABL uncat.
Russia					
Western Bering Sea, sample A	62	177	10	hex	ABL 11-0005
Western Bering Sea, sample B	64.54	179.32	10	hex	ABL 11-0004
Sea of Okhotsk, off Sakhalin Island	51.57	144.24	10	hex	ABL 11-0007
Sea of Okhotsk, off Sakhalin Island	52.54	144.12	10	hex	ABL 11-0006
Japan					
Soya Strait, off Wakkanai, Hokkaido	45.55	142.23	25	hex=13, ja=3, hn=9	UW 116840
Seto Inland Sea, Akashi, Hyogo	34.38	135	30	ja	FAKU 130979-131008
Nohara Maizuru, Kyoto	35.45	135.3	12	ja	UW 153060
Ise Bay	34.73	136.68	50	ja	UW 153061
Ofunato, Iwate	38.5	141.8	6	hn	FAKU 130767- 130774

Tamura-Nei model (1993) and included mean divergence and range of divergence between each species pair, as well as ranges of divergence within each species. Because divergences between the sequences were large, all sequences, including those of the Atlantic specimens and the *Uranoscopus* sequence, were analyzed for substitution saturation of the mitochondrial

COI sequence by using Xia's method (Xia et al., 2003) in DAMBE, vers. 5.3.109 (Xia, 2013).

Morphology

Counts of median-fin rays and internal features were taken from radiographs; other counts were taken from

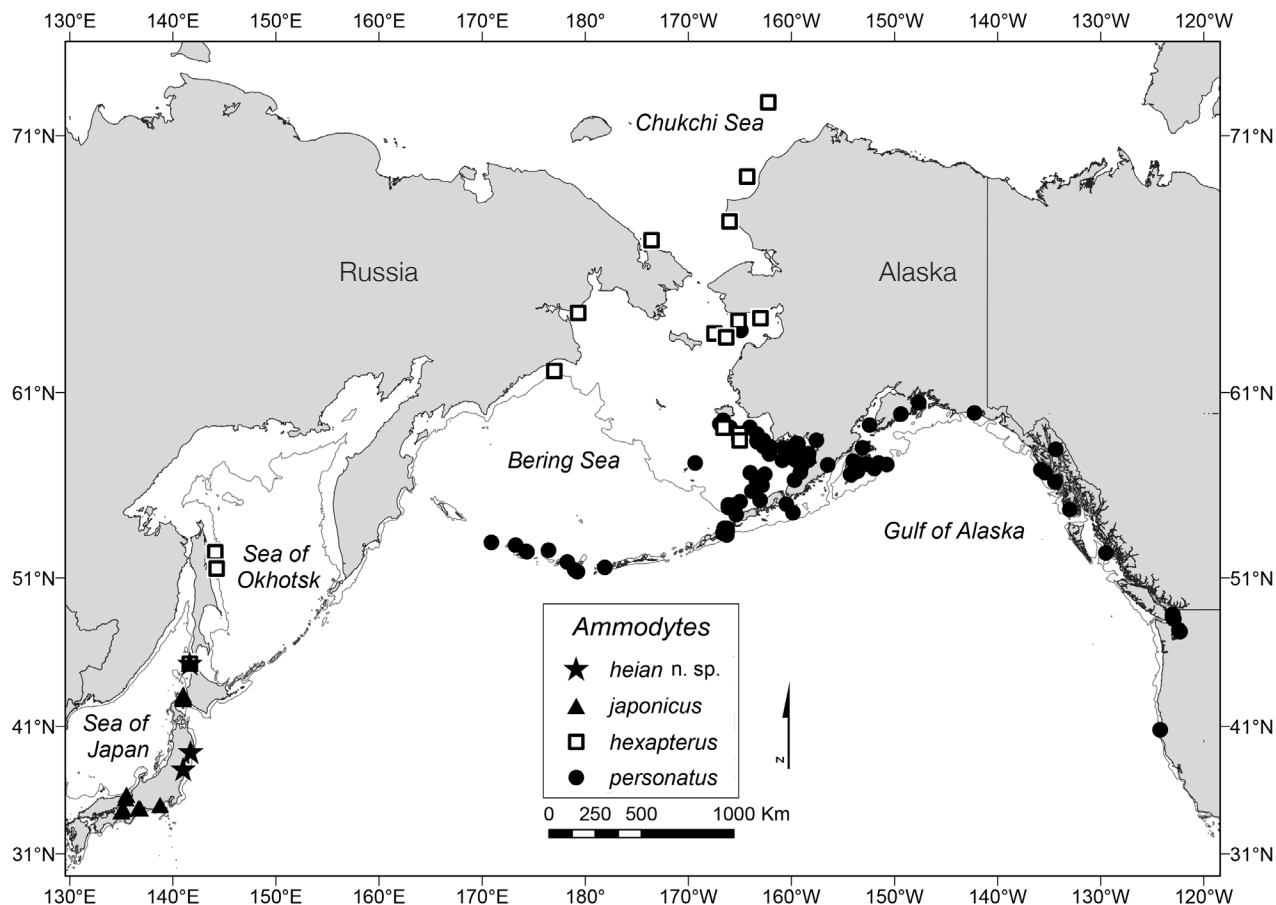


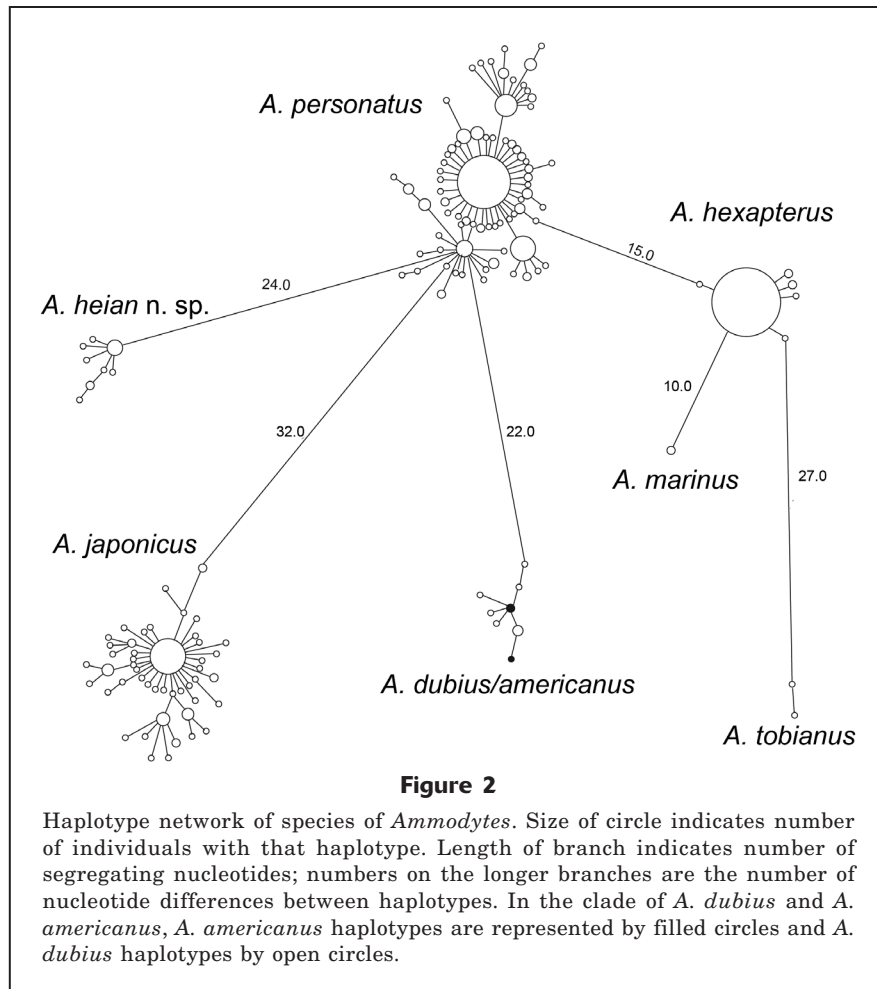
Figure 1

Distribution of species of *Ammodytes* of the North Pacific region based on material examined. Genetic material, listed in Table 1, was collected from 2000 to 2013. Morphological material is listed in Appendix 1. The gray line indicates the 200-m depth contour.

the left side and supplemented with right-side counts when the left side was damaged. Counts of dorsal-fin rays were made according to the method of Nizinski et al. (1990) and began with the first visible ray and excluded the 1 or 2 anterior rayless pterygiophores, and these counts included the last 2 rays that were each supported by a pterygiophore. Counts of anal-fin rays included all visible rays, the last 2 rays each supported by a pterygiophore. Anterior anal-fin pterygiophores were anterior to the first pterygiophore supported by the first haemal spine and did not include the anteriormost 1 or 2 rayless pterygiophores. Pectoral-fin ray counts did not include the rudimentary ventralmost ray. Pigmented pectoral-fin rays were the dorsalmost rays with evident melanophores and, because pigment appears consistently with development, counts of these rays are presented for specimens larger than 100 mm in standard length (SL) only. Gill rakers of the lower arch included the raker at the junction between upper and lower parts of the arch. Dermal plicae included those anterior and posterior to the lateral-line pores.

When these plicae were incomplete or not aligned in parallel rows, counts were supplemented from the right side. The first caudal vertebra was defined as the first centrum with a long haemal spine, and the centrum fused to the hypural plate was counted as the last vertebra.

Unless indicated otherwise, SL was used throughout this study, always measured from the tip of the snout. Measurements were taken according to the methods of Hubbs and Lagler (1958), with these additions: the length of the prepectoral process (a flap-like axillary process at the dorsal base of the pectoral fin) was measured from the dorsal base of the pectoral fin to the tip of the process, and prepectoral length was measured from the same point on the pectoral-fin base to the snout tip. Measurements and counts are presented in species descriptions as the range for all material examined, followed by the value for the holotype, lectotype, or neotype in parentheses, when intraspecific variation is indicated. Statistical analyses were performed with Statgraphics Centurion XV, vers. 15.2 (StatPoint Tech-



nologies Inc., Warrenton, VA), Spotfire S+ 8.2 (TIBCO Software Inc., Palo Alto, CA), and SPSS 11.5.1 (IBM, Armonk, NY). Using the Bonferroni method to adjust for multiple comparisons, we considered differences significant at $P < 0.05$.

More than 600 specimens were examined morphologically for meristic and morphometric data or for meristic data only. For all specimens identified genetically or by geographic range, meristic frequency distributions are presented. A reduced data set of 214 genetically identified specimens that had a complete suite of meristic and morphometric character data was used to conduct both univariate and multivariate analyses. Arcsine-transformed morphometric ratios (with SL as denominator) were tested to meet the assumptions of normality and equality of variance required for analysis of covariance (ANCOVA). A Kruskal-Wallis nonparametric test was used to test for differences in all characters with heterogeneous variances. Differences were considered significant at $P < 0.001$. A stepwise discriminant function analysis was conducted with morphometric and meristic data to establish the relative significance of characters in distinguishing the species and to identify specimens preserved in formalin with-

out tissues available for genetic identification. Morphometric data were standardized by dividing values by SL. The robustness of the discriminant function analysis was tested with a leave-one-out cross-validation procedure conducted in SPSS 11.5.1. Allometry was evaluated by plotting each measurement divided by head length (HL) against SL.

Results

Genetics

In the 560-bp COI sequences, 152 haplotypes were identified at 176 polymorphic sites, with no insertions or deletions. Seven monophyletic clades emerged from the sequence analysis of Pacific and Atlantic specimens. Each clade included many singleton haplotypes and up to 4-bp differences radiating from a common haplotype (Fig. 2).

Four clades within the North Pacific region were represented in the haplotype network of *Ammodytes* (Fig. 2). We refer to these clades as *A. personatus* (range: throughout the eastern North Pacific Ocean from Cali-

Table 2

Genetic distance calculated in MEGA 6 (Tamura et al., 2013) with the Tamura and Nei (1993) model for species of *Ammodytes*. On the diagonal, which is indicated with a gray background, is the range of distances among haplotypes within each species. Mean distance between each species pair is below the diagonal. Above the diagonal is the range of distances among all haplotypes between each species pair. *Ammodytes dubius* and *A. americanus* are reported together because the samples exhibited identical sequence patterns.

	<i>hexapterus</i>	<i>personatus</i>	<i>japonicus</i>	<i>heian</i>	<i>marinus</i>	<i>dubius/ americanus</i>	<i>tobianus</i>	<i>Uranoscopus</i>
<i>hexapterus</i>	0–0.004	0.029–0.043	0.059–0.074	0.044–0.052	0.004–0.005	0.033–0.047	0.044–0.051	0.274–0.280
<i>personatus</i>	0.031	0–0.013	0.056–0.077	0.043–0.056	0.022–0.032	0.034–0.049	0.052–0.066	0.276–0.290
<i>japonicus</i>	0.065	0.065	0–0.013	0.063–0.076	0.059–0.070	0.059–0.082	0.070–0.087	0.274–0.282
<i>heian</i>	0.047	0.049	0.068	0–0.007	0.040–0.046	0.051–0.063	0.057–0.068	0.265–0.273
<i>marinus</i>	0.005	0.027	0.063	0.042	0	0.032–0.041	0.042–0.045	0.282
<i>dubius/americanus</i>	0.04	0.043	0.068	0.057	0.036	0–0.009	0.049–0.059	0.281–0.289
<i>tobianus</i>	0.048	0.058	0.079	0.062	0.044	0.055	0.004	0.276–0.282
<i>Uranoscopus</i>	0.276	0.282	0.277	0.268	0.282	0.286	0.279	0

fornia to the Aleutian Islands and the southeastern Bering Sea), *A. hexapterus* (range: Chukchi Sea, northern and western Bering Sea, and Sea of Okhotsk), *A. japonicus* (range: Sea of Japan and Seto Inland Sea), and a new species (range: Pacific Ocean side of northern Japan and Soya Strait) (Fig. 1). Only 3 clades of Atlantic species emerged from the analyses; specimens identified morphologically as *A. dubius* or *A. americanus* as defined by Nizinski et al. (1990) were homogenous at the COI gene (as also noted by McCusker et al., 2013). *Ammodytes marinus* was closely related to *A. hexapterus*, differing by up to 10 bp. At 8 of these sites, however, *A. marinus* appeared to be heteroplastic or otherwise ambiguous. These results indicate that further investigation of *Ammodytes* of the North Atlantic Ocean is warranted.

Differentiation between clades within the North Pacific region ranged from 15 to 32 nucleotide polymorphisms. *Ammodytes personatus* differed from *A. hexapterus* by a minimum of 2.7% (15 of 560 bp), from *A. japonicus* by 5.7%, and from the new species by 4.3%. Percent divergence between *A. hexapterus* and *A. japonicus* was 6.4% and between *A. hexapterus* and the new species, 4.8%. The percent divergence between the 2 species in Japan, *A. japonicus* and the new species, was 6.4%. Sequence divergences, corrected for saturation, between each species pair were similar and are reported in Table 2. The index of substitution saturation was significantly below both the symmetrical and asymmetrical critical values ($P=0.000$) for all tests, indicating little evidence for substitution saturation within the COI DNA sequences among *Ammodytes* or between out-groups.

