# Reassessment of multiple species of Gymnelus (Teleostei: Zoarcidae) in Pacific Arctic and boreal regions 

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#### Abstract

Recently described new nominal species and resurrected species in the eelpout genus Gymnelus Reinhardt 1834 were reassessed for validity using fresh material collected in Pacific Arctic regions and a large body of data from a previous systematic review of the genus. The analysis reported here included both DNA barcodes and morphology. Only two species were validated: G. viridis (Fabricius 1780) and G. hemifasciatus Andriashev 1937. The latter species occurred as two morphotypes for which there is some evidence of difference in ecological preference, but the available environmental data are not robust enough to firmly identify or verify ecophenotypes.


Key words: Zoarcidae, Gymnelus, eelpouts, Gymnelus hemifasciatus, Gymnelus viridis, Arctic, boreal Pacific, DNA barcoding, ecophenotype

## Introduction

Species of the eelpout genus Gymnelus Reinhardt 1834 are found on the sea floor in shallow Arctic and boreal marine waters. In a systematic review of Gymnelus material Anderson (1982) confirmed the validity of four species (G. hemifasciatus Andriashev 1937, G. popovi [Taranetz \& Andriashev 1935], G. retrodorsalis Le Danois 1913, and G. viridis [Fabricius 1780]) and described one new species (G. pauciporus Anderson 1982), for a total of five in the genus. Subsequently Chernova (1998a) redescribed G. viridis and resurrected a synonym, G. bilabrus Andriashev 1937; revised the descriptions of G. retrodorsalis and G. pauciporus and described a new species G. andersoni (Chernova 1998b); redescribed G. hemifasciatus and described a new species G. knipowitschi (Chernova 1999a); described four other new Gymnelus species from Arctic seas (Chernova 1999b) and four from Far Eastern seas (Okhotsk Sea, northwestern Pacific Ocean, western Bering Sea; Chernova 2000); and suggested a restoration of $G$. popovi to its original genus, Commandorella Taranetz \& Andriashev 1935 (Chernova 2000). Those actions tripled the number of species in Gymnelus, even with removal of Commandorella. In Pacific Arctic and boreal regions, some of the new nominal species of Gymnelus have been considered phenotypic variants exhibiting morphological plasticity previously known in other eelpouts (mainly polychromatism and variability in cephalic lateralis canals and pores), or ecophenotypes of two widely distributed and recognized species: G. viridis (Fabricius 1780) and G. hemifasciatus Andriashev 1937 (e.g., Mecklenburg et al. 2002; Anderson \& Fedorov 2004; Mecklenburg et al. 2011).

This paper deals primarily with the two species represented in recent ichthyological and fisheries oceanography investigations in Bering Strait and the East Siberian, Chukchi, and Beaufort seas: the halfbarred pout, Gymnelus hemifasciatus, and fish doctor, G. viridis. These species have long been familiar to field and laboratory scientists and observers in northern Pacific regions. Accumulation of fresh material for the current analysis began with the first expedition of the Russian-American Long-Term Census of the Arctic (RUSALCA) in 2004, during which Russian and American scientists' identifications of the Gymnelus species differed
(Mecklenburg et al. 2007). Since then, we have collected material from two more RUSALCA expeditions in 2009 and 2012, and several other expeditions from 2006 to 2013 conducted by other programs; the disagreement over identifications continues. For instance, Chernova (e.g., 2009a, b; pers. comm. 2004-2014) identifies the RUSALCA and other Pacific Arctic material we identify as $G$. hemifasciatus to the new species $G$. knipowitschi Chernova 1999 and G. platycephalus Chernova 1999, while relegating the material we identify as G. viridis to Gymnelus sp. or G. bilabrus.

Our observations and data do not support recognition of the new species as being distinct nor the resurrection of G. bilabrus. It is important to resolve the taxonomy of these multiple nominal forms because considering them all as distinct species affects assessments of biodiversity by overestimating numbers of species present and, consequently, can give a false idea of the nature of the Arctic fish fauna.

In the fresh samples used in the present analysis, Chernova (2009a,b; pers. comm. 2004-2014) has identified, at different times, G. barsukovi, G. bilabrus, G. knipowitschi, and G. platycephalus. In a taxonomic checklist of the Zoarcidae (Anderson \& Fedorov 2004), those names were considered to be synonyms of G. hemifasciatus and $G$. viridis. We bring recent data from DNA sequencing (barcoding) and morphological examination to resolution of the problem.

In addition to the genetic distances revealed by DNA barcoding, analysis of the fresh sample focuses on coloration and the supratemporal commissure and lateralis pores which Chernova gave as major identifying features for the several nominal forms. For the cephalic lateralis system, the major identifying character specified is whether nominal forms possess a complete or incomplete supratemporal commissure across the back of the head, with usually three (complete commissure) or two (incomplete) lateralis pores. Published accounts indicate that this is a variable character in Pachycara crossacanthum (Anderson 1989), Magadanichthys skopetsi (Shinohara et al. 2004), Greenland to Pacific Arctic G. viridis (Anderson 1982), and the nominal G. andersoni (Chernova 1998b). Several species of boreal Lycodes Reinhardt 1831 exhibit variation in the completeness of lateralis canals, especially the supratemporal, as well (Anderson, unpubl.). In Bothrocara Bean 1890 the supratemporal commissure was found to be present, but pore distribution is variable (Anderson et al. 2009). In Lycenchelys scaurus (Garman 1899) the supratemporal commissure and three pores is typical, but four fish $(9.5 \%)$ had the commissure complete but lacked pores, two also had the commissure complete but had only the median pore present, and two had the commissure interrupted with only the two lateral pores present (Anderson 1995).

Published accounts also indicate variability in coloration within other eelpout species and coloration is often given as a diagnostic character. Lycodes marisalbi Knipowitsch 1906 can be uniformly brown or have white bars (Møller 2000). Lycodes pallidus Collett 1879 also has a uniformly brownish morphotype and one with light crossbars (Møller et al. 2001). Lycodes seminudus Reinhardt 1837 has at least two monochrome morphotypes, including dark gray to almost black and pinkish white (Mecklenburg, unpubl.), as well as a distinctly banded form (Jensen 1904; McAllister et al. 1981; Møller \& Jørgensen 2000). Lycodes yamatoi Toyoshima 1985 has dark and light color forms with the light morphotype exhibiting individually variable banding (Balanov \& Kukhlevskii 2011). Lycodes nakamurae (Tanaka 1914) also has dark and light color forms with variable intermediate morphotypes (Saveliev et al. 2014). Bothrocara hollandi (Jordan \& Hubbs 1925) has two color forms, a "white" type (pale pinkish) and a "black" type (dark brown or blackish) that are depth-dependent (Okiyama 2004). Chernova also used coloration in the diagnoses of Gymnelus species and has described variations within some species, including the nominal forms G. knipowitschi (Chernova 1999a) and G. platycephalus (Chernova 1999b).

Additional analysis of the data presented by Anderson (1982) completes this reassessment of the nominal species. Since the fresh sample is restricted to material from the Pacific Arctic region, the analyses of nominal species described from the Pacific boreal region, including waters around the western Aleutian Islands and the Pacific Ocean off southeastern Kamchatka, depend primarily on Anderson's (1982) original data.

## Material and methods

The material referred to as the fresh sample includes 221 specimens collected from 2004 to 2013 from the eastern East Siberian Sea, the Chukchi Sea, the western Beaufort Sea, and the northern Bering Sea including Bering Strait. It comprises specimens obtained by the first author during participation in research cruises, specimens provided frozen from other cruises, and specimens from a 2013 survey which were provided from the University of Alaska

Museum. Specimens were photographed and measured for total length (TL) on board, or in the laboratory within a month after receipt of the frozen samples. Some (31, or 14\%) specimens had been fixed in formalin before receipt, but all specimens were available less than 9 months after collection while color patterns were still clearly evident and shrinkage from fixation was minimal. Identifications to species were made according to characters given by Anderson (1982), especially color patterns since they were so clear in the fresh material. (In old preserved material with loss of color patterns diagnostic characters include number of pectoral-fin rays, the position of the dorsal-fin origin relative to the pectoral-fin base, and in more difficult cases, numbers of vertebrae.)

