Comparative morphology of pre-extrusion larvae, *Sebastes mentella* and *Sebastes norvegicus* (Pisces: Sebastidae) in Icelandic waters

A. R. Vergara*†, Þ. Sigurðsson** and F. Saborido-Rey*
**Instituto de Investigaciones Marinas, IIM-CSIC, Calle Eduardo Cabello 6, 36208 Vigo,Spain*
*and **Marine Research Institute, Skulagotu 4, 101 Reykjavik, Iceland*
† Tel.: +34 986231930; email: albarvergara@iim.csic.es

Abstract

This study evaluated potential differences in morphology of unextruded larvae from *Sebastes mentella* and *Sebastes norvegicus* in Icelandic waters. Fifty-four larvae of each species were measured, and 18 measurements were recorded for each specimen (morphometric, meristic and pigmentation patterns). Pre-extrusion larvae of *S. norvegicus* were longer than those of *S. mentella*. Additionally, there were significant differences in morphometric, meristic and pigmentation characters between pre-extrusion larvae of these species. Pigmentation of *S. mentella* differed from that of *S. norvegicus* in several aspects. Dorsal and ventral body pigmentation tended to begin more posteriorly in *S. mentella*, therefore, the overall length of these pigmented areas tended to be longer in *S. norvegicus*.

Key words: meristics; morphology; North Atlantic Ocean; pigmentation; redfish.

INTRODUCTION

Redfish (genus *Sebastes*) are members of the species-rich family Sebastidae; in the North Atlantic Ocean *Sebastes* is represented by four species. North Atlantic redfish species are morphologically remarkably similar; therefore, their identification has been controversial and remains difficult because of overlapping meristic and other morphological characters (Ni, 1982; Power & Ni, 1985; Rubec *et al*., 1991; Saborido-Rey, 1994; Pampoulie & Daníelsdóttir, 2008).

Sebastes are viviparous, the eggs being fertilized internally (Saborido-Rey *et al*., 2004), and spawning is characterized by the parturition or extrusion of between 40 000 and 400 000 pelagic larvae annually (Magnússon & Magnússon, 1995). Embryonic development within gonads of individual *Sebastes* is synchronous. After parturition, *Sebastes* larvae lead a pelagic existence of varying duration, and are one of the most abundant fish larvae in the Irminger Sea south-west of Iceland and off the Flemish Cap (47º N; 45º W) throughout all years and seasons surveyed (Serebryakov *et al*., 1984). Discrimination of species among redfish larvae is complex because the morphological characters used for adults and juveniles cannot be used for identifying species during the larval stages (Penney, 1987). Also, none of the characters studied for larvae has given clear separation of species (Moser *et al*., 1977; Serebryakov, 1982).

The ability to identify larvae of *Sebastes* has increased dramatically in recent years. They are easily recognized as members of *Sebastes* (Moser *et al*., 1977; Matarese *et al*., 1989; Moser, 1996), but the early stages have not yet developed species-distinguishing characteristics and incorrect identifications have complicated descriptions of larvae of *Sebastes* from the North Atlantic Ocean (Magnússon, 1981; Penney, 1985; Kendall, 1991; Moser & Boehlert, 1991; Gray *et al*., 2006).

Thus, a detailed examination of the morphology of unextruded larvae of *Sebastes mentella* Travin 1951 and *Sebastes norvegicus* (Ascanius 1772) [regarded as a name valid by some authors as much as *Sebastes marinus* (L. 1758), Eschmeyer (2012)] was carried out. The characters (morphometrics, meristic and pigmentation variables) were examined as potential criteria for species identification, based on a comparative morphology of unextruded larvae from females in the area of south-west Iceland.

MATERIALS AND METHODS

Sampling locations covered mainly the fishing grounds around Iceland. The collection of samples followed general agreement among researchers involved in the REDFISH project (unpubl. data) during 2000 and 2002. In this project, characteristics of gas-bladder musculature were used to identify adults of *S. mentella* and *S. norvegicus* (Saborido-Rey, 1994). Adult female *S. mentella* and *S. norvegicus* containing larvae were collected off south-west Iceland by stratified random bottom trawling from research surveys. The sampling strategy was to process specimens >25 cm total length (L_T), because smaller specimens are considered to be immature (Saborido-Rey, 1994). Gonads were removed, placed in microperforated plastic bags and then placed in a plastic barrel with 3,6% buffered formaldehyde.

Late-stage pre-extrusion larvae of both species, with yolk sacs fully reabsorbed or nearly so, were used in a comparative morphological analysis. Only fully developed larvae were used to ensure that interspecific differences were not affected by variations in developmental stage. Because of this requirement, only 7 of 103 ovaries showed suitable late-stage pre-extrusion larvae (7%). Three female *S. norvegicus* were collected in 2000 and four female *S. mentella* were collected in 2002.