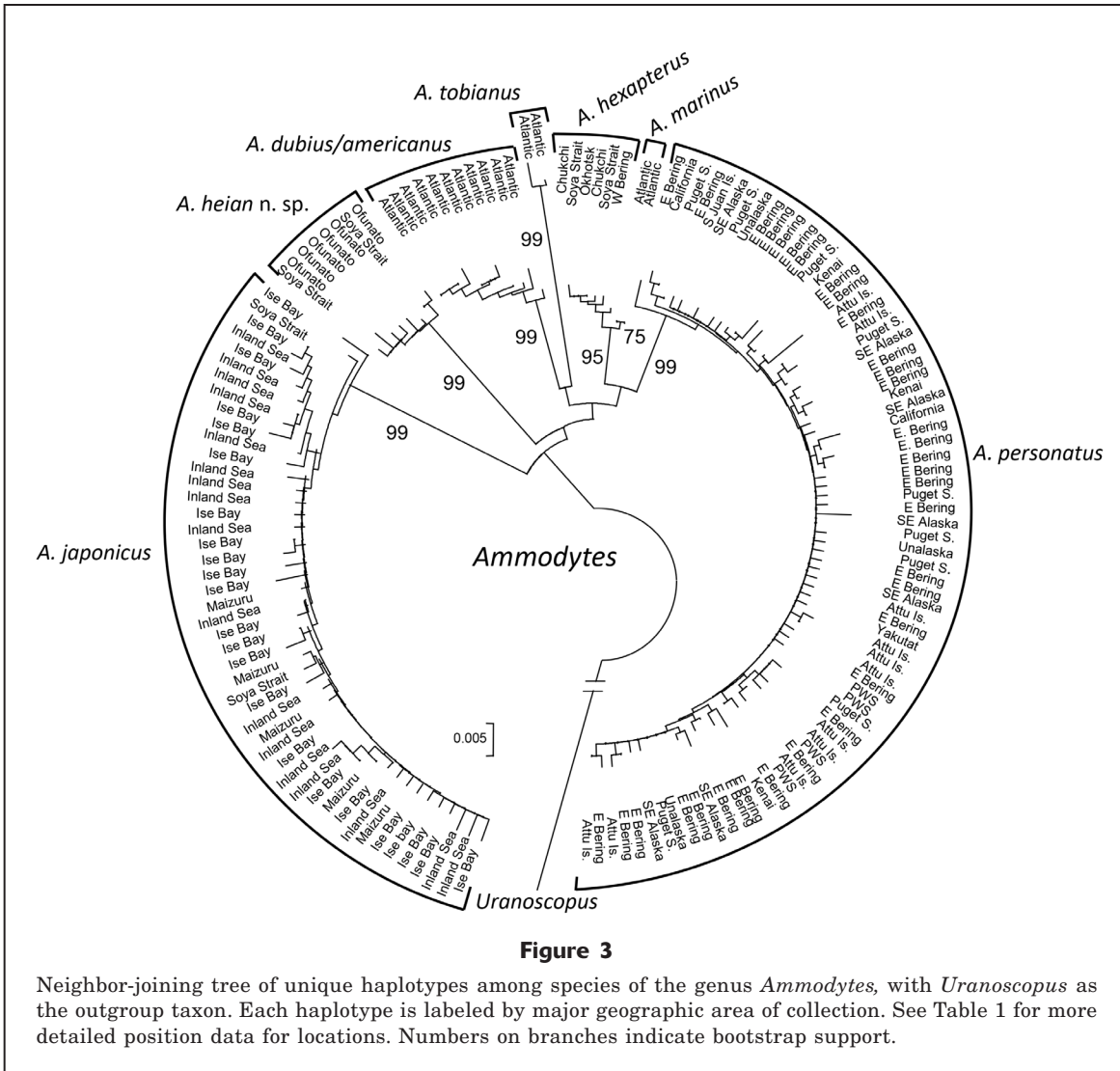
In all genetic analyses, 4 monophyletic and highly divergent groupings among Pacific specimens were observed, representing 4 distinct species in the region of the North Pacific Ocean. Bootstrap support of the

phylogenetic results was high (95–99%) for all species clades (Fig. 3). Summaries of the variation in the groupings within the phylogenetic trees, by method, are represented by trees of consensus sequences of each highly supported species clade (Fig. 4). These phylogenetic resolutions differed only in the position of *A. personatus* as sister of the *A. dubius* and *A. americanus* clade or sister of the *A. hexapterus* and *A. marinus* clade. The low bootstrap values indicate that neither of these resolutions is well supported by these data. Intraspecific variation differed within the 4 clades (Table 3). The 2 clades representing *A. japonicus* and the new species displayed the highest levels of gene diversity (0.50 and 0.53), followed by a high level of diversity within *A. personatus* (0.31), which exhibited 3 secondary nodes of haplotypes. Specimens within these secondary branches were not geographically related (Fig. 3). *Ammodytes hexapterus* was nearly monomorphic, with a low level of genetic diversity (0.04): only 6 single transitions were detected in 143 individuals.

All COI sequences reported in GenBank and the Barcode of Life Database (BOLD) for *Ammodytes* of the North Pacific region were aligned in CodonCode Aligner. Each sequence clearly corresponded with 1 of the 4 species described in this article (Table 4).

Morphology

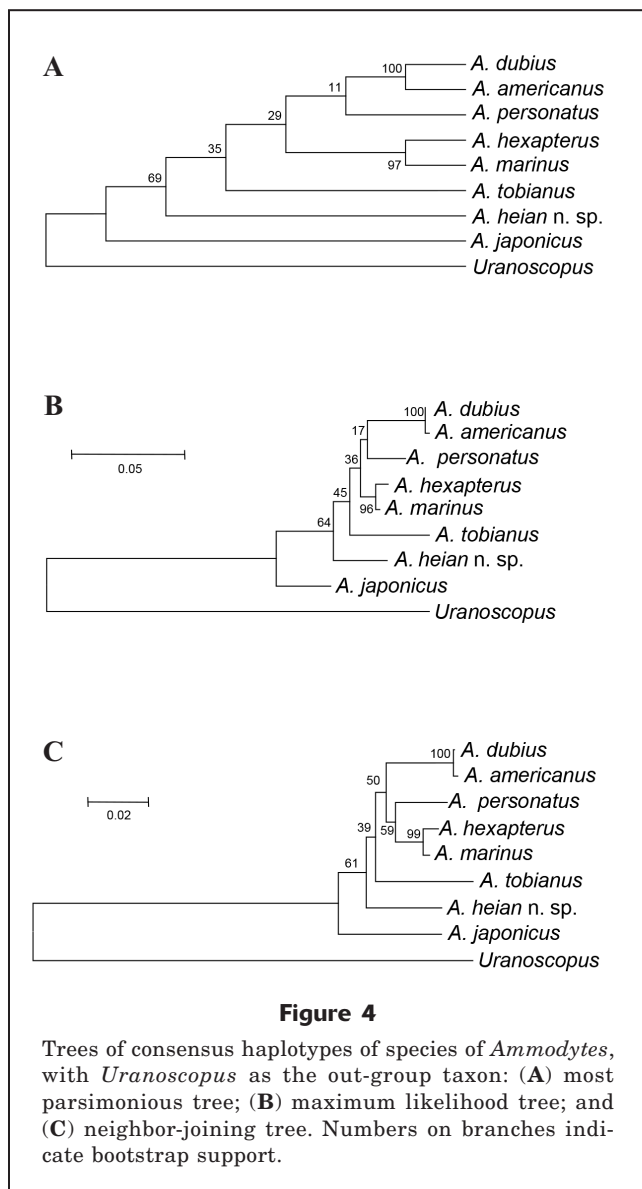
Meristic characters Among meristic characters of specimens identified genetically and with a complete suite of morphological characters, only counts of total gill rakers, lateral-line pores, dermal plicae, and pectoral-fin rays met variance assumptions necessary to conduct an ANCOVA (Table 5). Counts of gill rakers differed between *A. japonicus*, *A. hexapterus*, and *A. personatus*; counts in the new species and *A. personatus* did not differ significantly from each other, but each had sig-



nificantly higher counts than either *A. japonicus* or *A. hexapterus*. Counts of lateral-line pores differed significantly among all species: *A. personatus* had the lowest counts, followed by *A. hexapterus*, *A. japonicus*, and the new species with higher counts. Pectoral-fin rays differed significantly only in the new species, which had significantly higher counts than all other species. All other meristic characters violated the equality of variance assumption required for ANOVA and were tested by using the nonparametric Kruskal-Wallis test. With the exception of gill rakers of the lower arch and caudal-fin rays, all characters were significantly different between 2 or more species (Table 5). Importantly, the new species exhibited higher counts of anal-fin rays and anterior anal-fin pterygiophores. Meristic character frequencies are presented in Tables 6–8.

Morphometric characters Among morphometric characters of specimens identified genetically and with a com-

plete suite of morphological characters, only caudal peduncle depth, caudal peduncle length, preanal length, and anal-fin base length met variance assumptions necessary to conduct an ANCOVA (Table 5). The caudal peduncle was significantly deeper in *A. personatus* than in *A. hexapterus* and the new species (which were not significantly different from each other), as well as in *A. japonicus*, in which this character was significantly more slender than it was in all other species. The caudal peduncle was also longer in *A. hexapterus* and *A. personatus* (which were not significantly different from each other) than in the new species and *A. japonicus*, in which it was shorter than it was in all other species. The preanal length was significantly longer in *A. personatus* and was significantly shorter in the new species than in all other species. The anal-fin base was significantly longer in *A. japonicus*, followed by the new species, *A. hexapterus*, and *A. personatus*. Other characters were tested with the Kruskal-Wallis



test and, with the exception of gill raker length, all differed significantly between 2 or more species (Table 5). Most significantly, the new species had a smaller orbit, wider interorbital space, and longer prepectoral process than all other species, and *A. personatus* had a shorter preanal length than all other species (Table 5). All species exhibited ontogenetic allometry in orbit size and pectoral-fin length: the orbit was proportionately longer and deeper and the pectoral fin was longer in smaller individuals. In *A. japonicus* alone, gill rakers were proportionally longer in smaller individuals.

Discriminant function analysis All 3 discriminant functions obtained in this analysis were significant (Wilks's lambda; $P < 0.0001$). All specimens of the 2 species of *Ammodytes* of the eastern and northern parts of the North Pacific Ocean (*A. personatus* and *A. hexapterus*)

were distinguished from specimens of the 2 species of *Ammodytes* found only in waters off Japan (*A. japonicus* and the new species) on the first discriminant axis (Fig. 5). Scores were calculated from the following first discriminant function equation:

$$D_1 = -0.991 (od) - 0.413 (iow) + 0.465 (pb) + 0.379 (pl) + 0.914 (cpvl) + 0.048 (pdl) + 0.423 (ppl) + 0.230 (gr) - 0.192 (llp) + 0.146 (dp) - 0.270 (ap) + 0.875 (pcv) + 0.445 (cv) - 62.266,$$

where D_1 = the first discriminant score of an individual; od = orbit depth divided by HL; iow = interorbital width divided by HL; pb = pectoral-fin base depth divided by HL; pl = pectoral fin length divided by HL; $cpvl$ = caudal peduncle ventral length divided by HL; pdl = predorsal length divided by HL; ppl = prepectoral length divided by HL; gr = the number of gill rakers on the entire gill arch; llp = the number of lateral-line pores; dp = the number of dermal plicae; ap = the number of anal-fin pterygiophores anterior to the first haemal spine; pcv = the number of precaudal vertebrae; and cv = the number of caudal vertebrae.

A specimen with a score above 0 was identified as an individual of an eastern or northern Pacific species (either *A. personatus* or *A. hexapterus*); scores below 0 indicated the specimen was a species of Japan (either *A. japonicus* or the new species).

On the second discriminant axis, all but 3 specimens of *A. japonicus* and the new species were distinguished from each other (95.0%; Fig. 5). Three specimens identified genetically as *A. japonicus* were misclassified as the new species (Fig. 5). Among individuals identified as *A. personatus* or *A. hexapterus*, 98.6% were distinguished from each other, the exceptions being a specimen genetically identified as *A. personatus* and misclassified as *A. hexapterus* and 2 specimens genetically identified as *A. hexapterus* but misclassified as *A. personatus*. Scores on the second discriminant axis were calculated with the second discriminant function equation:

$$D_2 = -0.334 (od) - 0.578 (iow) - 2.674 (pb) + 0.818 (pl) + 0.958 (cpvl) + 0.446 (pdl) - 0.765 (ppl) + 0.031 (gr) + 0.027 (llp) - 0.007 (dp) - 0.675 (ap) - 0.265 (pcv) + 0.170 (cv) - 2.458,$$

where D_2 = the first discriminant score of an individual; od = orbit depth divided by HL; iow = interorbital width divided by HL; pb = pectoral-fin base depth divided by HL; pl = pectoral fin length divided by HL; $cpvl$ = caudal peduncle ventral length divided by HL; pdl = predorsal length divided by HL; ppl = prepectoral length divided by HL; gr = the number of gill rakers on the entire gill arch; llp = the number of lateral-line pores; dp = the number of dermal plicae; ap = the number of anal-fin pterygiophores anterior to the first haemal spine; pcv = the number of precaudal vertebrae; and cv = the number of caudal vertebrae.

Most specimens with a score above 0 were identified as either *A. hexapterus* or *A. japonicus*; scores below 0

Table 3

Genetic indices for the 4 species of *Ammodytes* of the North Pacific region. n =sample size; H =number of haplotypes; S =number of polymorphic sites; h =haplotype diversity; π =average nucleotide diversity; and SE=standard error.

	n	H	S	h (SE)	π (SE)
<i>A. hexapterus</i>	143	6	5	0.1500 (0.39)	0.0002 (0.0003)
<i>A. personatus</i>	229	75	64	0.8100 (0.02)	0.0030 (0.0020)
<i>A. japonicus</i>	95	47	47	0.8471 (0.36)	0.0049 (0.0029)
<i>A. heian</i> n. sp.	15	8	8	0.8476 (0.08)	0.0027 (0.0019)

identified most specimens as either *A. personatus* or the new species.

The cross-validation procedure correctly classified 95.3% of the specimens. Of 76 specimens of *A. japonicus* and the new species, 3 specimens of *A. japonicus* were misidentified as the new species. Of 136 specimens of *A. hexapterus* or *A. personatus*, 4 specimens of *A. hexapterus* were misidentified as *A. personatus*.

Systematics

Ammodytes Linnaeus, 1758

Ammodytes (Artedi) Linnaeus, 1758:247 (type *A. tobianus* Linnaeus).

Argyrotaenia Gill, 1861:40 (type *A. vittatus* DeKay, 1842).