The genetic analysis included 67 successfully barcoded specimens (Table 1) from the cruises in 2007 through 2012; barcoding was not an established method at the time of the 2004 cruise, and some of the material from 2012 and 2013 was received already fixed in formalin. In preparation for genetic analysis, the first author removed muscle tissue from the fresh and frozen specimens from the right side well posterior to the anus after wiping the skin clean with an alcohol swab. The specimens were photographed with a barcode sample number label, color strip, and ruler included in each photograph. Lateral views were photographed at a minimum, and many specimens were also photographed in dorsal and ventral view. Notes were taken on coloration for specimens which were not photographed and tissue-sampled.

Tissue samples were placed in $95 \%$ ethanol and the whole specimens were fixed in $10 \%$ buffered seawaterformalin solution. After fixation specimens were rinsed in water and stored in $70 \%$ ethanol before deposition in three museums: California Academy of Sciences, San Francisco (CAS); University of Alaska Museum, Fairbanks (UAM); and the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

Tissue samples were sent to the Biodiversity Institute of Ontario, University of Guelph, Canada, for DNA barcoding as contributions to the Fish Barcode of Life initiative. DNA barcoding, which sequences a standard region of the mitochondrial cytochrome $c$ oxidase 1 gene (COI), followed the protocol described by Steinke et al. (2009a). Sequence data were submitted to the Barcode of Life Data system (BOLD, http://www.barcodinglife.org, see Ratnasingham \& Hebert [2007]) and to GenBank (accession numbers in Table 1). Specimen and collection data, sequences, specimen images, and trace files are provided in the public dataset "Gymnelus GenBank [DSGYMGB]" on BOLD. Neighbor-joining (NJ) analyses and genetic distance calculations were executed with MEGA version 5.0 (Tamura et al. 2011). The Kimura 2-parameter (K2P) distance metric (Kimura 1980) was employed for all sequence comparisons and analyses. Confidence in estimated relationships of NJ tree topologies was evaluated by a bootstrap analysis with 1,000 replicates using MEGA version 5.0.

The DNA barcodes were supplemented by morphological observations of the barcoded material as well as numerous other specimens, including some of those studied by Chernova (1998a,b, 1999a,b, 2000, pers. comm.). Specimens of the fresh sample, as well as some from earlier collections, archived in the CAS and UAM were examined together by the authors at the CAS in June 2014. The second author measured standard length (SL), examined the supratemporal commissure for completeness and counted the supratemporal (occipital) and temporal (postorbital) pores (the most variable in eelpouts), and determined sex by observation of the gonads (young) or color of the anal fin (Anderson 1982). We standardized our terminology for the coloration patterns and noted the pattern for each specimen. Notation was taken on whether a depressed fusion of the center of the upper lip was present or absent - a condition in the original diagnosis of G. bilabrus (Andriashev 1937) which Anderson (1982) found in only four specimens and Chernova (1998a) found to be absent in a smaller sample.

Original data from Anderson (1982) were also used; see methodology described therein.

## Results

DNA sequencing. The DNA barcodes for the 67 Gymnelus specimens successfully sequenced place them in two clades: 47 in G. hemifasciatus and 20 in G. viridis (Fig. 1). The results are similar to those for a somewhat smaller sample reported earlier (Mecklenburg et al. 2011). The two clades are clearly separate, yet closely related. The species are separated by only $1.2 \%$ sequence divergence (range $0.8-1.9 \%$ ). There is little intraspecific variation in either clade: $0.4 \%$ for $G$. hemifasciatus and $0.1 \%$ for G. viridis. As can be seen from the NJ tree (Fig. 1), the minor genetic variation seen is not consistent by coloration, sex, or geographic location.

The barcodes from specimens identified as $G$. knipowitschi by Chernova (e.g., CAS 228491, UAM 5520, UAM 5521, ZIN uncatalogued in Table 1) or similar to them (as in, e.g., Mecklenburg et al. 2007; Balushkin et al. 2011),
including those that could be identified as $G$. knipowitschi from her key (Chernova 2000), fall within the $G$. hemifasciatus clade. In Fig. 1, those are the specimens labeled with an S to indicate the solid-band morphotype (described below). Barcodes from specimens similar to specimens identified by Chernova as G. platycephalus (e.g., Mecklenburg et al. 2007; Balushkin et al. 2011) also fall within the G. hemifasciatus clade. In Fig. 1, those are the sequences designated by a T as the typical morphotype. No specimens in our fresh sample could be identified as $G$. platycephalus from the key published in Chernova (2000). The barcodes from specimens similar to G. bilabrus and G. barsukovi identified by Chernova (e.g., Mecklenburg et al. 2007; Balushkin et al. 2011) fall within the G. viridis clade. We were not able to morphologically distinguish between G. barsukovi and G. bilabrus in the fresh sample except that the males of G. viridis appeared to equate to G. barsukovi and the females to G. bilabrus (designated by male and female symbols in Fig. 1).

Coloration. The fresh sample ( $\mathrm{N}=221$ ), including specimens barcoded as well as others examined, comprised $179(81 \%)$ G. hemifasciatus and 42 G. viridis (19\%). The coloration of the specimens indicated three morphotypes: two which are sexually dimorphic morphotypes of $G$. hemifasciatus and one sexually dimorphic morphotype of $G$. viridis.

The G. hemifasciatus sample included what we call the typical and the solid-band variations. Solid-banded $G$. hemifasciatus (Fig. 2) include full-banded males and half-banded females similar in coloration to that described for the nominal species G. knipowitschi by Chernova (1999a: male, fig. 1; female, fig. 3). The males have full dark bands extending ventrally to the anal fin, and the females have half bands not extending below midbody. The bands are solid, not broken by pale mottling or spots, and have relatively straight sides. The full-banded adult males all had black anal fins. The coloration in both sexes, except for the black anal fin, was evident even in very small specimens (Fig. 2) and the specimens could be sexed by coloration alone. The coloration of the females matched the description by Chernova for the females of G. knipowitschi (Chernova 1999a) as well as the holotype and paratype of G. diporus (Chernova 2000), which also were females. Of the 179 G. hemifasciatus specimens in the fresh sample, 85 ( $47.5 \%$ ) were the solid-banded form. Of those, 37 ( $43.5 \%$ ) were full-banded males and 48 $(56.5 \%)$ were half-banded females.

The coloration of the form we refer to as the typical morphotype of G. hemifasciatus (Fig. 3) is similar to that described by Andriashev (1937: holotype, fig. 23) as G. hemifasciatus and by Chernova (1999a), in part, as G. hemifasciatus in her redescription of this species. It is called typical for its similarity to Andriashev's holotype, although it is not necessarily typical in the sense of being the most common morphotype. Both males and females of the typical morphotype are variegated, with full bands reaching the anal fin anteriorly, bands transitioning to a checkered or indistinct pattern posteriorly, and mottling on the head, nape, and, usually, all along the dorsum. The coloration is evident even in very small juveniles of both sexes and discrimination between males and females only becomes obvious externally when the males turn orange and develop black anal fins (Fig. 3). Chernova (1999a:7) included this pattern of coloration, although not the colors themselves, in the diagnosis of the redescribed $G$. hemifasciatus ("Coloration with dark transversal bands disappears toward the tail"). Of the 179 G. hemifasciatus in the fresh sample, $94(52.5 \%)$ were the typical morphotype; $31(33 \%)$ of those were males and $63(67 \%)$ were females.

Males and females of G. viridis in the fresh sample (Fig. 4) had broad dark bands mottled with white, similar to Anderson's (1982) type 3. Coloration was most similar to that shown and described for G. bilabrus by Andriashev (1937: fig. 20) and Chernova (1998a: fig. 2a,b). In fresh condition, females were ivory colored with reddish brown bands mottled with white or ivory. The adult males were dark grayish brown with darker, almost black, broad mottled bands on the body, orange head, and orange and black pectoral fins (Fig. 4). The mottled bands were indistinct and not clearly discernible from the dark background color in adult males. In preservative the orange color turns pale gray.

None of the other color variations of G. viridis observed in Anderson's (1982) material or in the specimens from the Canadian high Arctic collected by Green \& Mitchell (1997) were observed in our fresh sample. Anderson's (1982) specimens (Table 2) included many from more regions around the Arctic and more coloration variants than those of our fresh sample. Some differences could be due to the indistinct coloration in older preserved specimens but some also to true regional differences. For instance, in the fresh sample specimens from the Beaufort Sea were from the western (Alaskan) area of the sea only, and variation in coloration in G. viridis has been observed to be greater in the eastern (Canadian) part of the Beaufort Sea (e.g., Green \& Mitchell 1997; Mecklenburg, unpubl.).