All other gonads of collected *Sebastes* either contained unhatched eggs or hatched larvae in early developmental stages (93%). The percentage of suitable larvae that were collected from the gonads and in good condition to be photographed and measured was low because of prolonged preservation. Consequently, only randomly selected samples of 54 larvae were measured from each species.

Several images were taken of each larva with a video camera connected to a stereo microscope. All photographed larvae were measured using the software QWin (Leica Imaging Systems; www.leica-microsystems.com). A total of five morphometric measurements were taken (Fig. 1), comprising: (1) standard length (L_S), the distance along the midline of the body from the tip of the snout to the end of the urostyle; (2) pre-anal length (L_{PRA}), the distance along the midline of the body from the tip of the snout to the anus; (3) head depth (H_D), along a vertical line through the centre of the eye; (4) body depth at the anus (B_D) and (5) eye diameter (D_E), maximum horizontal eye diameter.

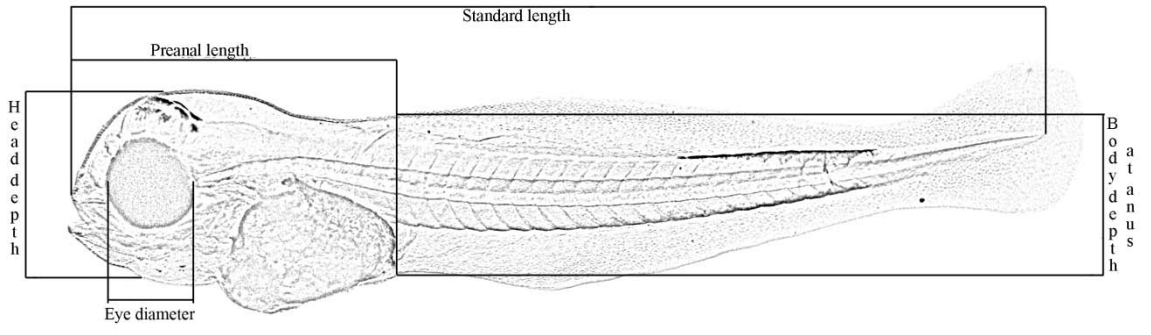

Fig. 1. *Sebastes* spp. larva showing base points for measurements.

Three meristic measurements were recorded, comprising: total body myomeres (*M*), number of pre-anal myomeres (M_{PRA}) and number of postanal myomeres (M_{POA}). Furthermore, a total of 10 pigmentation patterns were recorded, comprising: postanal myomere on which the anteriormost melanophore on the dorsum begins ($P_{D\text{-}B}$) and ends ($P_{D\text{-}E}$); postanal myomere on which the anteriormost melanophore on the ventrum begins ($P_{V\text{-}B}$) and ends ($P_{V\text{-}E}$); total length, in myomeres, of the dorsal ($P_{D\text{-}T}$) and the ventral body melanophore line ($P_{V\text{-}T}$) and melanophore pattern located on the ventrum (P_V), at the nape (P_N), on the dorsum (P_D) and on top of the brain (P_H, see Table I).

Table I. Pigmentation patterns of pre-extrusion larvae of *Sebastes mentella* and *Sebastes norvegicus.*

Melanophores	**1**	**2**	**3**	**4**
On the ventrum M_V	Expanded, separate	Expanded, not separate	Expanded, separate + not separate	Expanded + contracted
At the nape M_N	Single expanded	One or more contracted	No pigment	No pigment
On the dorsum M_D	Line for more than half the total extent of the melanophore pattern	Line less than half the total extent of the melanophore pattern	No pigment	No pigment
On top of brain M_H	Distinct merging into a solid cap	All separate	No pigment	No pigment

Statistical Analyses

Mean values of L_S and mass did not show any significant difference between the females from which pre-extruded larvae were extracted and selected (both $P > 0{,}5$); for this reason, the maternal influences [age, size and condition of females on egg and larval quality (Sogard *et al*., 2008)] were not considered in this study.

The means of each variable between species were compared by *t* -test. This study used a *t* -Test for unequal variances (the homogeneity assumption could have been violated, indicated by the Levene test), because the results between equal variances and unequal variances were practically indistinguishable (Zar, 1999).

Discriminant analysis (Bookstein, 1991) was used to identify characters with the best potential for future classification of planktonic larvae (classification power of each morphological character, using stepwise insertion of variables). Stepwise insertions of variables were used to minimize the sum of unexplained variance for all groups and to eliminate redundant variables. Three different discriminant functions were determined: (1) only morphometric variables were used, (2) only meristic and pigmentation patterns were used and (3) all variables and measurements were combined. Although discriminant analysis assumes that the discriminating variables have normal distributions, in practice, strict adherence to the technique is not required (Mardia *et al*., 1992). Statistical analyses were carried out using IBM SPSS Statistics 19 for Windows (www-01.ibm.com/software/analytics/spss/products/statistics).