Diagnosis

Body elongate, covered with small cycloid scales situated at right angles along oblique dermal plicae below lateral line. Lateral line incomplete, straight, unbranched, 3–4 scale rows below the dorsal-fin base. Ventrolateral dermal fold extends from isthmus along edge of belly and above anal fin. Median ventral fold present, extending from isthmus to vent. Premaxilla protractile, with well-developed ascending process. Anterior ends of maxillae not broadened and not touching each other but connected by tendon. Teeth absent. Dorsal fin long, origin anterior to posterior tip of pectoral fin, anterior 1–3 pterygiophores inserted between neural spines 6–7, 7–8, 8–9, or 9–10. Pectoral fin pointed, rays 6–7 longest, rays 3–10 bifurcate, other rays simple. Pelvic fins absent. Vertebrae 59–78.

Description

Body elongate, slender, depth about 10–15 times into SL. Body anterior to vent longer than posterior portion, distance from snout to anal-fin origin about 60–70% SL. Head elongate, with long pointed snout. Mouth

large, superior: upper jaw protractile, with elaborate cartilages supporting premaxilla (Pietsch, 1984); lower jaw projecting, mandible with strong and sharp symphyseal process. Orbit moderately large, length 5 to 6 times into HL. Gill membranes separate, free from isthmus. Gill rakers long and slender, 20–31 on first arch.

Body covered with small cycloid scales: scales below lateral line situated along 106–198 oblique dermal plicae, fading to scale rows on caudal peduncle, scales above lateral line 3–4, and scales on belly between median ridge and ventrolateral fold 3–4. Head naked. Lateral line straight, unbranched, incomplete, extending from above operculum to posterior portion of anal fin. Pored lateral line scales 106–185.

Dorsal-fin rays 49–69, simple except for few posterior-most. Dorsal fin long, with origin anterior to tip of pectoral fin. Anal-fin rays 24–36, simple except for few posterior-most. Anal fin about half the length of dorsal fin, with origin at 66% of body. Pectoral-fin rays 11–17, rays 7–9 longest. Pelvic fins absent. Caudal fin forked. Total vertebrae 59–78, precaudal vertebrae 33–49, caudal vertebrae 21–28.

Ammodytes hexapterus Pallas, 1814

Arctic sand lance [Japanese name: Kita-ikanago]

Figures 6A and 7A; Tables 5–7

Ammodytes hexapterus Pallas, 1814:226 (original description; types lost; circumboreal, Kamchatka, Kuril and Aleutian islands, American coast, Baltic Sea).

Ammodytes tobianus personatus Popov, 1931:145 (Nagaeva Bay, northern Sea of Okhotsk).

Ammodytes hexapterus hexapterus Lindberg, 1937:87 (Commander Islands, Avachinskaya Bay, Ayan Bay, Shantar Islands, Terpenia Bay, Gulf of Tartary).

Neotype

UAM 2813, 126.5 mm, Russia, Chukchi Sea, 67.4093°N, 173.5757°W, RUSALCA 2012, station CL10, PSBT, haul 16, 13 September 2012 (GenBank Accession KJ137280), herein designated.

Table 4

Cytochrome oxidase c subunit 1 sequences of *Ammodytes* of the North Pacific region mined from GenBank (www.ncbi.nlm.nih.gov) and Barcode of Life Database (BOLD; www.boldsystems.org) with GenBank accession number, BOLD sequence identification (ID), general location of collection, current name assigned to the sequence data in GenBank and BOLD (Current ID), and “revised” name (Revised ID), which refers to the species in this study with which the sequence aligned.

GenBank accession	BOLD sequence ID	Location	Current ID	Revised ID
<i>A. hexapterus</i>				
HQ712266	DSFAL117-07	Chukchi Sea	<i>hexapterus</i>	<i>hexapterus</i>
HQ712267	DSFAL118-07	Chukchi Sea	<i>hexapterus</i>	<i>hexapterus</i>
HQ712268	DSFAL157-07	Chukchi Sea	<i>hexapterus</i>	<i>hexapterus</i>
HQ712269	DSFAL282-07	N. Bering Sea	<i>hexapterus</i>	<i>hexapterus</i>
HQ704752		N. Bering Sea	<i>hexapterus</i>	<i>hexapterus</i>
HQ704753		N. Bering Sea	<i>hexapterus</i>	<i>hexapterus</i>
HQ704754		N. Bering Sea	<i>hexapterus</i>	<i>hexapterus</i>
HM421764	DSFAL626-09	Chukchi Sea	<i>hexapterus</i>	<i>hexapterus</i>
HM421765	DSFAL627-09	Chukchi Sea	<i>hexapterus</i>	<i>hexapterus</i>
	DSFIB095-11	Arctic Ocean	<i>hexapterus</i>	<i>hexapterus</i>
	DSFAL703-11	Arctic Ocean	<i>hexapterus</i>	<i>hexapterus</i>
	DSFAL709-11	Arctic Ocean	<i>hexapterus</i>	<i>hexapterus</i>
	DSFAL712-11	Arctic Ocean	<i>hexapterus</i>	<i>hexapterus</i>
	DSFIB090-11	Arctic Ocean	<i>hexapterus</i>	<i>hexapterus</i>
	TZAIC156-05	Hudson Bay	<i>hexapterus</i>	<i>hexapterus</i>
	TZAIC160-05	Hudson Bay	<i>hexapterus</i>	<i>hexapterus</i>
	TZAIC176-05	Hudson Bay	<i>hexapterus</i>	<i>hexapterus</i>
<i>A. personatus</i>				
FJ666917	GBGC9217-09	Bering Sea	<i>hexapterus</i>	<i>personatus</i>
FJ666918	GBGC9216-09	Bering Sea	<i>hexapterus</i>	<i>personatus</i>
FJ666919	GBGC9215-09	Bering Sea	<i>hexapterus</i>	<i>personatus</i>
FJ666920	GBGC9214-09	Bering Sea	<i>hexapterus</i>	<i>personatus</i>
FJ666921	GBGC9213-09	Bering Sea	<i>hexapterus</i>	<i>personatus</i>
HQ712264	DSFAL019-07	Kodiak Island	<i>cf. personatus</i>	<i>personatus</i>
HQ712265	DSFAL257-07	Kodiak Island	<i>cf. personatus</i>	<i>personatus</i>
	FMV428-09	Vancouver Island, BC	<i>hexapterus</i>	<i>personatus</i>
	FMV429-09	Vancouver Island, BC	<i>hexapterus</i>	<i>personatus</i>
<i>A. japonicus</i>				
FJ666901	GBGC9212-09	Yellow Sea	<i>personatus</i>	<i>japonicus</i>
FJ666902	GBGC9211-09	Yellow Sea	<i>personatus</i>	<i>japonicus</i>
FJ666903	GBGC9210-09	Yellow Sea	<i>personatus</i>	<i>japonicus</i>
FJ666904	GBGC9209-09	Yellow Sea	<i>personatus</i>	<i>japonicus</i>
FJ666905	GBGC9208-09	Yellow Sea	<i>personatus</i>	<i>japonicus</i>
FJ666906	GBGC9207-09	Yellow Sea	<i>personatus</i>	<i>japonicus</i>
FJ666907	GBGC9206-09	Yellow Sea	<i>personatus</i>	<i>japonicus</i>
FJ666908	GBGC9219-09	East China Sea	<i>personatus</i>	<i>japonicus</i>
FJ666909	GBGC9218-09	East China Sea	<i>personatus</i>	<i>japonicus</i>
FJ666910	GBGC9205-09	Sea of Japan (=East Sea)	<i>personatus</i>	<i>japonicus</i>
FJ666911	GBGC9204-09	Sea of Japan (=East Sea)	<i>personatus</i>	<i>japonicus</i>
FJ666912	GBGC9203-09	Sea of Japan (=East Sea)	<i>personatus</i>	<i>japonicus</i>
FJ666913	GBGC9202-09	Sea of Japan (=East Sea)	<i>personatus</i>	<i>japonicus</i>
FJ666914	GBGC9201-09	Sea of Japan (=East Sea)	<i>personatus</i>	<i>japonicus</i>
EU266366	GBGC7790-09	no location noted	<i>personatus</i>	<i>japonicus</i>
HQ711864	ANGBF1790-12	Shandong, China	<i>personatus</i>	<i>japonicus</i>
JQ738429	ANGBF2227-12	no location noted	<i>personatus</i>	<i>japonicus</i>
JQ738549	ANGBF2283-12	no location noted	<i>personatus</i>	<i>japonicus</i>
JQ738551	ANGBF2284-12	no location noted	<i>personatus</i>	<i>japonicus</i>
JQ738553	ANGBF2285-12	no location noted	<i>personatus</i>	<i>japonicus</i>
JQ738552	ANGBF4508-12	no location noted	<i>personatus</i>	<i>japonicus</i>
JQ738550	ANGBF4509-12	no location noted	<i>personatus</i>	<i>japonicus</i>
JQ738428	ANGBF4565-12	no location noted	<i>personatus</i>	<i>japonicus</i>
<i>A. heian</i> n. sp.				
FJ666915	GBGC9200-09	Sea of Japan (=East Sea)	<i>personatus</i>	<i>heian</i>
FJ666916	GBGC9199-09	Sea of Japan (=East Sea)	<i>personatus</i>	<i>heian</i>

Table 5

Proportional morphometric and meristic characters of species of *Ammodytes* of the North Pacific region, based on genetically identified specimens for which all of both types of data were collected. Standard length (SL) and head length are given in millimeters. Morphometric data are given in percent SL and presented as the range, followed by the mean and standard deviation (SD). Species listed in superscript are statistically different from the species in ordinary type, as determined by analysis of covariance or Kruskal-Wallis (KW) tests as appropriate. pr=*A. personatus*; hx=*A. hexapterus*; ja=*A. japonicus*; hn=*A. heian* new species (n. sp.); and NS=non-significant.

	<i>A. hexapterus</i>		<i>A. personatus</i>		<i>A. japonicus</i>		<i>A. heian</i> n. sp.		Significance
	n	Range (Mean [SD])	n	Range (Mean [SD])	n	Range (Mean [SD])	n	Range (Mean [SD])	
Standard length	63	89.0–257.3 (149.6 [46.2])	73	61.2–273.6 (148.9 [85.2])	60	86.0–162.3 (122.5 [27.5])	17	119.6–225.9 (204.7 [23.1])	KW: <0.001
Head length	63	18.7–23.3 (20.7 [1.1])	73	18.8–25.4 (22 [2.2])	60	17.6–22.2 (20.0 [1.4])	17	18.8–22.1 (19.7 [0.8])	hx ^{pr,ja,hn} , pr ^{hx,ja,hn} ; ja ^{hx,pr} ; hn ^{hx,pr}
Morphometrics									
Orbit length	63	2.3–4.0 (3.1 [0.5])	73	2.3–5.1 (3.6 [0.9])	60	2.3–3.8 (3.0 [0.4])	17	2.1–3.4 (2.5 [0.3])	KW: <0.001
Orbit depth	63	2.5–4.0 (3.2 [0.4])	73	2.3–4.8 (3.5 [0.8])	60	2.4–4.3 (3.3 [0.5])	17	2.1–3.2 (2.6 [0.2])	KW: <0.001
Depth at dorsal-fin origin	63	6.1–10.7 (8.6 [1.1])	73	6.7–11.6 (8.8 [1.2])	60	5.8–10.5 (8.8 [1.0])	17	8.8–10.9 (9.8 [0.6])	KW: <0.001
Depth at anal-fin origin	63	6.0–10.3 (8.2 [1.1])	73	6.7–11.1 (8.6 [0.9])	73	6.7–11.1 (8.9 [1.2])	17	8.7–10.9 (9.7 [0.6])	KW: <0.001
Snout length	63	4.7–6.9 (5.7 [0.4])	73	5.1–7.0 (5.9 [0.5])	60	4.8–6.4 (5.5 [0.4])	17	5.1–6.2 (5.5 [0.2])	KW: <0.001
Interorbital width	63	1.9–3.5 (2.7 [0.4])	73	2.6–3.7 (3.2 [0.2])	60	2.6–3.8 (3.1 [0.3])	17	3.1–3.7 (3.4 [0.2])	KW: <0.001
Upper jaw length	63	5.8–7.8 (6.6 [0.5])	73	4.8–8.9 (7.2 [1.1])	60	5.3–7.7 (6.4 [0.6])	17	5.5–7.2 (6.2 [0.4])	KW: <0.001
Lower jaw length	63	8.2–10.3 (9.0 [0.5])	73	7.5–11.5 (9.6 [1.2])	60	7.7–10.9 (8.9 [0.8])	17	7.7–9.0 (8.5 [0.3])	KW: <0.001
Gill raker length	63	1.6–2.9 (2.1 [0.2])	73	1.5–3.0 (2.2 [0.3])	60	1.4–3.0 (2.1 [0.4])	17	1.7–2.6 (2.1 [0.2])	KW: <0.001
Prepectoral process length	63	1.2–3.7 (2.0 [0.4])	73	1.0–3.0 (2.0 [0.4])	60	1.3–2.7 (2.0 [0.3])	17	1.5–3.0 (2.4 [0.3])	KW: <0.001
Pectoral-fin base depth	63	1.9–2.7 (2.3 [0.2])	73	2.1–3.3 (2.6 [0.3])	60	2.0–3.0 (2.5 [0.3])	17	2.0–2.7 (2.4 [0.2])	KW: <0.001
Pectoral fin length	63	8.5–11.8 (10.1 [0.7])	73	8.2–13.4 (10.5 [1.6])	60	7.6–10.7 (9.4 [0.7])	17	7.7–10.5 (8.8 [0.6])	KW: <0.001
Caudal fin length	63	8.0–10.9 (9.4 [0.6])	73	8.0–11.4 (9.6 [1.1])	60	7.2–11.9 (9.3 [0.8])	17	8.6–10.1 (9.2 [0.4])	NS
Caudal peduncle depth	63	2.1–3.1 (2.6 [0.2])	73	2.3–3.0 (2.7 [0.2])	60	2.1–3.5 (2.5 [0.2])	17	2.4–2.8 (2.5 [0.1])	<0.001
Caudal peduncle length	63	4.2–5.7 (5.1 [0.3])	73	3.9–5.9 (4.9 [0.4])	60	2.8–5.4 (3.9 [0.4])	17	3.7–5.1 (4.6 [0.4])	<0.001

Table 5 (continued)