FIGURE 1. Neighbor-joining tree for 67 COI sequences of Gymnelus hemifasciatus and G. viridis collected in 2007-2012 from the Bering, East Siberian, Chukchi, and Beaufort seas. The Barcode of Life Datasystem (BOLD) process ID number, sample number as submitted to BOLD, coloration, sex, and ocean region are given. All G. viridis are the mottled-band morphotype (M). The G. hemifasciatus sample includes the typical morphotype (T) and the solid-band morphotype (S). The morphotypes are described in the text and shown in Figs. 2-4. Numbers below nodes represent bootstrap values (only values above 75 are shown). The scale bar represents K2P distance.


FIGURE 2. Examples of the solid-band morphotype of Gymnelus hemifasciatus in the fresh sample.


FIGURE 3. Examples of the typical morphotype of Gymnelus hemifasciatus in the fresh sample.


FIGURE 4. Examples of Gymnelus viridis in the fresh sample. All were the mottled-band morphotype.
TABLE 1. (Continued)

| Species | Locality | Latitude | Longitude | Date collected | Catalog number | BOLD ID | Barcode ID | GenBank no. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| G. hemifasciatus | W Beaufort Sea | 71.326 | -151.100 | 28-Sep-2012 | UAM 3697 | DSFIB248-13 | BEAU2012-51 | KM987626 |
| G. hemifasciatus | W Beaufort Sea | 71.028 | -150.100 | 22-Sep-2012 | UAM 3698 | DSFIB349-13 | BEAU2012-52 | KM987631 |
| G. hemifasciatus | NW Chukchi Sea | 71.440 | -174.861 | 17-Sep-2009 | UAM 5520 | DSFAL568-09 | RUSALCA09-84 | GU804880 |
| G. hemifasciatus | NW Chukchi Sea | 71.418 | -174.814 | 17-Sep-2009 | UAM 5521 | DSFAL569-09 | RUSALCA09-85 | GU804881 |
| G. hemifasciatus | NE Chukchi Sea | 70.060 | -167.164 | 8-Jul-2008 | UAM 5752 | DSFAL396-08 | OSHOR08-50 | HQ712410 |
| G. hemifasciatus | SE Chukchi Sea | 66.202 | -168.659 | 7-Jul-2008 | UAM 5804-01 | DSFAL356-08 | OSHOR08-10 | HQ712409 |
| G. hemifasciatus | SE Chukchi Sea | 68.187 | -167.197 | 12-Jul-2008 | UAM 5831-01 | DSFAL350-08 | OSHOR08-04 | HQ712405 |
| G. hemifasciatus | SE Chukchi Sea | 68.187 | -167.197 | 12-Jul-2008 | UAM 5831-02 | DSFAL351-08 | OSHOR08-05 | HQ712406 |
| G. hemifasciatus | SE Chukchi Sea | 68.187 | -167.197 | 12-Jul-2008 | UAM 5831-07 | DSFAL352-08 | OSHOR08-06 | HQ712407 |
| G. hemifasciatus | SE Chukchi Sea | 68.187 | -167.197 | 12-Jul-2008 | UAM 5831-08 | DSFAL353-08 | OSHOR08-07 | HQ712408 |
| G. hemifasciatus | SE Chukchi Sea | 66.202 | -168.659 | 7 -Jul-2008 | UAM 5994 | DSFAL419-08 | OSHOR08-73 | HQ712411 |
| G. hemifasciatus | W Beaufort Sea | 70.452 | -145.088 | 17-Aug-2011 | UAM 6271-01 | DSFAL718-11 | BEAU2011-21 | KM987616 |
| G. hemifasciatus | W Beaufort Sea | 70.452 | -145.088 | 17-Aug-2011 | UAM 6271-02 | DSFAL717-11 | BEAU2011-20 | KM987635 |
| G. hemifasciatus | NE Chukchi Sea | 71.489 | -163.373 | 23-Aug-2009 | UAM 6295 | DSFIB043-11 | COMIDA09-05 | KM987618 |
| G. hemifasciatus | W Beaufort Sea | 70.960 | -149.572 | 23-Aug-2011 | UAM 6296-01 | DSFIB199-12 | BEAU2011-120 | KM987619 |
| G. hemifasciatus | W Beaufort Sea | 70.960 | -149.572 | 23-Aug-2011 | UAM 6296-02 | DSFIB198-12 | BEAU2011-119 | KM987633 |
| G. hemifasciatus | W Beaufort Sea | 70.960 | -149.572 | 23-Aug-2011 | UAM 6297 | DSFIB201-12 | BEAU2011-122 | KM987642 |
| G. hemifasciatus | NE Chukchi Sea | 69.820 | -163.881 | 24-Aug-2010 | UAM 6331 | DSFIB050-11 | AKCH10-06 | KM987641 |
| G. hemifasciatus | W Beaufort Sea | 71.734 | -153.526 | 28-Aug-2011 | UAM 6345-01 | DSFIB102-11 | BEAU2011-113 | KM987625 |
| G. hemifasciatus | W Beaufort Sea | 71.734 | -153.526 | 28-Aug-2011 | UAM 6345-02 | DSFIB101-11 | BEAU2011-112 | KM987623 |
| G. hemifasciatus | W Beaufort Sea | 71.593 | -155.037 | 31-Aug-2011 | UAM 6389-02 | DSFIB089-11 | BEAU2011-100 | KM987639 |
| G. hemifasciatus | NE Chukchi Sea | 71.300 | -157.204 | 5-Sep-2011 | UAM 6458 | DSFIB120-11 | AKMAP2011-17 | KM987627 |
| G. hemifasciatus | NE Chukchi Sea | 71.160 | -160.193 | 7-Sep-2011 | UAM 6480 | DSFIB134-11 | AKMAP2011-31 | KM987620 |

TABLE 1. (Continued)

| Species | Locality | Latitude | Longitude | Date collected | Catalog number | BOLD ID | Barcode ID | GenBank no. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| G. hemifasciatus | NE Chukchi Sea | 71.166 | -160.211 | 7-Sep-2011 | UAM 6482-01 | DSFIB122-11 | AKMAP2011-19 | KM987634 |
| G. hemifasciatus | East Siberian Sea | 71.650 | 179.550 | 11-Sep-2009 | ZIN uncataloged | DSFAL546-09 | RUSALCA09-62 | GU804875 |
| G. viridis | NE Chukchi Sea | 69.999 | -168.405 | 5-Sep-2007 | CAS 230053-01 | DSFAL097-07 | BASIS2007-35 | HQ712416 |
| G. viridis | NE Chukchi Sea | 69.999 | -168.405 | 5-Sep-2007 | CAS 230053-02 | DSFAL098-07 | BASIS2007-34 | HQ712415 |
| G. viridis | NE Chukchi Sea | 69.999 | -168.405 | 5-Sep-2007 | CAS 230053-03 | DSFAL099-07 | BASIS2007-33 | HQ712414 |
| G. viridis | NE Chukchi Sea | 69.999 | -168.405 | 5-Sep-2007 | CAS 230055-01 | DSFAL095-07 | BASIS2007-36 | HQ712417 |
| G. viridis | NE Chukchi Sea | 69.999 | -168.405 | 5-Sep-2007 | CAS 230055-02 | DSFAL096-07 | BASIS2007-37 | HQ712418 |
| G. viridis | NE Chukchi Sea | 69.999 | -168.405 | 5-Sep-2007 | CAS 230055-03 | DSFAL100-07 | BASIS2007-32 | HQ712413 |
| G. viridis | NE Chukchi Sea | 69.999 | -168.405 | 5-Sep-2007 | CAS 230055-04 | DSFAL101-07 | BASIS2007-31 | HQ712412 |
| G. viridis | NE Bering Sea | 64.492 | -170.441 | 15-Sep-2007 | CAS 230182-05 | DSFAL275-07 | BASIS2007-204 | HQ712419 |
| G. viridis | NE Chukchi Sea | 70.898 | -164.567 | 12-Aug-2007 | CAS 230317 | DSFAL303-07 | OSHORO2007-21 | HQ712420 |
| G. viridis | NE Chukchi Sea | 70.839 | -160.686 | 9 -Sep-2011 | CAS 235295 | DSFIB125-11 | AKMAP2011-22 | KM987614 |
| G. viridis | W Beaufort Sea | 71.028 | -150.100 | 22-Sep-2012 | CAS 236447-01 | DSFIB286-13 | BEAU2012-05 | KM987640 |
| G. viridis | W Beaufort Sea | 71.217 | -150.100 | 22-Sep-2012 | UAM 2980 | DSFIB285-13 | BEAU2012-04 | KM987638 |
| G. viridis | W Beaufort Sea | 71.028 | -150.100 | 22-Sep-2012 | UAM 3699 | DSFIB350-13 | BEAU2012-53 | KM987624 |
| G. viridis | SE Chukchi Sea | 66.202 | -168.659 | 7-Jul-2008 | UAM 5989 | DSFAL415-08 | OSHOR08-69 | HQ712422 |
| G. viridis | W Beaufort Sea | 70.452 | -145.088 | 17-Aug-2011 | UAM 6272 | DSFAL719-11 | BEAU2011-22 | KM987630 |
| G. viridis | W Beaufort Sea | 70.670 | -145.104 | 17-Aug-2011 | UAM 6275 | DSFAL716-11 | BEAU2011-19 | KM87636 |
| G. viridis | W Beaufort Sea | 71.246 | -153.117 | 1-Sep-2011 | UAM 6417-02 | DSFIB086-11 | BEAU2011-97 | KM987629 |
| G. viridis | NE Chukchi Sea | 71.300 | -157.204 | 5-Sep-2011 | UAM 6459-01 | DSFIB121-11 | AKMAP2011-18 | KM987617 |
| G. viridis | NE Chukchi Sea | 71.300 | -157.204 | 5-Sep-2011 | UAM 6459-02 | DSFIB127-11 | AKMAP2011-24 | KM987628 |
| G. viridis | NE Chukchi Sea | 71.224 | -157.983 | 6-Sep-2011 | UAM 6473-01 | DSFIB118-11 | AKMAP2011-15 | KM987622 |

TABLE 2. Distribution of occipital (supratemporal) pores and three color patterns in Gymnelus viridis around the Arctic from data in Anderson (1982). N is the number of specimens.

| Region | Number of occipital pores |  |  |  |  |  | Color patterns |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 0 | 1 | 2 | 3 | 4 | N | Monotone | Mottled bands | Solid bands | N |
| Greenland | 1 | 0 | 75 | 6 | 2 | 84 | 6 | 23 | 6 | 35 |
| Eastern Canada | 3 | 0 | 21 | 46 | 3 | 73 | 18 | 25 | 10 | 53 |
| Beaufort and Chukchi seas | 3 | 0 | 15 | 39 | 0 | 57 | 13 | 29 | 10 | 52 |
| Bering Sea | 0 | 0 | 0 | 22 | 1 | 23 | 7 | 13 | 9 | 29 |
| Siberian seas | 2 | 0 | 2 | 6 | 0 | 10 | 4 | 5 | 1 | 10 |
| Total specimens | 9 | 0 | 113 | 119 | 6 | 247 | 48 | 95 | 36 | 179 |
| Standard length (mm) |  |  |  |  |  |  | 56-242 | 39-192 | 32-179 |  |

As in previous studies (e.g., Anderson 1982), in both G. hemifasciatus and G. viridis in the fresh sample one or more black spots bordered with white (ocelli) were sometimes present on the dorsal fin. No difference in the frequency or position of ocelli was found among the morphotypes or sexes.

Occipital pores and supratemporal commissure. The postorbital (temporal) pores showed little variation in the fresh sample and Anderson's (1982) sample, with nearly all exhibiting four pores bilaterally, and further reporting is restricted to the occipital (supratemporal) pores. They were observed in 204 specimens of the fresh sample (Table 3). No appreciable differences between males and females were found so they are grouped in Table 3. The majority ( $60.0 \%$ ) of specimens of the solid-band G. hemifasciatus morphotype had two occipital pores (pattern 1-0-1) and an incomplete commissure, followed by $22.7 \%$ with three pores (pattern 1-1-1) and a complete commissure. Other patterns appeared to be related to failure of pores to open externally in young specimens. Most ( $88.8 \%$ ) of the typical morphotype of G. hemifasciatus had three occipital pores and $4.5 \%$ had two with the median pore missing. The rest had various combinations with a pore doubled or others missing.

TABLE 3. Occipital (supratemporal) pore counts and lengths of 204 specimens of Gymnelus hemifasciatus and G. viridis in the fresh sample.

| Variable | G. hemifasciatus, typical morphotype |  | G. hemifasciatus, solid-band morphotype |  | G. viridis |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | \% | N | \% | N | \% |
| Occipital pore counts |  |  |  |  |  |  |
| 1-1-1 | 79 | 88.8 | 17 | 22.7 | 38 | 95.0 |
| 1-0-1 | 4 | 4.5 | 45 | 60.0 | 0 | 0.0 |
| 1-0-0 or 0-0-1 | 2 | 2.3 | 7 | 9.3 | 0 | 0.0 |
| 0-0-0 | 1 | 1.1 | 6 | 8.0 | 0 | 0.0 |
| 0-1-1 or 1-1-0 | 1 | 1.1 | 0 | 0.0 | 0 | 0.0 |
| 2-1-1 | 2 | 2.3 | 0 | 0.0 | 1 | 2.5 |
| 1-2-1 | 0 | 0.0 | 0 | 0.0 | 1 | 2.5 |
| Total specimens | 89 | 100.1 | 75 | 100.0 | 40 | 100.0 |
| Total length (mm) | 63-176 |  | 50-159 |  | 45-256 |  |
| Standard length (mm) | 60-163 |  | 48-144 |  | 42-220 |  |

In data from Anderson (1982), no clear pattern regionally was seen for G. viridis in the number of occipital pores except for a tendency for two pores around Greenland, three pores in the Bering Sea, and either two or three pores in eastern Canadian waters and the Beaufort and Chukchi seas (Table 2). In the fresh sample, primarily from
the Beaufort and Chukchi seas, nearly all (95.0\%) G. viridis had three pores with complete supratemporal commissures (Table 3). This shows that in order to understand coloration, sex, the supratemporal commissure and its pores, and geography one needs a very large sample size.

Distribution of the fresh sample. The geographic distributions of $G$. viridis and the two morphotypes of $G$. hemifasciatus in the fresh sample are shown in Fig. 5. In all, Gymnelus specimens taken at 60 stations from 2004 to 2013 are represented. Gymnelus viridis was taken at $20(33 \%)$ of those stations, the typical morphotype of $G$. hemifasciatus at $18(30 \%)$, and the solid-band morphotype at $36(60 \%)$. Although it appears from the maps that the solid-band morphotype of $G$. hemifasciatus mostly occurs more northerly than the typical morphotype, this could be an artifact of the sample. The solid-band morphotype also occurs in more southerly locations (e.g., Balushkin et al. 2011). It could also reflect preference for different environmental conditions. For instance, sediments with a high proportion of sand are more typical of the southern part of the sampling area (Fig. 5).


FIGURE 5. Distribution of Gymnelus specimens in the fresh sample on bottom sediments. A, index map. B, G. viridis. C, typical morphotype of $G$. hemifasciatus. D, solid-band morphotype of $G$. hemifasciatus. Sediment map based on data from U.S. Department of Commerce, NOAA (1987).

More specimens of the typical morphotype of G. hemifasciatus are included in the fresh sample but the solidband morphotype was taken at twice as many stations (Table 4). The typical morphotype was often represented by greater numbers per haul than the solid-banded one, but being museum voucher specimens, the sample is probably biased.

TABLE 4. Summary of bottom depth, temperature, and salinity at stations where Gymnelus specimens in the fresh sample were taken by bottom trawls and for which the environmental data are available.

| Environmental variable | G. hemifasciatus, typical morphotype |  | G. hemifasciatus, solid-band morphotype |  | G. viridis |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Range | No. stations | Range | No. stations | Range | No. stations |
| Depth (m) | 32-100 | 18 | 33-101 | 36 | 20-100 | 20 |
| Temperature ( ${ }^{\circ} \mathrm{C}$ ) | -1.5 to 10.5 | 14 | -1.8 to 6.9 | 29 | -1.8 to 10.5 | 18 |
| Salinity | 30.62-32.90 | 14 | 31.25-33.44 | 29 | 28.73-33.44 | 18 |

Gymnelus viridis was frequently taken in the same hauls with one or the other morphotype of $G$. hemifasciatus. In contrast, the two morphotypes of G. hemifasciatus were taken together in the same tow only once. In that instance (UAM 47835) a female of the typical morphotype ready to spawn was taken with two females (halfbanded) and a juvenile male (full-banded) of the solid-band form. The spawning female had 1-1-1 occipital pores, one half-banded female had $1-0-1$, the other half-banded female had 1-1-1, and the juvenile male had 1-0-1. That one odd catch was at a depth of 100 m and was the only one where the typical form of $G$. hemifasciatus was taken so deep.