	<i>A. hexapterus</i>		<i>A. personatus</i>		<i>A. japonicus</i>		<i>A. heian</i> n. sp.		Significance
	n	Range (Mean [SD])	n	Range (Mean [SD])	n	Range (Mean [SD])	n	Range (Mean [SD])	
Predorsal length	63	24.9–29.8 (27.2 [1.3])	73	23.1–30.8 (27.2 [2.1])	60	22.6–27.8 (25.2 [1.4])	17	23.5–27.3 (25.7 [1.0])	KW: <0.001 hx ^{ja} , pr ^{ja} , hn, ja ^{bx} , pr ^{hn} , hn ^{pr} , ja
Prenasal length	63	60.3–67.4 (64.3 [1.6])	73	61.8–69.1 (65.5 [1.4])	60	60.8–69.9 (64 [1.3])	17	60.7–66.2 (63.5 [1.6])	<0.001 hx ^{pr} , hn, pr ^{bx} , ja, hn, ja ^{pr} , hn, hn ^{bx} , pr ^{ja}
Dorsal-fin base length	63	63.8–71.4 (68 [1.5])	73	63.2–74.0 (68.3 [3.1])	60	67.6–77.3 (71.2 [1.9])	17	69.2–72.0 (70.7 [0.9])	KW: <0.001 hx ^{ja} , hn, pr ^{ja} , hn, ja ^{bx} , pr, hn ^{bx} , pr
Anal-fin base length	63	27.6–32.6 (30.2 [1])	73	26.8–32.4 (29.6 [1.1])	60	30.0–34.8 (32.5 [0.9])	17	28.9–34.6 (32.1 [1.3])	<0.001 All
Prepectoral length	63	17.7–22.5 (19.6 [1.2])	73	17.9–24.5 (21.0 [1.8])	60	16.5–21.3 (18.7 [1.3])	17	17.3–20.4 (18.5 [0.7])	KW: <0.001 hx ^{pr} , ja, hn, pr ^{bx} , ja, hn, ja ^{bx} , pr, hn ^{bx} , pr
Meristics									
Dorsal-fin rays	63	56–63 (58.9 [1.5])	73	56–65 (60.4 [2.8])	60	53–60 (56.2 [1.5])	17	55–60 (57.9 [1.5])	KW: <0.001 hx ^{pr} , ja, pr ^{bx} , ja, hn, ja ^{pr} , pr ^{bx} , hn, hn ^{pr} , ja
Anal-fin rays	63	27–33 (30.1 [1.3])	73	27–33 (29.5 [1.5])	60	27–31 (29.2 [0.9])	17	30–33 (31.9 [1.0])	KW: <0.001 hx ^{pr} , ja, hn, pr ^{bx} , hn, ja ^{bx} , hn, hn ^{pr} , ja
Anterior anal-fin pterygiophores	63	8–14 (10.8 [1.6])	73	7–13 (9.8 [1.3])	60	8–12 (10.0 [0.8])	17	10–13 (11.8 [0.8])	KW: <0.001 hx ^{pr} , ja, hn, pr ^{bx} , hn, ja ^{bx} , hn, hn ^{bx} , pr ^{ja}
Pectoral-fin rays	63	13–16 (14.5 [0.6])	73	13–16 (14.3 [0.8])	60	13–17 (14.3 [0.7])	17	14–17 (15.0 [0.8])	<0.005 hx ^{hn} , pr ^{hn} , ja ^{hn} , hn ^{bx} , pr ^{ja}
Pigmented pectoral-fin rays	58	2–6 (4.2 [0.9])	34	3–7 (5.3 [0.9])	56	4–11 (6.9 [1.5])	20	4–10 (5.9 [1.0])	KW: <0.001 hx ^{pr} , ja, pr ^{bx} , ja, hn, ja ^{pr} , hn, hn ^{bx} , ja
Gill rakers (total)	63	24–29 (26.7 [1.1])	73	24–30 (27.3 [1.5])	60	21–29 (24.1 [1.6])	17	26–30 (27.9 [1.0])	<0.001 hx ^{pr} , ja, hn, pr ^{bx} , ja, hn, ja ^{pr} , hn, hn ^{bx} , ja
Gill rakers (upper arch)	63	4–6 (4.5 [0.6])	73	4–6 (4.9 [0.4])	60	4–5 (4.6 [0.5])	17	4–5 (4.9 [0.4])	KW: <0.001 hx ^{pr} , hn, pr ^{bx} , ja, hn, ja ^{pr} , hn, hn ^{bx} , ja
Gill rakers (lower arch)	63	20–24 (22.2 [1])	73	19–26 (22.5 [1.5])	60	17–24 (19.5 [1.4])	17	21–25 (23.1 [0.9])	KW: <0.001 hx ^{ja} , hn, pr ^{ja} , ja ^{pr} , ja ^{pr} , hn ^{bx} , hn, hn ^{pr} , ja
Pseudobranchs	19	8–16 (10.5 [1.9])	37	9–19 (12.1 [2.6])	31	9–14 (10.4 [1.3])	13	12–17 (14.2 [1.9])	<0.001 hx ^{pr} , hn, pr ^{bx} , ja, hn, ja ^{pr} , hn, hn ^{bx} , pr ^{ja}
Lateral line pores	63	121–152 (137.2 [7.9])	73	114–158 (132.2 [8.4])	60	134–160 (147.3 [5.6])	17	146–185 (159.6 [9.0])	<0.001 All
Dermal plicae	63	143–172 (159.5 [8.0])	73	139–179 (155.3 [8.2])	60	147–174 (160.2 [6.1])	17	157–198 (174.5 [8.6])	<0.001 hx ^{pr} , hn, pr ^{bx} , ja, hn, ja ^{pr} , hn, hn ^{pr} , hn
Precaudal vertebrae	63	42–47 (44.1 [1.2])	73	42–49 (44.8 [1.7])	60	37–43 (40.1 [1.1])	17	39–43 (41.8 [1.3])	KW: <0.001 All
Caudal vertebrae	63	21–27 (24.2 [1.3])	73	23–26 (24.4 [0.9])	60	21–25 (22.6 [0.8])	17	22–25 (23.6 [0.8])	KW: <0.001 hx ^{ja} , hn, pr ^{ja} , hn, ja ^{bx} , pr ^{hn} , hn ^{bx} , pr ^{ja}
Total vertebrae	63	66–71 (68.4 [1.1])	73	66–73 (69.1 [2])	60	60–66 (62.8 [1.2])	17	63–67 (65.3 [1.2])	KW: <0.001 All
Principal caudal-fin rays	63	14–17 (15.2 [0.5])	68	13–18 (15.3 [0.8])	60	15–18 (15.4 [0.7])	17	15–17 (15.3 [0.7])	NS

Table 6

Counts of dorsal-fin rays, anal-fin rays, anterior anal-fin pterygiophores, pectoral-fin rays, pigmented pectoral-fin rays, and caudal-fin rays in species of *Ammodytes* of the North Pacific region. Pigmented pectoral-fin rays are reported only for specimens larger than 100 mm in standard length.

	Dorsal-fin rays																<i>n</i>	
	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65		66
<i>A. hexapterus</i>							9	20	28	26	15	10	2	2				113
<i>A. personatus</i>						4	19	41	39	56	50	40	18	17	8	1		293
<i>A. japonicus</i>	1	5	4	6	12	21	20	12	7	5	2						95	
<i>A. heian</i> n. sp.						2	2	3	6	8	2						23	
	Anal-fin rays										<i>n</i>							
	25	26	27	28	29	30	31	32	33									
<i>A. hexapterus</i>			2	18	22	49	26	10	2	130								
<i>A. personatus</i>	1	1	15	44	65	106	40	19	2	292								
<i>A. japonicus</i>		1	2	14	37	24	8	3	1	90								
<i>A. heian</i> n. sp.						3	7	5	8	23								
	Anterior anal-fin pterygiophores								<i>n</i>									
	7	8	9	10	11	12	13	14										
<i>A. hexapterus</i>	1	8	39	26	25	13	9	4	126									
<i>A. personatus</i>	4	23	61	96	75	27	5		291									
<i>A. japonicus</i>	1	6	24	36	12	4			83									
<i>A. heian</i> n. sp.				2	7	11	3		23									
	Pectoral-fin rays						<i>n</i>											
	13	14	15	16	17													
<i>A. hexapterus</i>	6	47	48	1		103												
<i>A. personatus</i>	37	135	54	7		233												
<i>A. japonicus</i>	6	50	32	2	1	91												
<i>A. heian</i> n. sp.		7	11	4	1	23												
	Pigmented pectoral-fin rays											<i>n</i>						
	2	3	4	5	6	7	8	9	10	11								
<i>A. hexapterus</i>	3	14	25	18	3						63							
<i>A. personatus</i>		19	20	28	12	5					84							
<i>A. japonicus</i>			3	10	14	15	14	6		1	63							
<i>A. heian</i> n. sp.			1	5	6	4	3		1		20							
	Principal caudal-fin rays							<i>n</i>										
	13	14	15	16	17	18												
<i>A. hexapterus</i>		1	99	19	2		122											
<i>A. personatus</i>	1	2	240	26	8	1	278											
<i>A. japonicus</i>		2	73	13	5	1	94											
<i>A. heian</i> n. sp.			19	2	2		23											

Diagnosis

A species of *Ammodytes* distinguished from *A. japonicus* by significantly more total vertebrae (65–72 vs. 59–66) and precaudal vertebrae (40–47 vs. 36–43), fewer

pored lateral-line scales (121–152 vs. 132–163) and dermal plicae (143–172 vs. 144–182), more dorsal-fin rays (56–63 vs. 50–60), and fewer pigmented pectoral-fin rays (2–6 vs. 4–11). It is further distinguished from the new species by its significantly larger orbit (12–

Table 7

Counts of precaudal, caudal, total vertebrae, and gill rakers of the lower arch in specimens of species of *Ammodytes* of the North Pacific region that were analyzed in this study.

	Precaudal vertebrae															<i>n</i>
	36	37	38	39	40	41	42	43	44	45	46	47	48	49		
<i>A. hexapterus</i>					1	2	14	32	52	19	9	3			132	
<i>A. personatus</i>						2	9	52	80	66	51	25	9	1	295	
<i>A. japonicus</i>	1	12	9	27	33	18	6	1							108	
<i>A. heian</i> n. sp.				2	5	1	9	6							23	
	Caudal vertebrae									<i>n</i>						
	21	22	23	24	25	26	27	28								
<i>A. hexapterus</i>	1	6	22	34	46	18	5		113							
<i>A. personatus</i>	3	9	50	103	89	35	6		295							
<i>A. japonicus</i>	5	23	43	23	8	3		2	107							
<i>A. heian</i> n. sp.		2	6	14	1				23							
	Total vertebrae															<i>n</i>
	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	
<i>A. hexapterus</i>							2	6	26	44	35	16	3	1	133	
<i>A. personatus</i>							2	16	43	62	61	42	39	27	4	296
<i>A. japonicus</i>	1	3	16	29	45	18	5	1								117
<i>A. heian</i> n. sp.	2	7	2	10	2	23										
	Lower gill rakers												<i>n</i>			
	16	17	18	19	20	21	22	23	24	25	26					
<i>A. hexapterus</i>					4	12	33	14	7	2		72				
<i>A. personatus</i>			1	1	23	54	64	48	13	11	1	217				
<i>A. japonicus</i>	2	9	12	25	19	5	2	3	4		1	82				
<i>A. heian</i> n. sp.			1		2	5	9	5	1			23				

21% HL vs. 11–15% HL), more total vertebrae (65–72 vs. 63–67) and precaudal vertebrae (40–47 vs. 39–43), fewer pored lateral line scales (121–152 vs. 142–185) and dermal plicae (143–172 vs. 156–198), and fewer pigmented pectoral fin rays (2–6 vs. 4–10). This species is distinguished from *A. personatus* and all other species of the North Pacific region by a unique COI haplotype (GenBank Accession KJ137280; Appdx. 2).

Description

Body elongate, slender, depth at dorsal-fin origin 27.5–56.9% HL (43.6% HL), depth at anal-fin origin 28.0–55.4% HL (39.3% HL), depth at caudal peduncle 9.5–15.3% HL (12.0% HL). Head long, 18.7–22.2% SL (21.7% SL). Snout long, 23.0–30.0% HL (26.9% HL). Mouth large: upper jaw 27.0–36.0% HL (30.9% HL); lower jaw 36.0–50.0% HL (43.3% HL). Orbit moderately large, 12.0–21.0% HL (18.2% HL). Gill rakers long, slender, 4–6 (5) on upper part of arch, 20–25 (23)

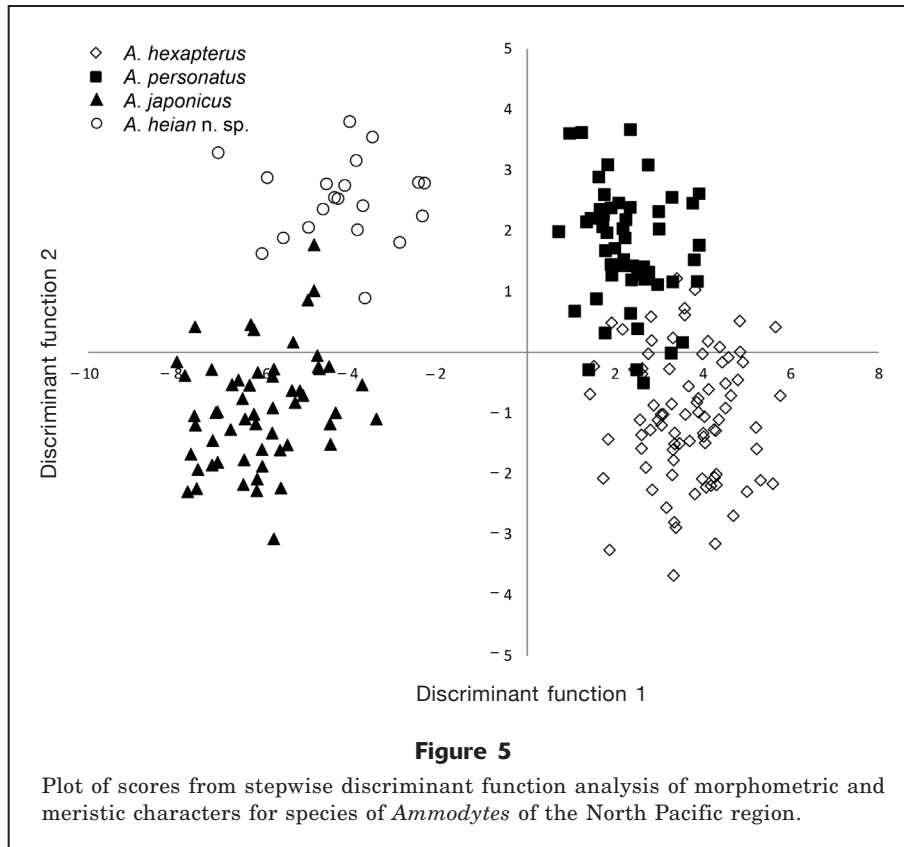
on lower part, 25–30 (28) total, longest raker length 7.4–12.7% HL (11.3% HL). Pseudobranchs 9–16 (11).

Pored lateral-line scales 121–152 (125). Scales below lateral line situated along 143–172 (149) oblique dermal plicae.

Dorsal-fin rays 56–63 (59). Anal-fin rays 27–33 (30), 7–14 (9) pterygiophores anterior to first caudal vertebra. Pectoral-fin rays 13–16 (15), rays 2–6 (4) pigmented. Total vertebrae 65–72 (68), precaudal vertebrae 40–47 (44), caudal vertebrae 21–27 (24).