Taken at face value the maximum depths for the two morphotypes of G. hemifasciatus are similar (Table 4). However, only one typical G. hemifasciatus was taken at 100 m ( 1 of 18 stations, $6 \%$ ); the others were taken at depths of 60 m or less ( 17 of 18 stations, $94 \%$ ). The solid-band form was caught more often ( 8 of 36 stations, 22\%) at depths greater than 60 m , to 101 m . It also was caught more often at negative temperatures ( 14 of 29 stations with temperature data, $48 \%$ ) than the typical form ( 2 of 14 stations, $14 \%$ ). Gymnelus viridis is reported to be a shallower-water species than G. hemifasciatus (e.g., Anderson 1982; Mecklenburg et al. 2002) and this was reflected in G. viridis being caught at the shallowest, least saline stations and less frequently at negative temperatures. Temperatures were negative at only 3 of the 19 stations (15\%) where G. viridis was taken.

The information on substrate from observation of net contents, grain size in sediment grabs, and observations by remotely operated vehicle at the stations where Gymnelus were taken is incomplete and difficult to assess. Most sites had high proportions of sand and mud in various combinations, which is characteristic of the region. Net contents indicated that the solid-band morphotype of G. hemifasciatus tended to be found on substrates with a high proportion of mud mixed with some combination of sandy mud, gravel, and shell hash, whereas the typical morphotype was more often associated with muddy sand and rougher substrate including shell hash, gravel, rock, cobble, and boulders. Gymnelus viridis was most often taken on the rougher substrates, and more often with the typical form of $G$. hemifasciatus (nine stations) than with the solid-band form (four stations). The same impression was gained from plots of the collection localities on a map of sediment types (Fig. 5). A few localities fell outside the areas for which the sediments have been mapped, but of the 18 localities for G. viridis that were on mapped sediments, 15 ( $83 \%$ ) were on gravelly substrate (Fig. 5B). All 16 (100\%) of the locations with sediment data for the typical morphotype of G. hemifasciatus were on gravelly substrate, and none on mud or sand without gravel (Fig. 5C). All 27 ( $100 \%$ ) of the localities for the solid-band morphotype of G. hemifasciatus that are within mapped sediment areas had a high proportion of mud; $13(48 \%)$ were on smooth mud, sandy mud, or muddy sand without gravel and none on primarily gravel substrate (gravel or muddy gravel; Fig. 5D).

Review of the nominal forms. Below we assess each of Chernova's new names on the basis of her diagnostic and other identifying characters. A major difficulty in assessing these nominal forms has been the inconsistency in her unquantified diagnostic characters from one form to another. The diagnoses reflect an arbitrariness in choosing characters which we demonstrate in Tables 5 and 6 . In boldface type are those characters used in Chernova's diagnoses (mostly given as the quantified character value from the descriptive part, rather than, e.g., "eye large" or "small gill opening") and those in regular typeface are those used in diagnoses of other nominal forms not used in all, taken also from the descriptive parts of those forms. As will be shown, many of the characters often were based on ontogenetic or sexually polymorphic features.

TABLE 5. Diagnostic and other identifying characters of nominal forms of Gymnelus hemifasciatus. Boldface type indicates values given as diagnostic; other values are from the descriptions of type specimens (Chernova 1999a, 2000).

| Character | $\begin{gathered} \text { G. knipowitschi } \\ \mathrm{N}=14: 67-142 \mathrm{~mm} \text { TL } \end{gathered}$ | $\begin{gathered} \text { G. diporus } \\ \mathrm{N}=2: 79,107 \mathrm{~mm} \mathrm{TL} \end{gathered}$ | $\begin{gathered} \text { G. soldatovi } \\ \mathrm{N}=5: 101-111 \mathrm{~mm} \mathrm{TL} \end{gathered}$ |
| :---: | :---: | :---: | :---: |
| Supratemporal commissure | Incomplete | Incomplete | Complete |
| Color bands, number | 14-15 | "Up to 18" | 0 (dorsal mottling) |
| Predorsal length, \% TL | 17-21 | 18.2-18.9 | 16.4-19.2 |
| Head width, \% HL | 48-58 | 50.0-55.6 | 46.0-58.0 |
| Eye diameter, \% HL | 22.6-29.8 | 23.8-24.4 | 22.3-25.0 |
| Snout length, \% HL | 21.8-26.1 | 16.9-20.8 | 23.7-25.8 |
| Gill slit length, \% HL | 18.2-26.7 | 23.1-25.0 | 23.5-28.1 |
| Pectoral fin length, \% HL | 41.0-53.0 | 53.6-54.0 | 44.0-53.0 |
| Pectoral base height, \% P length | 37.0-50.0 | 40.0-42.0 | 35.0-45.0 |
| Retrorse dorsal fin origin? | No | No | No |
| Free dorsal fin pterygiophores | 0-2 | Not given | 0-1 |
| Vertebrae, total | 86-94 | 88-94 | 88-94 |

## Gymnelus hemifasciatus Andriashev 1937

(Figs. 2 and 3)
Three nominal species were erected that we consider variant phenotypes of G. hemifasciatus: G. knipowitschi Chernova 1999a, G. diporus Chernova 2000, and G. soldatovi Chernova 2000 (Table 5).

Gymnelus knipowitschi, described from 14 types with 73 other specimens listed, basically distributed from the Barents Sea eastward to Arctic Canada including the Bering Sea, was diagnosed by having an incomplete supratemporal commissure, 14-15 dark transverse bars, 0-2 free dorsal-fin pterygiophores, 86-94 vertebrae, and several morphometric characters overlapping with other nominal forms (Table 5). Head width and length are often sexually dimorphic in many eelpouts (e.g., some Atlantic Lycenchelys [Goode \& Bean 1896, figs. 277, 278, 282]; Gymnelus [Anderson 1982]; Pachycara brachycephalum [Anderson 1988]). Both head length and width are sexually dimorphic in G. hemifasciatus (Anderson 1982) but this is not discussed by Chernova (1999a, 2000), probably owing to her small sample sizes. We found a mistranslation in the English language version of Chernova (1999a:2) that reads "Head wide and shallow (wider than longer)" that should read (our translation) ". . . (wider than deep)". A "large" eye was purported to be sexually dimorphic, but with greatly overlapping values between the sexes; the values are statistically insignificant at $\mathrm{N}=14$ (Chernova 1999a:2). Pectoral fin length was also purported to be sexually dimorphic based on the same sample.

Gymnelus diporus, described from two females, a juvenile and a subadult from the Commander Islands and the Pacific Ocean off southeastern Kamchatka, was diagnosed in having an incomplete supratemporal commissure as above, in not having a posteriorly shifted dorsal fin origin (the same in both G. knipowitschi and G. soldatovi), a narrow and long pectoral fin, short snout, up to 18 vertical bands, and small size (up to 107 mm TL, but $\mathrm{N}=2$ ). Compared to G. knipowitschi we find only a shorter snout length non-overlapping in these two specimens (Table 5) among Chernova's (1999a, 2000) characters. However, we discern no significant differences in the one illustration (Chernova 2000: fig. 4) of this form with either G. knipowitschi or G. soldatovi (Chernova 1999a: figs. 1, 3; Chernova 2000: fig. 1) and ascribe the difference in snout lengths to perhaps accuracy of measurement due to preservation, or individual or ontogenetic variation. Compared to G. soldatovi only the complete supratemporal commissure, lack of well-defined dark bands, and the snout length distinguish that form (Table 5). We refer to the G. diporus form as "half-banded" G. hemifasciatus, which are females of the solid-band morphotype (females halfbanded, males full-banded).

Gymnelus soldatovi, described from five types and six other specimens from the Okhotsk Sea and Kuril Islands, was diagnosed in having a complete supratemporal commissure with three occipital pores, few vertebrae
(mistranslated in English version as a "high" vertebral number), cylindrical body, "wide" head, large snout, small gill opening, "wide" (meaning high base) pectoral fin, and small size (to 111 mm TL). Vertebral number, head width, snout length (except in G. diporus), gill slit length, and pectoral base height all overlap with the other two nominal forms (Table 5). We regard the feature "cylindrical body" a non-character reflecting either a preservation artifact in these pliable fishes, or general, individual robustness. A mistranslation in the English language edition of the description of G. soldatovi gives females with the black anal fin whereas Chernova (2000:10) in the original edition correctly states it is the males with this feature (our translation).

## Gymnelus viridis (Fabricius 1780)

(Fig. 4)

Four nominal species were erected that we consider variant phenotypes of G. viridis: G. barsukovi Chernova 1999b, G. platycephalus Chernova 1999b, G. gracilis Chernova 2000, and G. obscurus Chernova 2000.

Gymnelus barsukovi, described from 10 types and 13 other specimens from the Laptev Sea eastward to the Beaufort Sea including the northern Bering Sea, was diagnosed in having a complete supratemporal commissure with three occipital pores, "numerous" vertebrae, a cylindrical body, a "wide" head, "small" eye, "large" mouth (probably upper jaw length), large size, and uniform dark coloration. Vertebral number greatly overlaps that of the other nominal forms (Table 6). We consider "cylindrical body" a non-character as it can be biased by compaction during preservation of these pliable fishes, or it may be a reflection of an individual's general robustness due to the larger size of this form. This also applies to head width, eye diameter, and upper jaw length (Table 6). We do not know the criteria of how Chernova (1999b:349) decided that individuals $156-187 \mathrm{~mm}$ were immature nor to which sex she was referring, but if females were examined they may simply have recently spawned. Gymnelus viridis females mature at about $110-120 \mathrm{~mm} \mathrm{SL}$, seen in a few mottled-band females by Anderson (1982:31) and shown here in Fig. 6.


FIGURE 6. Female G. viridis of the mottled-band, or "G. bilabrus," morphotype, $12-13 \mathrm{~cm}$ in length, guarding her 5-day-old eggs. The fish was collected at Resolute, Cornwallis Island, central Arctic Canada, and bred and spawned at the Vancouver Aquarium, British Columbia, Canada. Photograph by Danny Kent, Vancouver Aquarium.

Gymnelus platycephalus, described from seven types and four other specimens from the Bering and Chukchi seas, was diagnosed in having a complete supratemporal commissure with three occipital pores, a "low, flat" head, "high, laterally compressed" body, "small" mouth, "low" number of jaw teeth, a "large" gill opening, small size, and adult males "with a closed mouth, the lower jaw fits inside the upper jaw" (or mouth subterminal). We consider the overlapping head depth and mouth size (upper jaw length) nondiagnostic as is body depth except in the juveniles described (see below) as G. gracilis. A "low number" of jaw teeth reflects an ontogenetically variable character in many zoarcids including Gymnelus (e.g., Anderson 1982, 1989, 1995), impossible to compare to other nominal forms as sizes were not given. We deem the subterminal mouth of males as nondiagnostic since Chernova's female holotype shows a subterminal mouth as well (Chernova 1999b: fig. 8a). Coloration was described as including a "fine uniform netted-cellular pattern." None of the material in our fresh sample fits the description of this form, although Chernova (2009a,b; pers. comm.) identified several of the RUSALCA specimens and several from other recent collections as G. platycephalus that we identify as G. hemifasciatus. None of our $G$. hemifasciatus or $G$. viridis in the fresh sample had coloration even remotely like the only illustration of $G$. platycephalus with a pattern (Chernova 1999b: fig. 8b), a preservative-faded adult male collected 11 September 1950 (Anderson 1982:73). Anderson recorded for the 1982 review, but did not elaborate, three specimens as "spotted" or "speckled" that closely fit this morphotype. One from Somerset Island, Arctic Canada (NMC 760102), had a complete supratemporal commissure with three occipital pores, and two specimens, one from southwestern Greenland (ZMUC uncatalogued, "specimen 26") and one from Baffin Island, Canada (NMC 771501D), had incomplete commissures with two occipital pores.

Gymnelus gracilis, described from six juvenile specimens, 47-82 mm TL, from the Pacific Ocean off the coast of Kamchatka near Cape Afrika, was diagnosed in having an interrupted supratemporal commissure with two occipital pores, a "not" posteriorly shifted dorsal-fin origin, a very thin body, small head, few teeth, and coloration of "numerous (about 46) transverse dark bands." The character "not having a posteriorly shifted dorsal-fin origin" is incorrect (unless being compared to G. retrodorsalis), as the dorsal origin is placed above the middle of the pectoral fin (Chernova 2000: fig. 5) and there are two free dorsal pterygiophores, a variable character, with the fin origin associated with vertebrae 4-6 (see Anderson 1994:13). We regard the head length and width, and slender body as ontogenetic features, with the lower values typical of juvenile eelpouts.

Gymnelus obscurus, described from three northwestern Bering Sea young adults, was diagnosed in having a complete supratemporal commissure with three occipital pores, a "large" gill opening, "small" eye, wide interorbital distance, "intense" pigmentation (body uniformly dark), and adult males with a subterminal mouth. Gill opening length (in these short openings) overlaps only with G. barsukovi but as the sample size for all these nominal forms is so small, we regard this as insignificant (Table 6). Eye diameter greatly overlaps the other nominal forms. Chernova (2000: fig. 7) has accurately depicted sexual dimorphism in head width, to which interorbital width is redundant (Table 6). None of the specimens in our fresh sample matches the diagnosis or description.

Gymnelus bilabrus was originally described from three specimens (Andriashev 1937) and redescribed by Chernova (1998a) from the holotype and eight nontypes collected from the Bering and Beaufort seas. Andriashev (1937) mainly distinguished G. bilabrus from G. viridis by its adnate upper lip (hence the name), which Anderson (1982:32) found in four additional G. viridis specimens, its deeper and narrower head, which Anderson (1982) showed were sexually dimorphic in Gymnelus, and its "marbled" (mottled) coloration. However, Andriashev (1937) reported one specimen was not of the marbled pattern but had "wide brown bars" and "irregular small and large light, dark-edged spots" (translation).

Among important characters used by Chernova (1998a), G. bilabrus was a form with a complete supratemporal commissure (as were all her G. viridis morphotypes except the juveniles named G. gracilis), the anterior placement of the dorsal fin origin (but predorsal length greatly overlapping the other forms), and the sexually dimorphic head length not overlapping in the juvenile G. gracilis form (Table 6). Chernova (1998a) compared G. bilabrus (9 specimens) with G. viridis ( 17 specimens), an inadequate sample size we believe, especially when total ranges of values of both meristic (such as pectoral-fin rays) and morphometric characters (such as placement of the dorsal-fin origin and the dimorphic head width) are discussed. We refer to this phenotypic variant as the mottled-band form of G. viridis (Figs. 4, 6).
TABLE 6. Diagnostic and other identifying characters of nominal forms of Gymnelus viridis. Boldface type indicates values given as diagnostic; other values are from the descriptions of type and other specimens (Chernova 1998, 1999b, 2000).

| Character | G. barsukovi <br>  <br>  <br> $\mathrm{N}=10: 156-243 \mathrm{~mm} \mathrm{TL}$ | G. platycephalus <br> $\mathrm{N}=7: 85-143.5 \mathrm{~mm} \mathrm{TL}$ | G. gracilis <br> $\mathrm{N}=6: 47-87 \mathrm{~mm} \mathrm{TL}$ | G. obscurus <br> $\mathrm{N}=3: 122-156 \mathrm{~mm} \mathrm{TL}$ | $\mathrm{N}=9: 53-191 \mathrm{~mm}$ TL |
| :--- | :---: | :---: | :---: | :---: | :---: |

*Head pores with variation in suborbitals were given as diagnostic (Chernova 1998). As these are typical of all Gymnelus species, they are not repeated here. The diagnosis includes the holotype and eight non-types.


FIGURE 7. Summary neighbor-joining tree of COI sequence divergences between Gymnelus hemifasciatus, G. viridis, and another zoarcid, Lycodes seminudus. The Gymnelus samples include specimens from the Bering, East Siberian, Chukchi, and Beaufort seas. The L. seminudus sample includes material from the Greenland Sea and Baffin Bay as well as the Chukchi and Beaufort seas. Numbers at nodes represent bootstrap values. The number of specimens follows each species name. The scale bar represents K2P distance.