Distribution

On the basis of material examined, we determined that *Ammodytes hexapterus* ranges from the Soya Strait off Wakkanai, Hokkaido, Japan, through the Sea of Okhotsk, the western and northeastern Bering Sea, and into the Chukchi Sea (Fig. 1). In the eastern Bering Sea, its range overlaps with that of *A. personatus* south to Norton Sound, the Pribilof Islands, Kuskokwim Bay,



and Unimak Pass (Fig. 1). Published sequences in GenBank indicate *A. hexapterus* is also distributed in the Beaufort Sea and Hudson Bay, Canada (Table 4).

Etymology

The specific name *hexapterus* is derived from *hex* meaning “six” and *aptera* literally meaning “without wings,” likely referring to the lack of pelvic fins in this species. We propose the common name “Arctic sand lance,” replacing the name “Pacific sand lance,” which we assign to *A. personatus*, to more properly reflect its distribution.

Remarks

No type material is extant for *Ammodytes hexapterus* (Svetovidov, 1978, 1981). Because of the close morphological similarity but distinct genetic signature of species of *Ammodytes*, we, therefore, designate UAM 2813 from the Chukchi Sea as the neotype. Among species of *Ammodytes*, only *A. hexapterus* is known from the Chukchi Sea. The species was described originally from material obtained at uncertain locations during Russian expeditions into the Bering and Chukchi seas.

Duncker and Mohr (1939) uncertainly synonymized *A. hexapterus* under *A. dubius*, despite the priority by date of *A. hexapterus*. Following Nizinski et al. (1990),

we identified *A. dubius* morphologically and found COI sequence data to support the species-level separation of *A. hexapterus* and *A. dubius*, although *A. dubius* itself was genetically indistinguishable from *A. americanus* in the COI region.

Ammodytes personatus Girard, 1856 Pacific sand lance Figures 6B and 7B; Tables 5–7

Ammodytes personatus Girard, 1856:137 (original description; no types known; possibly USNM 612, 3 specimens, the lot is missing; Cape Flattery, Washington).

Ammodytes alascanus Cope, 1873:30 (original description; syntypes ANSP 8956–57, 2 specimens; Sitka, Alaska).

Ammodytes aleutensis Duncker and Mohr, 1939:20 (in part; original description; paralectotypes ZMB 14235, 5 specimens, 87.0–114.5 mm, Unalaska, Alaska, *Albatross*, 16 June 1890).

Neotype

UW 152354, 124.0 mm, Washington, Strait of Juan de Fuca, off Miller Peninsula, 48.4°N, 122.9°W, 25 April 2013, A. Kagley (GenBank Accession KJ137281), herein designated.

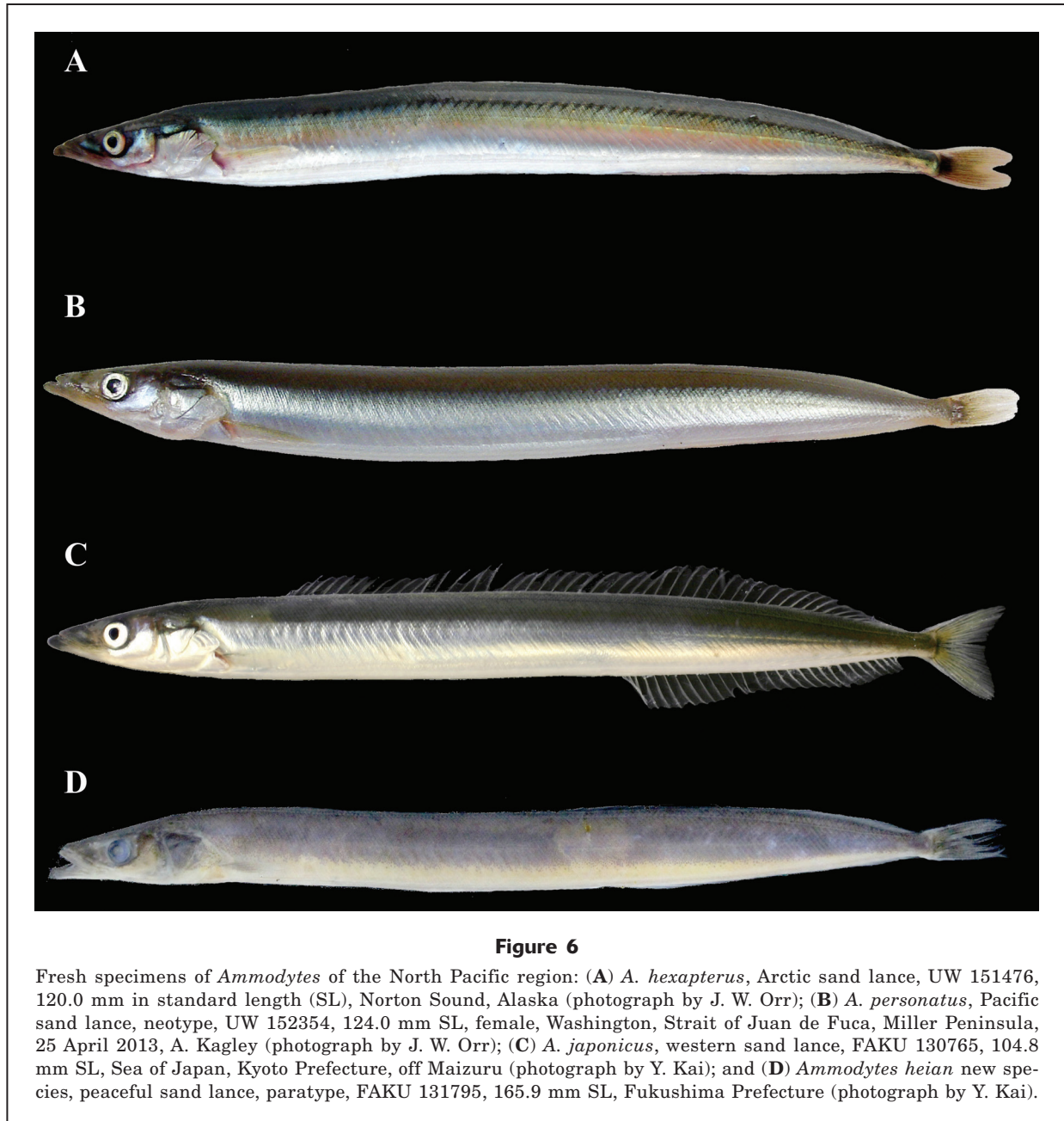


Figure 6

Fresh specimens of *Ammodytes* of the North Pacific region: (A) *A. hexapterus*, Arctic sand lance, UW 151476, 120.0 mm in standard length (SL), Norton Sound, Alaska (photograph by J. W. Orr); (B) *A. personatus*, Pacific sand lance, neotype, UW 152354, 124.0 mm SL, female, Washington, Strait of Juan de Fuca, Miller Peninsula, 25 April 2013, A. Kagley (photograph by J. W. Orr); (C) *A. japonicus*, western sand lance, FAKU 130765, 104.8 mm SL, Sea of Japan, Kyoto Prefecture, off Maizuru (photograph by Y. Kai); and (D) *Ammodytes heian* new species, peaceful sand lance, paratype, FAKU 131795, 165.9 mm SL, Fukushima Prefecture (photograph by Y. Kai).

Diagnosis

A species of *Ammodytes* distinguished from *A. japonicus* by having significantly more total vertebrae (65–73 vs. 59–66) and precaudal vertebrae (41–49 vs. 36–43), more dorsal-fin rays (56–66 vs. 50–60), and fewer pigmented pectoral-fin rays (3–7 vs. 4–11). It is further distinguished from the new species by its narrower body (depth at dorsal-fin origin 24–53% HL vs. 33–57% HL; depth at anal-fin origin 33–52% HL vs. 27–55% HL), larger orbit (12–18% HL vs. 11–15% HL), fewer pored lateral-line scales (114–170 vs. 142–185) and dermal plicae (139–193 vs. 156–198), more total vertebrae (65–73

vs. 63–67) and precaudal vertebrae (41–49 vs. 39–43), and fewer pigmented pectoral-fin rays (3–7 vs. 4–10). It is distinguished from *A. hexapterus* and all other species of the North Pacific region by a unique COI haplotype (GenBank Accession KJ137281; Appdx. 2).

Description

Body elongate, slender, depth at dorsal-fin origin 27.2–53.5% HL (45.2% HL), depth at anal-fin origin 25.8–52.2% HL (42.1% HL), depth at caudal peduncle 10.0–15.0% HL (13.9% HL). Head long, 18.8–25.4% SL (20.3% SL). Snout long, 23.1–29.9% HL (27.8% HL).

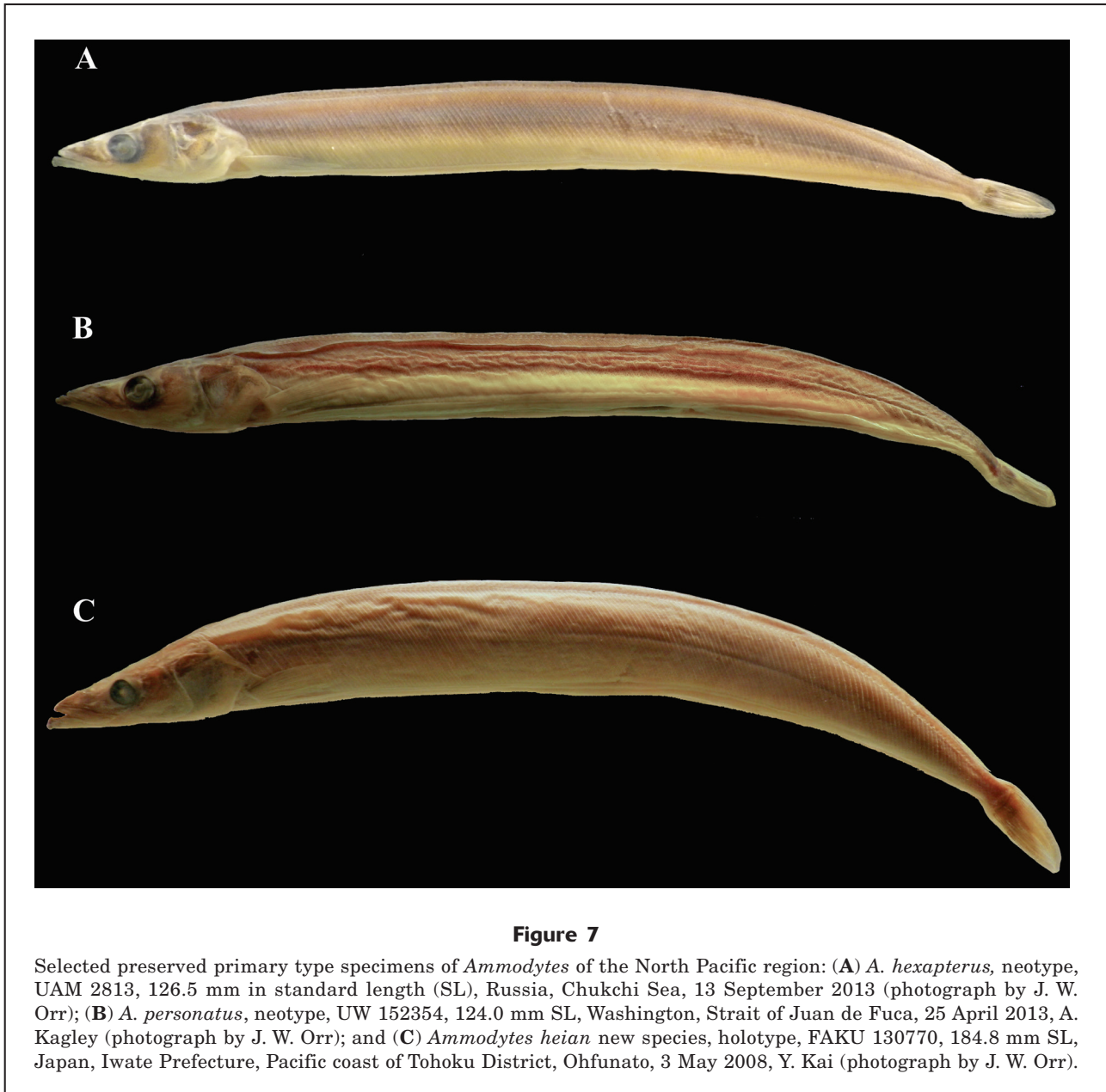


Figure 7

Selected preserved primary type specimens of *Ammodytes* of the North Pacific region: (A) *A. hexapterus*, neotype, UAM 2813, 126.5 mm in standard length (SL), Russia, Chukchi Sea, 13 September 2013 (photograph by J. W. Orr); (B) *A. personatus*, neotype, UW 152354, 124.0 mm SL, Washington, Strait of Juan de Fuca, 25 April 2013, A. Kagley (photograph by J. W. Orr); and (C) *Ammodytes heian* new species, holotype, FAKU 130770, 184.8 mm SL, Japan, Iwate Prefecture, Pacific coast of Tohoku District, Ohfunato, 3 May 2008, Y. Kai (photograph by J. W. Orr).

Mouth large: upper jaw 29.8–35.8% HL (30.2% HL); lower jaw 40.5–48.0% HL (41.7% HL). Orbit moderately large, 11.5–18.8% HL (14.7% HL). Gill rakers 22–30 (28), long, 8.2–12.4% HL (9.5% HL), slender, 4–6 (4) on upper part of arch, 18–26 (24) on lower part. Pseudo-branches 8–19 (10).

Pored lateral-line scales 114–170 (126). Scales below lateral line situated along 139–193 (150) oblique dermal plicae.

Dorsal-fin rays 56–66 (58). Anal-fin rays 25–33 (27), 7–13 (9) pterygiophores anterior to first caudal vertebrae. Pectoral-fin rays 13–16 (14), rays 3–7 (3) pigmented. Total vertebrae 65–73 (69), precaudal vertebrae 40–47 (44), caudal vertebrae 21–27 (25).

Distribution

On the basis of material examined, we determined that *Ammodytes personatus* ranges from California to the Gulf of Alaska, west to Attu Island in the Aleutian Islands, and north to Norton Sound in the northeastern Bering Sea (Fig. 1). In the eastern Bering Sea, its range overlaps with that of *A. hexapterus* in Norton Sound, the Pribilof Islands, Kuskokwim Bay, and Unimak Pass (Fig. 1). *Ammodytes personatus* (as *A. hexapterus*) has been reported also from as far south as Balboa Island in Southern California (Love et al., 2005). Unpublished sequence data of Turanov and Kartavtsev (2014) suggest that *A. personatus* may range from Bering Island

into the Sea of Okhotsk, a conclusion that will require further analysis of specimens from these areas.