## Discussion

About $98 \%$ of the species included in the barcode reference library developed for studies of Pacific Arctic marine fishes (Mecklenburg et al. 2011) exhibited distinct barcodes, allowing their unambiguous identification. Most species showed little intraspecific variation (adjusted mean $=0.3 \%$ ), but a few species had multiple lineages showing much more divergence and likely include overlooked species. Such lineages in Icelus Krøyer 1845 and Mallotus Cuvier 1829 were highlighted (Mecklenburg et al. 2011). In contrast, a few other genera or species contained two or more putative species that lacked barcode divergence. Such cases could reflect hybridization, young taxa, or taxonomic over-splitting (Steinke et al. 2009b). In the earlier Gymnelus sample and the expanded fresh sample the specimens, which would have been identified as various species using Chernova's (1998a, 1999a,b) descriptions, fell into only two groups (G. hemifasciatus and G. viridis) that lacked in-group divergence, supporting the conclusion that Chernova's nominal forms represent a case of over-splitting. The complete lack of any coherence of specimens within the groups by geography, sex, or coloration disallows identifying the observed morphotypes as young taxa. Although the sequences in the G. hemifasciatus clade displayed a relatively high degree of variability, the variability is well within the range reported in prior barcoding studies on fishes (e.g., Steinke et al. 2009a; Ward et al. 2009). DNA sequences only from the Pacific Arctic were included in the present study and the G. viridis sample included only the mottled-band morphotype. The DNA sequences from G. viridis in the fresh sample of Pacific Arctic individuals are just $\sim 0.3 \%$ different from G. viridis taken off southern Greenland and the Gulf of St. Lawrence. In essence, although there is a difference between Pacific Arctic and Atlantic populations it is not enough to indicate they are different species (D. Steinke, Biodiversity Institute of Ontario, pers. comm. 2014).

Identifications made by experts of fish specimens which are nevertheless not compliant with barcoding expectations has been pointed to as the most difficult type of problem in assessing barcoding results (e.g., McCusker et al. 2012). Identifications of Gymnelus are an example of the problem. The results from COI sequencing of Gymnelus reflect the variability and lack of diagnostic strength of characters recently used (Chernova 1998a, 1999a, b, 2000) to describe species of Gymnelus. The barcodes do not support a set number of groups within each of the two species. The unreliability of coloration in particular for distinguishing species is further illustrated by the lack of genetic variability in the Lycodes seminudus sample at the barcode locus (Fig. 7) despite this species' rather significant variations in coloration. The $L$. seminudus sample includes uniformly white to black specimens from the continental slope off the Chukchi and Beaufort seas and distinctly banded specimens
from the deep fjords of northeastern Greenland and southern Baffin Bay off western Greenland and Baffin Island, Canada. Occurrence of one form is generally not exclusive of the other. Both forms have been taken in most regions (Jensen 1904), including the Pacific Arctic (Mecklenburg, unpubl.).

As we found with Gymnelus, Byrkjedal et al. (2014) evaluated three nominal species of fathead sculpin (Psychrolutidae: Cottunculus Collett 1875) and found that important morphological characters alone combined in a manner that made species identification impossible. Thus, they analyzed presumed diagnostic characters and compared morphological variation with that found in sequences of the COI gene. The sequences showed almost no variation despite the fact that the sequenced material spanned the whole range of character variation. Their analysis would not support recognition of more than one species.

Reviewing the identifications of Gymnelus specimens taken by the RUSALCA expeditions is important because of ongoing efforts to synthesize results of the program and because the situation illustrates problems with identifying Gymnelus material in the Pacific Arctic. In 2004 the RUSALCA collected 12 specimens of Gymnelus. The present authors examined them together a few days after the expedition and identified them as G. hemifasciatus and G. viridis. Examining them in 2005 and 2006, Chernova identified the G. hemifasciatus material as $G$. knipowitschi and G. platycephalus, and G. viridis as G. bilabrus. Reporting on the 2004 catch, the RUSALCA team compromised and referred to them as Gymnelus spp. in the text and included the alternate identifications in the captions to the photographs (Mecklenburg et al. 2007: fig. 3). Chernova (2009a,b; pers. comm.) identified the additional RUSALCA material from the expeditions in 2009 and 2012 ( 20 specimens) as G. platycephalus and G. knipowitschi and has relegated the one G. viridis caught in 2004 and another in 2012 to the status of "unidentified." The RUSALCA material identified as G. platycephalus by Chernova does not match the description (Chernova 1999b) of that nominal species, which, as we have shown, is a junior synonym of G. viridis. The specimens identified by Chernova in the recent sample as G. platycephalus are, according to our morphological analysis, examples of the typical form of $G$. hemifasciatus. None of the specimens taken by the nets on Pacific Arctic scientific cruises could be identified as G. platycephalus from the published description (Chernova 2000). Thus, Chernova's identifications conflict with her published descriptions. This has led to confusion among biologists identifying material from the RUSALCA and other Pacific Arctic surveys, as exemplified by the mistaken conclusion (Mecklenburg et al. 2011) that G. platycephalus is a synonym of G. hemifasciatus when it actually is a synonym of G. viridis.

The entire omission of G. viridis or one of its junior synonyms, such as G. bilabrus or G. barsukovi, from recent lists of Chukchi Sea fish species (Chernova 2009a,b; pers. comm.) is incomprehensible. The one specimen of $G$. viridis identified earlier by Chernova as G. bilabrus and later demoted to unidentified status is actually a good example of the bilabrus morphotype (see Mecklenburg et al. 2007: fig. 3). In fact, more than half the barcoded $G$. viridis specimens from our fresh sample (Fig. 1) are the bilabrus color morph of G. viridis, and most were taken in the Chukchi Sea. Moreover, Andriashev (1937) described G. bilabrus from Bering Strait material and reported (Andriashev 1952, 1954) G. viridis to be common in the Chukchi Sea.

The extreme rarity of catching the two morphotypes of G. hemifasciatus together suggests some ecological difference. Chernova (2000:8) suggested ecological differences among her new nominal species by stating that " $G$. knipowitschi prefers negative water temperatures and inhabits shallow areas up to 100 m (rarely to 175 m )," whereas " $G$. diporus was found under positive temperatures at depths from 123 to 200 m ." This difference could not be substantiated by only two specimens of G. diporus on which the description was based, and by bottom depths only to 100 m present in our Pacific Arctic sampling area. Besides, ecological differences recorded for collected specimens do not equate to validation of the presence of different species.

Anderson \& Fedorov (2004) suggested that some of the new nominal species of Gymnelus could be ecophenotypes of the previously described species, and there are strong indications of differences in the substrates, depths, and temperatures at which the G. hemifasciatus morphotypes in the fresh sample were taken. Both morphotypes of $G$. hemifasciatus were taken in a wide range of temperatures ( $-1.5^{\circ}$ to $10.5^{\circ} \mathrm{C}$, typical morphotype; $-1.8^{\circ}$ to $6.9^{\circ} \mathrm{C}$, solid-band morphotype [Table 4]), but the solid-band morphotype, which was most similar to the nominal form G. knipowitschi, was taken more often at negative temperatures $(48 \%$ of stations where it was caught) than the typical morphotype ( $14 \%$ ). It also often occurred at depths greater than $60 \mathrm{~m}(22 \%$ of stations where it was caught) whereas the typical form, except for one specimen, always occurred at depths of 60 m or less ( $94 \%$ of stations where caught). Observations of the substrate in net contents indicated that the typical morphotype of G. hemifasciatus was more often associated with harder and rougher substrate, including more gravel, shell hash,
cobble, and boulders, compared with the solid-band morphotype. The same impression was gained from plotting the catch localities on a map of the sediments in the region (Fig. 5), where it was seen that the solid-band morphotype of G. hemifasciatus occurred mostly on substrate with a high proportion of mud, including all mud or sandy mud with no gravel, whereas the typical or classic morphotype was found on sediments comprising all gravel or with a high proportion of gravel.

The discussion by Mallet (2008) of mosaic sympatry and maintenance of "ecotypes" (or ecophenotypes) in different habitats by their close proximity and opportunity for maintaining genetic continuity may have particular bearing for Gymnelus populations. Mosaic sympatry could explain the many variations within each species or morphotype. The morphotypes are regionally sympatric but are associated with different habitats within the regions. Many examples of such ecologically differentiated forms exist in nature; for instance, among fishes, freshwater and marine forms in sticklebacks (Gasterosteus aculeatus Linnaeus 1758) with differences in body armor (Bell \& Foster 1994) and adaptations to presence or absence of predators in guppies (Poecilia reticulata Peters 1859) reflected in head morphology and size at maturity (Torres-Dowdall et al. 2012). Gymnelus phenotypes may be another example. If corresponding genetic differences have arisen they are not detectable at the barcode locus.

To gain further understanding of the morphotypes within Gymnelus species it will be necessary to analyze catches for which environmental variables can be reliably quantified, rather than having to rely on voucher specimens which may not reflect actual numbers and proportions of species caught and which often have little environmental information associated with them. Moreover, the sparse ecological data that have been published may not always be accurate. For instance, although data were reported for G. viridis taken from the Beaufort and Chukchi seas by bottom trawl in 1977 (Frost \& Lowry 1983), examination of voucher specimens from 6 of the 12 stations at which G. viridis was reported to have been caught revealed they were misidentified G. hemifasciatus (Mecklenburg, unpubl.).

Several errors, exclusions, or misinterpretations among the new Russian papers require addressing here. Chernova (1998a) basically diagnosed Gymnelus viridis (17 specimens from eastern Canada and southwestern Greenland) as a form with relatively high vertebral counts (97-104), an interrupted supratemporal commissure, a relatively deep pectoral-fin base and other overlapping morphometric characters, and a monotonous coloration. Of the 59 monotone specimens studied by Anderson (1982) and our 2014 visit to the California Academy of Sciences, and identified as G. viridis, 22 ( $37.3 \%$ ) possessed an incomplete supratemporal commissure with two occipital pores and 37 ( $62.7 \%$ ) had complete commissures with three occipital pores ( $=G$. "barsukovi" or G. "obscurus" morphotypes depending on ontogenetic head and eye morphometry). Significantly, these morphotypes occurred together in four general localities: (1) southern Greenland (Julianehaab, Lindenowfjord); (2) eastern Arctic Canada off southern Baffin Island; (3) central Arctic Canada at Resolute, Cornwallis Island; and (4) the Beaufort Sea at Liverpool Bay, Canada. Two collections at Liverpool Bay (NMC 77-1259 and 77-1260) contained two monotone specimens each with a complete supratemporal commissure with three occipital pores, and one each with an incomplete commissure with two occipital pores. At Resolute two collections were made with the same conditions: NMC 65-355 is a monotone specimen with an incomplete supratemporal commissure and two occipital pores, and in NMC 62-399 are two monotone specimens with a complete commissure and three occipital pores. Among the material studied by Anderson (1982), Chernova (1998a:167) examined one specimen (ZMUC P76169) that both she and Anderson (1982) identified as G. viridis from southern Greenland but that Anderson found to have a complete supratemporal commissure with three occipital pores making it a G. "barsukovi" morphotype. Thus it appears that Chernova's (1998a) understanding of G. viridis omitted atypical natural variation owing to her small sample size and so relied on some selectivity. Other atypical conditions of characters were noted by Anderson (1982) and not mentioned by Chernova in her five papers. Of the 291 specimens Anderson (1982) examined of $G$. viridis, 6 ( $97-192 \mathrm{~mm} \mathrm{SL}$ ) lacked palatine teeth. They were from the Bering and Beaufort seas and central Arctic Canada. The interorbital pore was found in eight specimens of G. viridis (not seven as given by Anderson [1982:30]) from central and eastern Arctic Canada. Those two characters were accepted by Chernova (2000) in retaining the nominal genus Commandorella Taranetz \& Andriashev, 1935, which we reject. Absence of palatal teeth (either vomerine or palatine or both) is also characteristic of Lycodes cortezianus (Gilbert 1890), L. pacificus Collett 1879, and five species of Lycenchelys (Anderson 1994, 1995, 2006). Variation in other head pore counts in G. viridis is found in Anderson (1982:32). Data on branchiostegal ray condition was recorded for 204 of the 291 specimens. Ray number was usually six on each side $(6+6)$, but one specimen was found with formula $5+6$ and
two had $7+7$. Branchiostegal ray data were taken on 78 of the 113 specimens of $G$. hemifasciatus. The typical formula $6+6$ was found in 64 fish, and one had formula $6+7$, five had $5+6$, and eight had $5+5$.

In her synonymy of Gymnelus barsukovi Chernova (1999b:347) erroneously listed five ZIN lots (14146, $25332,34984,34988$, and 35423 ) studied by Anderson (1982) as well, to $G$. hemifasciatus. These in fact are specimens of G. viridis and were so listed by Anderson (1982:73).

Chernova (1999a) identified the specimen named Nemalycodes grigorjewi Herzenstein 1896 (ZIN 9688), from the Barents Sea as belonging to a species other than G. viridis, originally placed in synonymy with the latter by Knipowitsch (1901, 1908). The specimen is destroyed and unidentifiable, the description is nondiagnostic, there are three Gymnelus species in the Barents Sea (Anderson 1982: figs. 20, 25), and it was designated nomen dubium (Anderson 1982:56). However, Chernova (1999a:1), employing incorrect taxonomic procedure, placed the senior name N. grigorjewi as a synonym of her new nominal form G. knipowitschi. Near the end of this paper Chernova (1999a:7) states "... I tentatively consider N. grigorjewi as a synonym of the new species; at the same time, I believe that there is no basis yet to reinstate the specific name grigorjewi." This confusing taxonomic form appears, on the one hand, to make G. knipowitschi automatically a junior synonym of $N$. grigorjewi and, on the other hand, if Chernova does not want to "reinstate" the senior name, it would also appear that she may agree that the status of the name should remain a nomen dubium. We would avoid this kind of confusion and regard N. grigorjewi as a nomen dubium still.

Finally, three other nominal species of Gymnelus were described from western Russian Arctic seas and Svalbard: G. andersoni (Chernova 1998b) and G. esipovi and G. taeniatus (Chernova 1999b). As the areas and character evaluation are beyond the scope of this paper, we offer here just a few comments. All nominal forms have a retrograde dorsal-fin origin, thus resembling G. retrodorsalis Le Danois 1913, and similar meristics and morphometrics, but head canals and pore variation differ.

Gymnelus andersoni was described from 24 types, with 57 additional specimens listed ranging from the Barents to Laptev seas. It was diagnosed by its discontinuous suborbital (infraorbital) canal with few anterior and posterior pores, in conjunction with the supratemporal commissure "usually lacking" (Chernova 1998b:711). She found $7 \%$ of her sample ( 24 types and 57 others) possessed a partial supratemporal commissure with two lateral pores (pattern 1-0-1). Anderson's (1982) data concur and the second author's re-examination of his data found two lots (ZIN 14138: 5; 102-119 mm SL; and ZIN 14155: 2; 122, 124 mm SL ) with both the G. andersoni and typical G. retrodorsalis morphotypes from the same trawl haul. Chernova (1998b:714) listed only those specimens that fit her G. retrodorsalis diagnosis in that species' redescription and did not list the others which fit her G. andersoni. This again questions the diagnostic strength of the completeness of the supratemporal commissure (see above) and its variable pore distributions.

Gymnelus esipovi was described from nine types with four others listed ranging from Svalbard to the Kara Sea (Chernova 1999b). It was diagnosed by its discontinuous supratemporal commissure and its "comparatively high number of vertebrae," as well as the retrograde dorsal-fin origin and other characters we consider here (as with $G$. hemifasciatus and G. viridis above) as nondiagnostic: cylindrical body, large eye, numerous teeth, and small size. Vertebral counts for the type series are 98 (holotype) and 96-100 (paratypes) (Chernova 1999b:343). The second author's re-examination of his original (1982) data give vertebrae 95 (holotype) and 95-101 (paratypes) for seven specimens in three lots: ZIN 30558, ZIN 14139, and ZIN 29453. Comparing Chernova's nine specimens with Anderson's (1982) data on other Gymnelus specimens with the retrograde dorsal-fin origin and the incomplete supratemporal commissure, we find the vertebral count not especially "high" (see Anderson 1982: fig. 23). Thus, we consider G. esipovi a junior synonym of $G$. retrodorsalis Le Danois 1913. Further, the female paratype, 104 mm SL ( 106.5 mm TL) in ZIN 29453, has five occipital pores emanating from the supratemporal commissure instead of the usual two lateral ones, again diminishing the diagnostic strength of this feature.

Gymnelus taeniatus was described from a single juvenile female from Franz Josef Land (Chernova 1999b). It was diagnosed by its incomplete supratemporal commissure and six features we deem nondiagnostic. Because of its recent capture (collected 7 years before its description), especially of concern are the "high head and body" and very evident lateral line, conditions we know to significantly alter with time in preservative. Lacking additional comparative material from the area, this form appears to be a G. retrodorsalis with few (five) free dorsal pterygiophores (interneurals), not remarkable in other specimens from western Arctic Russia seen by Anderson (1982).

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