Etymology

The specific name *personatus* is derived from the Latin *personata* meaning “masked,” perhaps referring to a dark area on the head found in a few specimens. The author’s intent is uncertain, as the derivation of the name was not specified in the original description and type material is missing. Because most specimens do not have a masked appearance, we chose the common name of “Pacific sand lance.” Although this common name has been assigned previously to *A. hexapterus* (Nelson et al., 2004; Page et al., 2013), and the name has been applied to all eastern populations of the North Pacific region, *A. hexapterus* as now recognized is known in the Pacific Ocean only around the Kuril Islands, unlike *A. personatus*, which is found in the Pacific Ocean from the western Aleutian Islands to California.

Remarks

No type material is extant for *Ammodytes personatus*. Girard (1856) described the species from material collected by Lieutenant Trowbridge at Cape Flattery, Washington. Listed with the same collector and locality, USNM 612 likely composed at least part of the material used for the original description but is now missing and presumed lost (Williams³). Because of the close morphological similarity but distinct genetic signature of species of *Ammodytes*, we designate UW 116044 from the Strait of Juan de Fuca in the Salish Sea as the neotype. The locality is about 130 km east of the original type locality, and no other species of *Ammodytes* is known from the eastern North Pacific Ocean or Salish Sea.

Ammodytes japonicus Duncker and Mohr, 1939 Western sand lance [Japanese name: Ikanago] Figures 6C and 7C; Tables 5–7

Ammodytes personatus: Jordan, 1906:717, fig. 2 (in part; revision, all *Ammodytes* of the North Pacific region referred to *A. personatus*); Hashimoto and Kawasaki, 1981 (in part, “type N”); Han et al., 2012 (in part, “lineage B”).

Ammodytes japonicus Duncker and Mohr, 1939:20 (in part; original description; lectotype ZMH H142, 88.5 mm, Hokkaido, Japan; paralectotypes ZMH H143, 51 specimens, 6 of 51 examined, 64.0–86.7 mm, Otaru [=“Otaka”], Hokkaido, Japan).

Ammodytes aleutensis Duncker and Mohr, 1939:20 (original description; lectotype ZMH H139, 1 specimen, 81.0 mm, Otaru, Hokkaido, Japan; paralectotypes: ZMH H140, 1 specimen, 86.3 mm, Otaru

[=“Otaka”], Hokkaido, Japan; ZMH H141, 6 specimens, 62.0–73.2 mm, Kobe fish market, Japan; ZMB 14235, 5 specimens, 87–114.5 mm, Unalaska, Alaska).

Diagnosis

A species of *Ammodytes* distinguished from *A. hexapterus* by its significantly fewer total vertebrae (59–66 vs. 65–72) and precaudal vertebrae (36–43 vs. 40–47), more pored lateral-line scales (132–166 vs. 121–152) and dermal plicae (144–182 vs. 143–172), fewer dorsal-fin rays (50–60 vs. 56–63), and more pigmented pectoral-fin rays (4–11 vs. 2–6); from *A. personatus* by significantly fewer total vertebrae (59–66 vs. 65–73) and precaudal vertebrae (36–43 vs. 41–49), fewer dorsal-fin rays (50–60 vs. 56–66), and more pigmented pectoral-fin rays (4–11 vs. 3–7); and from the new species by its narrower body anteriorly (depth at dorsal-fin origin 32–53% HL vs. 33–57% HL), longer upper jaw (30–39% HL vs. 29–34% HL), larger orbit (12–20% HL vs. 11–15% HL), fewer pored lateral-line scales (132–163 vs. 142–185), and fewer dermal plicae (144–182 vs. 156–198). It is further distinguished from all other species of the North Pacific region by a unique COI haplotype (GenBank Accession KJ137283; Appdx 2).

Description

Body elongate, slender, depth at dorsal-fin origin 32.0–53.0% HL (38.4% HL), depth at anal-fin origin 33.0–57.0% HL (42.4% HL), depth at caudal peduncle 10.0–16.0% HL (11.3% HL). Head long, 17.6–24.5% SL. Snout long, 25.0–30.0% HL (28.8% HL). Mouth large; upper jaw 30.0–39.0% HL (32.8% HL); lower jaw 35.0–50.0% HL (43.5% HL). Orbit moderately large, 12.0–20.0% HL (15.8% HL). Gill rakers long, 7.5–13.4% HL, slender, 20–29 (31), 3–6 on upper part of arch, 16–26 on lower part. Pseudobranchs 7–14.

Pored lateral-line scales 132–163 (132). Scales below lateral-line situated along 144–182 (144) oblique dermal plicae.

Dorsal-fin rays 50–60 (51). Anal-fin rays 26–33 (30), 7–12 (9) pterygiophores anterior to first caudal vertebra. Pectoral-fin rays 13–17 (15), rays 4–11 pigmented. Total vertebrae 59–66 (63), precaudal vertebrae 36–43 (39), caudal vertebrae 21–28 (24).

Distribution

On the basis of material examined, we determined that *Ammodytes japonicus* ranges from the southern Sea of Okhotsk through the Sea of Japan into the Seto Inland Sea and the Pacific Ocean off the southern part of Japan (Fig. 1). In the southern Sea of Okhotsk, its range overlaps with that of *A. hexapterus* and the new species in the Soya Strait off Wakkanai, Hokkaido (Fig. 1). Data of Okamoto (1989), Kim et al. (2006, 2008, 2010), Han et al. (2012), and published sequences in GenBank indicate that *A. japonicus* also ranges to Kyushu, the

³ Williams, J. 2013. Personal commun. Department of Vertebrate Biology, National Museum of Natural History, Smithsonian Institution, Suitland, MD 20746.

East China Sea, the Yellow Sea, and the Pacific Ocean side of northern Japan, where its range overlaps with that of the new species (Table 4).

Etymology

The specific name *japonicus* is the Latinized adjectival form of *Japan*, meaning “of Japan.”

Remarks

We consider *Ammodytes aleutensis* to be a junior synonym of *A. japonicus*. In their original description, Duncker and Mohr (1939) included material from Unalaska Island, concluding erroneously that the species ranged throughout the Aleutian Islands. Meristic characters serve to identify those specimens as either *A. personatus* or *A. hexapterus*, and only *A. personatus* is recorded from the Aleutian Islands. Otherwise, all characters of the lectotype and other paralectotypes were well within the range of our genetically identified material for *A. japonicus*. Duncker and Mohr (1939) distinguished *A. japonicus* from *A. aleutensis* on the basis of meristic characters, as well as the position of the dorsal-fin origin (posterior to the center of the pectoral fin in *A. aleutensis* versus at the posterior end of the pectoral fin in *A. japonicus*), the posterior extension of the ventrolateral ridge (posterior to the second third of the anal fin and becoming reduced farther posterior versus extending posterior to the center of the anal fin). We find no differences among these morphometric characters in our material or in the pertinent type material examined.

The lectotype and 1 paralectotype of *A. aleutensis* and 1 lot of paralectotypes of *A. japonicus* (designated by Ladiges et al., 1958) were collected from “Otaka,” according to Duncker and Mohr (1939). We were unable to find a place with that name in Japan. However, in examining material at ZMH, we found that the original label for ZMH 143 (originally 13708) had been misinterpreted and should have been recorded as “Otaru,” a town on the western coast of Hokkaido.

***Ammodytes heian* Orr, Wildes, and Kai, new species**
Peaceful sand lance [New Japanese name: Oh-ikanago]
Figures 6D and 7D; Tables 5–7

Ammodytes personatus: Kawamura, 1940 (in part; cited in Ohshima, 1950; Onagawa and Moura bays); Hashimoto and Kawasaki, 1981 (in part, “type A”); Hashimoto, 1984 (in part, “group II”); Okamoto, 1989 (in part; off Rishiri Island, Wakkanai, Ryogoku Bay); Kim et al., 2010 (in part; specimens E11 and E30, table 1 and fig. 2); Han et al., 2012 (in part, “lineage A”).

Holotype

FAKU 130770, 184.8 mm, Japan, Iwate Prefecture, Pacific coast of Tohoku District, Ohfunato, 3 May 2008, Y. Kai.

Paratypes

FAKU 131506, 131507, 131795, 3 specimens, 148–165.9 mm, Japan, Fukushima Prefecture, Pacific coast of Tohoku District, Soma, 3 May 2008, Y. Kai; FAKU 130767–130769, 130771–131774, 7 specimens, 184.8–218.6 mm, Japan, Iwate Prefecture, Pacific coast of Tohoku District, Ohfunato, 3 May 2008, Y. Kai; UW 152685, 9 specimens, 202.9–225.9 mm, Japan, Hokkaido, off Wakkanai, 45.4492°N, 141.6446°E, Y. Kai.

Diagnosis

A species of *Ammodytes* distinguished from *A. hexapterus* by its significantly smaller orbit (11–15% HL vs. 12–21% HL), fewer total vertebrae (63–67 vs. 65–72), fewer precaudal vertebrae (39–43 vs. 40–47), more pored lateral-line scales (142–185 vs. 121–152), more dermal plicae (156–198 vs. 143–172), and more pigmented pectoral-fin rays (4–10 vs. 2–6). It is further distinguished from *A. personatus* by its deeper body (depth at dorsal-fin origin 40–57% HL vs. 24–53% HL; greater depth at anal-fin origin 39–55% HL vs. 33–52% HL), smaller orbit (11–15% HL vs. 12–18% HL), more pored lateral-line scales (142–185 vs. 114–170) and dermal plicae (156–198 vs. 139–193), fewer total vertebrae (63–67 vs. 65–73) and fewer precaudal vertebrae (39–43 vs. 41–49), and more pigmented pectoral-fin rays (4–10 vs. 3–7). It is further distinguished from *A. japonicus* by its deeper body anteriorly (depth at dorsal-fin origin 40–57% HL vs. 32–53% HL), shorter upper jaw (29–32% HL vs. 30–39% HL), smaller orbit (11–15% HL vs. 12–20% HL), more pored lateral-line scales (142–185 vs. 132–166) and more dermal plicae (156–198 vs. 144–182). It is further distinguished from all species of the North Pacific region by a unique COI haplotype (GenBank Accession KJ137282; Appdx. 2).

Description

Body elongate, slender, depth at dorsal-fin origin 40.1–57.6% HL (48.1% HL), depth at anal-fin origin 39.3–55.4% HL (48.1% HL), depth at caudal peduncle 11.2–14.0% HL (12.0% HL). Head long, 18.8–22.1% SL (20.1% SL). Snout long, 27.1–29.2% HL (28.5% HL). Mouth large: upper jaw 29.0–32.6% HL (32.2% HL); lower jaw 40.9–45.9% HL (43.7% HL). Orbit moderately sized, 11.1–15.2% HL (12.9% HL). Gill rakers 23–30 (27), long, 8.5–12.8% HL (11.0% HL), slender, 4–5 (4) on upper part of arch, 19–25 (23) on lower part. Pseudobranchs 10–17 (12).

Pored lateral-line scales 142–185 (158). Scales below lateral line situated along 156–198 (172) oblique dermal plicae.

Dorsal-fin rays 55–60 (56). Anal-fin rays 30–33 (31), 10–13 (12) pterygiophores anterior to first caudal vertebra. Pectoral-fin rays 14–17 (15), rays 4–10 (7) pigmented. Total vertebrae 63–67 (64), precaudal vertebrae 39–43 (42), caudal vertebrae 22–25 (22).

Distribution

On the basis of material examined, we determined that *Ammodytes heian* n. sp. ranges from the southern Sea of Okhotsk to the Pacific Ocean off the northern part of Japan (Fig. 1). In the southern Sea of Okhotsk, its range overlaps with that of *A. hexapterus* and *A. japonicus* in the Soya Strait off Wakkanai, Hokkaido (Fig. 1). Published sequences in GenBank (FJ666915, FJ666916) indicate that *A. heian* n. sp. also is found in the Sea of Japan (Table 4).

Etymology

The specific name *heian* is a transliteration of the Japanese word for “peace.” The holotype and paratypes were collected from waters off Fukushima and Iwate prefectures, before the earthquake and tsunami of March 2011.

Remarks

Early surveys of vertebral counts in *Ammodytes* by Kawamura (1940), Ohshima (1950), and Hashimoto and Kawasaki (1981) around Japan revealed significant variation in different regions. Populations from off Onagawa on the northeastern Pacific coast and in Moura Bay at the northern tip of Honshu (Ohshima, 1950, table 6, 61–66) are clearly different from populations in the Sea of Japan and farther south along the Pacific coast and match our data for *A. heian* n. sp. (Tables 5 and 7). Two populations examined by Hashimoto and Kawasaki (1981) had significantly different vertebral counts, as well as differences in life history characteristics. In a more comprehensive work, Hashimoto (1984) surveyed additional meristic characters, classifying populations around Japan into 3 groups: a northern group (“I”;=*A. hexapterus*) found in Japan only in Soya Strait; a northcentral group (“II”;=*A. heian* n. sp.) found on the northeastern Pacific Ocean side of Honshu and in the Sea of Japan from Tottori to the Soya Strait; and a southcentral group (“III”;=*A. japonicus*) found in the southern Sea of Japan, on the southcentral side of Honshu in the Pacific Ocean, and in the Seto Inland Sea.

Genetic research has consistently shown strong heterogeneity among populations around Japan (all originally identified as *A. personatus*), whether they are strictly considered as one species or potentially as more than one. Distributions of allozyme genotypes presented by Okamoto (1989) revealed 3 genetically isolated groups in Japan concordant with our results: a northern Japan group (likely representing *A. heian* n. sp., on the basis of the distribution of our material), a southern Japan group (= *A. japonicus*), a Kushiro and Wakkanai group (= *A. hexapterus*); also shown was a fourth group from Kodiak, Alaska (= *A. personatus*). Later work by Kim et al. (2006, 2008, 2010) with mtDNA also revealed genetic differences among populations around Korea. Through comparisons between our sequence

data and data in GenBank and BOLD, we identified 2 individuals of *A. heian* n. sp. from the Sea of Japan in the material of Kim et al. (2006, 2008, 2010; Table 4); all other individuals were identified by us as *A. japonicus*. Most recently, Han et al. (2012) found 2 lineages around Japan and in the Yellow Sea on the basis of analysis of the mitochondrial control region, concluding that further study with nuclear DNA markers is needed to clarify their taxonomic status. However, the morphological and COI sequence differences disclosed here as well as the isozyme analysis of Hashimoto and Kawasaki (1981) strongly support the conclusion that the lineages represent 2 species. Lineage A appears to represent *A. heian* n. sp., and Lineage B, *A. japonicus*.

Discussion

Our primary objective was to taxonomically revise the genus *Ammodytes* in the North Pacific Ocean and its fringing seas by examining morphological and mtDNA variation. Morphological and genetic analyses show that the genus *Ammodytes* comprises 4 species in the North Pacific region: *Ammodytes personatus*, ranging from California to the Aleutian Islands and eastern Bering Sea; *A. hexapterus*, ranging from the Hudson Bay in the east, through the Chukchi and Bering seas, to the western Pacific region in the Sea of Okhotsk and to Soya Strait between Hokkaido and Sakhalin islands; *A. japonicus*, found in the Sea of Japan, the Seto Inland Sea, the Pacific Ocean side of southern Honshu, and the Yellow Sea; and a new species, *A. heian*, herein described and found on the Pacific Ocean side of northern Honshu, in the Soya Strait, and in the Sea of Japan.

Although clearly distinct genetically, some species are morphologically similar to one another and, despite significant differences found among several characters, only combinations of morphometric and meristic characters serve to distinguish the species from one another. The species of the eastern or northern areas of the North Pacific region (*A. personatus* and *A. hexapterus*), together, can readily be distinguished from the species of the western North Pacific region (*A. japonicus* and *A. heian* n. sp.) on the basis of vertebral counts, but species within these pairs are nearly indistinguishable morphologically. To add to the challenge of species identification, ranges of *A. personatus* and *A. hexapterus* overlap in the northern Bering Sea, and *A. japonicus* and *A. heian* n. sp. were found together in our Soya Strait material; data from other authors strongly indicate that the latter 2 species are also found together in the Sea of Japan (Hashimoto, 1984; Kim et al., 2006, 2008, 2010; Han et al., 2012).

The distribution of each species generally corresponds well with general zoogeographic regions (Fig. 1). *Ammodytes personatus* exhibits an Aleutian–Oregonian distribution (Allen and Smith, 1988; Briggs, 1995; Logerwell et al., 2005) and is found in the eastern North Pacific Ocean from California to the Gulf of Alaska, the Aleutian Islands, and into the eastern Bering Sea, where to the north it is found sympatri-

cally with *A. hexapterus*. *Ammodytes hexapterus* exhibits an Arctic-Kuril distribution (Allen and Smith, 1988; Briggs, 1995; Logerwell et al., 2005), extending from the southern Sea of Okhotsk in the Soya Strait to the western Bering Sea, the northeastern Bering Sea, and into the Chukchi Sea. It may be a circum-Arctic species; sequence data in GenBank indicates that its range extends at least to the Beaufort Sea and Hudson Bay (Table 4). *Ammodytes japonicus* exhibits a distribution that encompasses the Sea of Japan and the Central Kuroshio Current area (Spalding et al., 2007), and this species is found on both coasts of Japan, in the Soya Strait, in the Sea of Japan, in the Seto Inland Sea, in the Yellow and East China seas (Kim et al., 2006, 2008, 2010), and on the southern Pacific coast of Japan. *Ammodytes heian* exhibits a distribution that consists of the northern Sea of Japan and northeastern Honshu (Spalding et al., 2007), having been found in the Soya Strait and on the northeastern Pacific coast of Japan.

A collection in the Soya Strait at Wakkanai, Japan, contained 3 species: *A. hexapterus*, *A. japonicus*, and *A. heian* n. sp. This distributional pattern is similar to the one based on allozyme data of Okamoto (1989), who found 3 “genetically distinct” groups around Japan, including 2 in the Soya Strait: a southern species ranging from Kyushu and the Seto Inland Sea to Sendai Bay (= *A. japonicus*), a more northern species from Iwate Prefecture to the northern Sea of Japan and Soya Strait (= *A. heian* n. sp.), and a third species on the Pacific Ocean side of Hokkaido off Kushiro and Soya Strait (= *A. hexapterus*). This strong geographic pattern may indicate that present-day, large-scale movement of sand lances is limited.

The genetic information presented in this article is meant to support the morphological data and describe the species of *Ammodytes* in the North Pacific region. It is not meant to provide a complete phylogenetic reconstruction of the genus *Ammodytes*. A productive look at phylogeny will require a more detailed study of *Ammodytes* of the Atlantic Ocean, as well as other members of the group. Although each clade of species is robust, the relationships among the Atlantic species are weak, as indicated by the low bootstrap branch support and alternative positions of *A. personatus* among Atlantic species in phylogenetic trees (Figs. 3 and 4). Additionally, Tajima D values (Tajima, 1989) indicate that the COI gene is likely under selection in *Ammodytes*.

Because selection can obscure phylogenetic patterns and because no literature is available to suggest a mutation rate in species of *Ammodytes*, we are reluctant to provide estimates of times of divergence between these species. *Ammodytes hexapterus* is nearly homogenous at COI and, because bottlenecks decrease molecular diversity, was likely derived from a founder population followed by rapid expansion, as indicated by the broad range over which it is homogenous. The lack of genetic divergence across haplotypes is typical for marine fishes that have experienced fluctuations in population size (Grant and Bowen, 1998). More information about the Atlantic species, and members of

other genera, may allow for a more robust examination of phylogeny in *Ammodytes*.

Our taxonomic revision of the sand lances of the genus *Ammodytes* in the North Pacific region resulted in the recognition of 4 species: *A. hexapterus*, *A. personatus*, *A. japonicus*, and the new species *A. heian*. Only 2 species, with a confused nomenclature, have been recognized as valid for the past several decades. Without a clear knowledge of the number of species present in the area, each with its unique life history and biology, the contributions of this genus to the ecosystem will be inadequately understood and successful management of these species will be impossible.

This study underscores the importance of increasing our knowledge of forage species. As scientists move to manage marine resources with an ecosystem-based approach, species at the base of the food web should be examined at least as rigorously as species of commercial interest. In this study, we uncovered aspects of the evolutionary history of the genus *Ammodytes* and its current-day isolation into 4 species in the ecosystem of the North Pacific Ocean and surrounding seas. Ecosystem models would benefit from further studies of the population structure within each species, as well as studies of the unusual life history of these sand- and water-dwelling species.

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Appendix 1

This appendix provides number and length of specimens, location, depth, and other details on the materials examined for this taxonomic revision of North Pacific sand lances of the genus *Ammodytes*: *A. hexapterus*, *A. personatus*, *A. japonicus*, and *A. heian* new species. Lengths are given in standard length.

Material examined

Ammodytes hexapterus 165 specimens (53.0–160.3 mm) examined, including the neotype listed in the species description in the main text. **Bering Sea:** UW 152677, 4 (70–75 mm), 72.0257°N, 162.2469°W, 28 m depth, FV *Alaska Knight*, cruise 201202, haul 98, 11 September 2012; UW 12728, 2 (142.0–170.7 mm), St. Lawrence Island, 63.6667°N, 167.4667°W, 22–40 m depth, RV *Deep Sea*, field numbers 49-10 to 49-14, 27 June 1949, H. Hildebrand; UW 150610, 150733, 151476, 16 (97.6–120.0 mm), 64.316°N, 163.0007°W, 12 m depth, FV *Vesteraalen*, cruise 201002, haul 74, 8 August 2010; UW 26820, 1 (93 mm), 63.5°N, 166.333°W, 27 m depth, RV *Deep Sea*, Area III. **Sea of Okhotsk:** ABL 11-0006, 50 (53–61 mm), 51.57°N, 144.24° E, 14 September 2009, O. Katugin; ABL 11-0007, 46 (117.0–160.3 mm), 52.54°N, 144.12°E, field number AhOS30, O. Katugin. **Chukchi Sea:** UAM 1255, 19 (83.0–159.0 mm), Alaska, 67.4093°N, 173.5757°W, RUSALCA 2012,

station CL10, PSBT, haul 16, 13 September 2012; UW 150611, 8 (113.0–129.5 mm), Alaska, 69.6674°N, 164.2905°W, surface, field number AkCh 011 OT5; UW 16914, 5 (82–87 mm), Alaska, Cape Thompson area, Chariot site, 68.1°N, 166°W. **Japan:** UW 116840, 13 (217.4–257.3 mm), off Wakkanai, Hokkaido, 45.4492°N, 141.6446°E, Y. Kai.

Ammodytes personatus 451 specimens (40.0–273.6 mm) examined, including the types listed in the species description in the main text. **Bering Sea:** UW 152678, 1 (75.0 mm), 58.01135°N, 160.2173°W, 49 m depth, FV *Aldebaran*, cruise 201101, haul 7, 6 June 2011; UW 110990, 2 (77–78 mm), 56.5667°N, 163.3833°W, 27 m depth, RV *Discoverer*, cruise 197701, station 89, haul 48, 27 August 1977; UW 110994, 2 (61–80 mm), 56.9167°N, 162.6°W, 27 m depth, RV *Discoverer*, cruise 197701, station 72, haul 31, 22 August 1977; UW 110997, 1 (72 mm), southern Bering Sea, 55.1022°N, 166.1181°W, 18 August 1977; UW 111017, 3 (55–68 mm), 56.23333°N, 163.3667°W, 27 m depth, RV *Discoverer*, cruise 197701, haul 30, 29 August 1977; UW 111027, 1 (74 mm), 55.4333°N, 164.9833°W, 27 m depth, RV *Discoverer*, cruise 197701, station 93, haul 52, 28 August 1977; UW 111043, 1 (83 mm), 56.3167°N, 162.85°W, 27 m depth, RV *Discoverer*, cruise 197701, haul 47, 27 August 1977; UW 111211, 1 (91 mm), 58.6667°N, 162.7167°W, 24 m depth, RV *Miller Freeman*, cruise 197501, haul 181, 8 October 1975; UW

112579, 1 (115 mm), 58.5134°N, 159.5233°W, 20 m depth, FV *Arcturus*, cruise 200001, haul 15, 26 May 2000, G. R. Hoff; UW 116094, 1 (242.0 mm), southeastern Bering Sea; UW 116096, 1 (94.6 mm), southeastern Bering Sea; UW 1361, 8 (82.7–106.9 mm) of 12, Alaska Peninsula, Big Lake near Kvichak River weir, 58.6667°N, 157.5667°W, 22 May 1929, C. Flock; UW 151465–151469, 5 (108.1–120.3 mm), 58.6538°N, 163.3465°W, 29 m depth, FV *Arcturus*, cruise 200901, haul 43, 10 June 2009; UW 151470–151472, 151490, 4 (140.0–174.5 mm), 57.0137°N, 159.1401°W, 32 m depth, FV *Alaska Knight*, cruise 201001, haul 5, 7 June 2010; UW 151473, 2 (80.0–169.8 mm), 57.9840°N, 158.3283°W, 33 m depth, FV *Aldebaran*, cruise 201001, haul 4, 7 June 2010; UW 151474, 3 (70.0–121.7 mm), 57.5001°N, 169.3437°W, 68 m depth, FV *Aldebaran*, cruise 201001, haul 104, 2 July 2010; UW 151475, 1 (102 mm), 58.3275°N, 162.0278°W, 45 m depth, FV *Aldebaran*, cruise 201001, haul 20, 10 June 2010; UW 151477, 1 (105.4 mm), 59.3179°N, 165.9568°W, 23 m depth, FV *Aldebaran*, cruise 201001, haul 72, 22 June 2010; UW 151478, 1 (105.6 mm), 57.9741°N, 162.1324°W, 34 m depth, FV *Alaska Knight*, cruise 201001, haul 20, 10 June 2010; UW 151479, 1 (79.4 mm), 57.6559°N, 160.8843°W, 56 m depth, FV *Aldebaran*, cruise 201001, haul 16, 10 June 2010; UW 151480, 1 (140.1 mm), Bering Sea, 57.9882°N, 158.9351°W, 38 m depth, FV *Aldebaran*, cruise 201001, haul 5, 7 June 2010; UW 151481, 1 (142.6 mm), 57.3101°N, 159.0668°W, 46 m depth, FV *Alaska Knight*, cruise 201001, haul 6, 7 June 2010; UW 151482, 1 (150.0 mm), 57.6559°N, 158.3651°W, 35 m depth, FV *Aldebaran*, cruise 201001, haul 3, 7 June 2010; UW 151483, 1 (78.0 mm), Bering Sea, 58.0087°N, 160.1893°W, 49 m depth, FV *Alaska Knight*, cruise 201001, haul 9, 8 June 2010; UW 151484, 1 (120.0 mm), 58.3435°N, 159.5522°W, 23 m depth, FV *Aldebaran*, cruise 201001, haul 6, 8 June 2010; UW 151485, 1 (120.0 mm), 57.67421°N, 159.6345°W, 48 m depth, FV *Arcturus*, cruise 200901, haul 7, 3 June 2009; UW 151486, 1 (112 mm), 59.6669°N, 166.609°W, 26 m depth, FV *Aldebaran*, cruise 201001, haul 75, 22 June 2010; UW 151488, 1 (73 mm), 59.3175°N, 164.0119°W, 21 m depth, FV *Arcturus*, cruise 200901, haul 46, 10 June 2009; UW 151489, 1 (147 mm), 58.3534°N, 162.7112°W, 30 m depth, FV *Alaska Knight*, cruise 201001, haul 24, 11 June 2010; UW 151492, 3 (65–120 mm), 58.2819°N, 159.9693°W, 39 m depth, FV *Alaska Knight*, cruise 201001, haul 8, 8 June 2010; UW 151493, 2 (70–110 mm), 58.6372°N, 162.707°W, 23 m depth, FV *Arcturus*, cruise 200901, haul 42, 9 June 2009; UW 17273, 1 (70.1 mm), 55.25°N, 166.1167°W, 29 August 1957, McCrery et al.; UW 22201, 1 (114 mm), Bering Sea, Bristol Bay, 58.4833°N, 159.3667°W, 14 m depth, FV *Mineshima Maru*, cruise 347, haul 629, 27 May 1988, Renko and Moore; UW 26830, 1 (131.6 mm), 57.75°N, 159.5333°W, FV *Silver Charlie*, 1 May 1981; UW 26836, 1 (198.3 mm), Bristol Bay, 57°N, 164°W, 1 October 1975; UW 29512, 4 (25–62 mm) of 7, 56.0028°N, 163.847°W, 91 m depth, cruise 77-1, tow 16/58, M. W. Brown; UW 45766, 1 (140.7 mm), 58.002°N, 159.6508°W, 39 m depth, FV *Arcturus*, cruise 199801, haul 7, 10 June 1998; UW 45884, 2 (209.3–212.0 mm), 54.7°N, 165.35°W, 150 m depth, FV *Arcturus*, cruise 199702, haul 310, G. R. Hoff; UW 46838, 1 (115 mm), 58.0109°N, 159.603°W, 38 m depth, FV *Aldebaran*, cruise 199901, haul 9, 24 May 1999, D. Nichol; UW 46853, 1 (105 mm), Kuskokwim Bay, 58.9790°N, 163.3502°W, 20 m depth, FV *Aldebaran*, cruise 199901, haul 25, 28 May 1999, D. Nichol. **Aleutian Islands:** UW 26835, 1 (129.5 mm), Amchitka Island, St. Makarins Bay, 51.37°N, 179.245°E, 25 June 1971, Palmisano; UW 154476, 2 (210 mm), off Amchitka Island, 51.9573°N, 178.2761°E, 74 m depth, FV *Ocean Explorer*, cruise 201201, haul 150, 14 July 2012, J. W. Orr; UW 152109, 2 (195–280 mm), off Tanaga Island, 51.6337°N, 178.0881°W, 62 m depth, FV *Ocean Explorer*, cruise 201201, haul 118, 6 July 2012, J. W. Orr; UW 112021, 1 (259 mm), off Yunaska Island, 53.1164°N, 170.92°E, 100 m depth, FV *Vesteraalen*, cruise 200001, haul 221, 16 July 2000, E. S. Brown; UW 116092, 1 (218.1 mm), 52.96829°N, 173.2401°E, 81 m depth, FV *Sea Storm*, cruise 200601, haul 136, 9 July 2006; UW 116093, 1 (225.2 mm), 52.96829°N, 173.2401°E, 81 m depth, FV *Sea Storm*, cruise 200601, haul 136, 9 July 2006; UW 116097–116207, 11 (223.4–273.6 mm), 52.5781°N, 174.3485°E, 89 m depth, FV *Sea Storm*, cruise 200601, haul 153, 14 July 2006, K. Dodd; UW 150280, 19 (226.6–259.5 mm), 52.6011°N, 174.2742°E, 86 m depth, FV *Sea Storm*, cruise 201001, haul 192, 1 August 2010, K. Maslenikov; UW 17252, 1 (65.0 mm), 52.65°N, 176.43°E, Allen and McCrery; UW 1728, 1 (87.0 mm), English Bay, Unalaska Island, 53.934°N, 166.25°W, MS *Dorothy*, 3 June 1930; UW 26846, 1 (148.0 mm), Amchitka Island, 51.5°N, 179°E, 4 October 1971; UW 48923, 6 (105–117 mm), Unalaska Island, 53.6733°N, 166.6483°W, 5 August 1962, Burdick and MacAllister; UW 48929, 16 (40–60 mm), Sedanka Island, Udamat Bay, 53.8036°N, 166.226°W, 15 August 1962; UW 48939, 4 (95–133 mm), Unalaska Island, Unalaska Bay, 53.9333°N, 166.517°W, station 3, 29 May 1962; UW 48950, 7 (103.0–124.1 mm), Unalaska Island, 53.6733°N, 166.6483°W, 5 August 1962, Burdick; UW 49045, 5 (50–72 mm), Alaska, Akun Island, Akun Bay, 55.25°N, 165.5°W, FV *Harmony* #7, 3 October 1962; UW 116091, 1 (233.1 mm), western Aleutian Islands. **Gulf of Alaska:** UW 152353, 2 (105–110 mm), 58.2917°N, 153.1155°W, 65 m depth, FV *Sea Storm*, cruise 200701, haul 159, 4 July 2007; UW 152352, 1 (128 mm), 59.4256°N, 152.4063°W, 67 m depth, FV *Sea Storm*, cruise 200701, haul 185, 7 July 2007; UW 152349, 9 (139.3–183.6 mm), Kodiak Island, Deadman Bay, 57.0667°N, 153.9378°W; UW 118906, 1 (155.0 mm), 57.0662°N, 153.6049°W, 79 m depth, FV *Pacific Explorer*, cruise 200901, haul 148, 26 June 2009, J. W. Orr; UW 119211, 1 (120 mm), 57.2218°N, 151.9528°W, 64 m depth, FV *Pacific Explorer*, cruise 200901, haul 156, 27 June 2009, J. W. Orr; UW 151487, 1 (148 mm), 54.8279°N, 159.8582°W, 49 m depth, FV *Sea Storm*, cruise 200901, haul 51, 5 June 2009; UW 14422, n=5, Squaw Harbor, Unga Island, Shumagin Islands, 55.3°N, 160.5°W, 30 August 1956, R. J. Mynre; UW 15497, 4

(70–105 mm), Gulf of Alaska, Uyak Bay, Kodiak Island, 57.6°N, 154°W, 10 July 1941, A. C. DeLacy et al.; UW 15610, 3 (90–123 mm), Alexander Archipelago, Shelikof Bay, Kruzof Island, 57.15°N, 135.8°W, 1 July 1960, Dryfoos; UW 16464, 4 (145–152 mm), 57.4167°N, 150.75°W, 4 June 1958; UW 20642, 8 (72–85 mm), Kodiak Island, Ugak Bay, 57.4517°N, 152.7019°W, U2-301-117, 20 June 1976, C. Harris and M. Hunter; UW 243, 1 (75 mm), Kodiak Island, Alitak, 56.9°N, 154.16°W, Crawford; UW 26825, 1 (95 mm), Kodiak Island, Ugak Bay, 57.4517°N, 152.701°W, 4 August 1923; UW 4002, 3 (70–90 mm), Kodiak Island, Lazy Bay, 56.9°N, 154.26°W, 8 May 1932; UW 4202, 4 (85–90 mm), Wide Bay, 57.4°N, 156.46°W, 31 May 1932; UW 45961, 1 (91 mm), 57.515°N, 151.5496°W, 147 m depth, FV *Vesteraalen*, cruise 200101, haul 177, 28 June 2001, J. W. Orr; UW 5301, 8 (112.0–120.2 mm), Prince of Wales Island, Tranquil Point in the Alexander Archipelago, 55°N, 133°W, 22 July 1939, Franett. **British Columbia:** UW 1734, 1 (83 mm), Hecate Strait, middle of Hecate Strait between Gander Island and Danger Rocks, 52.5°N, 129.5°W, 1 September 1931. **Washington:** UW 11329, 8 (66.1–107.1 mm), Puget Sound, Meadow Point, Seattle, 47.6°N, 122.3°W, 29 April 1955, A. DeLacy and class; UW 116044–116054, 11 (61.2–87.1 mm), Puget Sound, 48.7042°N, 123.014°W, 60–80 m depth, RV *Centennial*, site 10, sample V5, 6 November 2006, D. Gunderson and J. Blaine; UW 116055–116064, 10 (65.6–75.2 mm), Puget Sound, 48.69°N, 123.0161°W, 60–80 m depth, RV *Centennial*, site 28, sample V18, 6 November 2006, D. Gunderson and J. Blaine; UW 116065–116075, 11 (65.0–75.2 mm), Puget Sound, 48.5325°N, 123.0214°W, 60–80 m depth, RV *Centennial*, site 26, sample V16, 6 November 2006, D. Gunderson and J. Blaine; UW 116076–116090, 14 (63.6–79.8 mm), Puget Sound, 48.7136°N, 123.0161°W, 60–80 m depth, RV *Centennial*, site 31, sample V21, 6 November 2006, D. Gunderson and J. Blaine; UW 118502, 23 (68–83 mm), Salish Sea, San Juan Channel, south of Turn Island, 48.52°N, 122.95°W, 73–77 m depth, 24 April 2007, L. L. Britt; UW 118503, 8 (68.0–85.0 mm), Salish Sea, San Juan Channel, Jackson Beach, 48.52°N, 123°W, beach seine, 24 April 2007, L. L. Britt; UW 16754, 1 (125 mm), Puget Sound, Golden Gardens, 47.7°N, 122.4°W, 1 January 1963, R. B. Grinols; UW 26833, 11 (102.6–121.6 mm), Salish Sea, San Juan Island, Eagle Cove, 48.5°N, 123°W, Friday Harbor Lab 75-03-02, 20 June 1975, Fish 454a class. **California:** HSU 4802, 34 (77–108 mm), Humboldt Bay, 40.7621°N, 124.2152°W, 1 October 2009, A. Kinziger; UW 152676, 104 (60–77 mm), Hum-

boldt Bay, north jetty, 40.7621°N, 124.2152°W, 1 October 2009, A. Kinziger.

Ammodytes japonicus 138 specimens (30.0–160.9 mm) examined, including the types listed in the species description in the main text. FAKU 130765, 1 (104.8 mm), Japan, Nohara, Maizuru, Kyoto, 35.5°N, 135.4°E; FAKU 130979–131008, 30 (131.2–160.9 mm), Japan, Inland Sea, off Akashi, Hyogo, 34.5°N, 135°E, Y. Kai; FAKU 131055–131091, 28 (86.0–108.8 mm), Japan, off Shiroko, Aichi, Ise Bay, 34.734°N, 136.68°E, Y. Kai; FAKU W856, W914, W915, 125465, 130765, 5 (103.7–167.0 mm), Japan, Sea of Japan, Kyoto, Wakasa Bay, 35.8°N, 135.5°E, 1977; UW 153060, 17 (30.0–45.0 mm), Japan, Maizuru, 35.5°N, 135.4°E; UW 153061, 31 (30–32 mm), Japan, Ise Bay, 34.7°N, 136.8°E, 2006; UW 152684, 3 (208.0–218.9 mm), Japan, off Wakkanai, Hokkaido, 45.4492°N, 141.6446°E, 2007, Y. Kai; UW 16457, 5 (118.5–146.8 mm), Japan, Shizuoka Province, Suruga Bay, 35°N, 138.75°E, 15 May 1950, F. Wilke.

Ammodytes dubius 11 specimens (87.0–125.0 mm) examined. UW 152011, 10 (87–125 mm), western North Atlantic Ocean, Massachusetts, 41.7637°N, 69.8956°W; UW 4799, 1 (115 mm), Woods Hole, Massachusetts, 2 October 2012.

Ammodytes americanus 3 specimens (73.0–142.0 mm) examined. VIMS 12840, 1 (142 mm), western North Atlantic Ocean, Rhode Island Sound, 41.2355°N, 71.5519°W, 29 m depth, FV *Darana R*, cruise NM20100401, station 150, 6 May 2010; VIMS 12843, 1 (138 mm), western North Atlantic Ocean, Rhode Island Sound, 41.1764°N, 71.4936°W, 29 m depth, FV *Darana R*, cruise NM20100401, station 139, 5 May 2010; VIMS 12844, 1 (73 mm), western North Atlantic Ocean, Rhode Island Sound, 41.2937°N, 71.8408°W, 31 m depth, FV *Darana R*, cruise NM20100401, station 126, 11 May 2010.

Ammodytes marinus 2 specimens (133.0–155.0 mm) examined. ZMUC P61825–P61826, 2 (133–155 mm), Denmark, North Sea, Horns Rev, 55.47°N, 8.43°E, 2 July 2009.

Ammodytes tobianus 2 specimens (105.0–106.0 mm) examined. ZMUC P61815–P61816, 2 (105–106 mm), Denmark, Langeland, off Hjortholm, 55.9°N, 10.6°E, 1 May 2010.

Appendix 2

This appendix provides diagnostic mitochondrial DNA sequence data for North Pacific sand lances of the genus *Ammodytes*, including data for neotypes of *A. hexapterus* and *A. personatus* and for the holotype of *A. heinan* new species. The sequences are a partial

(560-base-pair) fragment from the cytochrome oxidase c subunit 1 region of the mitochondria.

Cytochrome oxidase c subunit 1 sequences

Ammodytes hexapterus

UAM 2813, neotype, GenBank Accession KJ137280.

COI sequence: tgtaatgccg gcgcaagga cgggcagggg
 aaggaggaga aggacggctg taatcagcac agtcacaca aata-
 aggtg tctgatactg ggaaatagcg ggaggtttca tattaataat
 tgtggtgatg aagttgattg ctccaagaat tgaagaaate cggc-
 taaat gcagagagaa gattgttaag tcaacagatg cacctgcgtg
 ggctagattt cggccaggg gtgggtatac agttcaaccg gtac-
 cagctc cagcttctac gcctgaagag gctaggagaa gaaggagggg
 ggtggggagg agtcaaaagc tcatgttatt tattcgaggg aatgc-
 tatgt cagggcgcc aatcattagg gggattagtc agtttccgaa ac-
 caccgatc ataattgta ttactataaa gaaaatcatt acgaatgcat
 gagcggtaac aattacgta tagatttggc cgtctctag gagggcgcc
 ggttgctaa gttctgctc gatgagcagg ctgagggctg tcccccat
 agcgctcaa gcacaaata

Ammodytes personatus

UW 152354, neotype, GenBank Accession KJ137281.

COI sequence: tgtaatgccg gcgcaagga cggggagggg
 gaggaggaga aggacggctg taatcagcac agtcacaca aata-
 aggtg tctgatactg agagatagcg ggaggtttca tgtaataat
 tgtggtgatg aagttgattg ctccaagaat cgaggagatc cggc-
 taaat gcagagagaa gattgttaag tcaacagatg cacctgcgtg
 ggctagattt cggccaggg gaggtatac agttcaaccg gtac-
 cagctc cagcttctac gcctgaagag gctaggagaa gaaggagggg
 ggtggggagg agtcaaaagc tcatgttatt tattcgaggg aatgc-
 tatat caggggcacc aatcattagg gggattagtc agtttccgaa ac-
 caccaatc ataattgta ttactataaa gaaaatcatt acgaatgcat
 gagcggtaac aattacgta tagatttggc catctctag gagggcgcc
 ggttgctaa gttctgctc gatgagcagg cttagagccg tcccccat
 agcgctcaa gcacaaata

Ammodytes japonicus

FAKU 130988, GenBank Accession KJ137283.

COI sequence: tgtaatgccg gcgcaagaa caggagggg
 gaggagaaga aggacggctg taatcagcac ggctcacaca aata-
 aaggtg tttgatactg ggagatagcg ggaggcttca tgtaataat
 tgtggtgatg aagttgattg ctccaagaat tgaagaaatt cggctaaat
 gcagggagaa gattgttaa tcaacagatg cacctgcgtg gggcagatt
 cggccaaag ggggtatac agttcaaccg gtaccggccc cagctctac
 gcctgaagag gctaagagaa gaagaaggga ggtggaaga agt-
 caaaagc ttatgttatt tattcgggga aatgctatat cagggcgcc
 aatcattagg gggattagtc agtttccaaa accaccaatc ataattgta
 ttactataaa gaaaatcatt acgaatgcat gagcggtaac aattacgta
 tagatttggc catctccgag gagggcgcc ggttgctaa gttcgcctc
 aatgagcagg cttagggccg tcccccat agcgctcaa gcacaaata

Ammodytes heian

FAKU 130770, holotype, GenBank Accession KJ137282.

COI sequence: tgtaatgccg gcgcaagaa caggagggg
 gaggagaaga aggacggctg taatcagcac ggctcacaca aata-
 aaggtg tttgatactg ggagatagcg ggaggcttca tgtaataat
 tgtggtgatg aagttgattg ctccaagaat tgaagaaatt cggctaaat
 gcagggagaa gattgttaa tcaacagatg cacctgcgtg gggcagatt
 cggccaaag ggggtatac agttcaaccg gtaccggccc cagctctac
 gcctgaagag gctaagagaa gaagaaggga ggtggaaga agt-
 caaaagc ttatgttatt tattcgggga aatgctatat cagggcgcc
 aatcattagg gggattagtc agtttccaaa accaccaatc ataattgta
 ttactataaa gaaaatcatt acgaatgcat gagcggtaac aattacgta
 tagatttggc catctccgag gagggcgcc ggttgctaa gttcgcctc
 aatgagcagg cttagggccg tcccccat agcgctcaa gcacaaata