RESULTS

Larvae collected from adult *S. mentella* were larger than those from *S. norvegicus*; mean L_S was significantly different (Table II). Similarly, body and head depth, eye diameter and pre-anal length were larger in *S. mentella*. Therefore, larvae of *S. mentella* appeared deeper bodied than those of *S. norvegicus* (Fig. 2). The ventral and dorsal rows of postanal melanophores, however, were longer in *S. norvegicus* (Table III).

Meristic and pigmentation variables were found to have significantly different means, except for the postanal myomere on which the posteriormost melanophore on the dorsum ends ($M_{D\text{-}E}$; Table III). Larvae of *S. norvegicus* tended to have more total body myomeres as well as more postanal and pre-anal myomeres than *S. mentella* [Fig. 3(a)]. The caudal (posterior) ends of the pigment pattern on the dorsum ($M_{D\text{-}E}$) and ventrum ($M_{V\text{-}E}$) were similar for most larvae of both species [Fig. 3(b), (c)].

Table II. Morphometric measurements of pre-extrusion larvae of *Sebastes mentella* and *Sebastes norvegicus.*

	Mean ± S.E. L_S (mm)	Mean ± S.E B_D (mm)	Mean ± S.E L_{PRA}(%)	Mean ± S.E H_D (mm)	Mean ± S.E D_E (mm)
S. mentella	7.43 ± 0.04	1.33 ± 0.01	34	1.44 ± 0.01	0.64 ± 0.007
S. norvegicus	6.18 ± 0.03	1.08 ± 0.01	33	1.20 ± 0.01	0.55 ± 0.005
t-Test	23.24	11.43	18.13	15.48	10.76
P	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05

L_S, standard length; B_D, body depth; L_{PRA}, pre-anal length; H_D, head depth; D_E, eye diameter.

Table III. Comparison of means of all meristic and pigmentation variables for *Sebastes mentella* and *Sebastes norvegicus.*

	M_{PRA}	M_{POA}	M	$P_{D\text{-}B}$	$P_{D\text{-}E}$	$P_{V\text{-}B}$	$P_{V\text{-}E}$	$P_{D\text{-}T}$	$P_{V\text{-}T}$	P_V	P_N	P_D	P_H
S. mentella	7.11	23.20	30.31	14.43	21.67	7.74	21.89	8.26	15.22	3.24	1.83	1.09	1.5
S. norvegicus	7.68	23.96	31.64	9.89	21.45	4.79	22.23	12.57	18.43	2.00	3.00	1.00	2.00
t-test	-7.30	-7.03	-11.75	18.42	1.34	13.65	-2.10	-15.85	-12.71	21.13	-8.70	2.33	-7.28
P	< 0.05	< 0.05	< 0.05	< 0.05	>0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05

M, total body myomeres; M_{PRA}, number of pre-anal myomeres; M_{POA}, number of postanal myomeres; $P_{D\text{-}B}$, postanal myomere on which the anteriormost melanophore on the dorsum begins; $P_{D\text{-}E}$, postanal myomere on which the anteriormost melanophore on the dorsum ends; $P_{V\text{-}B}$, postanal myomere on which the anteriormost melanophore on the ventrum begins; $P_{V\text{-}E}$, postanal myomere on which the anteriormost melanophore on the ventrum ends; $P_{D\text{-}T}$, total length, in myomeres, of the dorsal body melanophore line; $P_{V\text{-}T}$, total length, in myomeres, of the ventral body melanophore line; P_V, melanophore pattern located on the ventrum; P_N, melanophore pattern located at the nape; P_D, melanophore pattern located on the dorsum; P_H, melanophore pattern located on top of the brain.

Pigmentation patterns differed between species. The most noticeable difference was the line of melanophores on the ventrum; in *S. norvegicus* these were closely spaced dots (expanded, not separate). Also, in *S. norvegicus* the start of the pigment pattern on the dorsum [$P_{D\text{-}B}$; Fig. 3(b)] and ventrum [$P_{V\text{-}B}$; Fig. 3(c)] tended to be more anterior than in *S. mentella*. The lengths of the dorsal and ventral melanophore patterns ($P_{D\text{-}T}$ and $P_{V\text{-}T}$) for *S. mentella* were shorter, when measured in

myomere units, than the corresponding patterns in *S. norvegicus* [Fig. 3(b), (c)]. Neither species had subcaudal melanophores.

Fig. 2. Pre-extruded larvae: (a) *Sebastes mentella* (7,6mm standard length, L_S) and (b) *Sebastes norvegicus* (6,3mm L_S).

A discriminant analysis performed on the morphometric, meristic and pigmentation variables of pre-extrusion larvae of *S. mentella* and *S. norvegicus* showed that it is possible to separate the two species. The discriminant analysis explained 100% of the variance and discriminates between the species: 97,8% of pre-extrusion larvae were correctly classified according to their morphometric variables, 100% of preextrusion larvae were correctly classified according to their meristic and pigmentation traits and all variables combined. The difference in the centroids of morphological, meristic and pigmentation traits was significant (see Wilk's λ and χ^2 in Table IV).

Nevertheless, none of the characters would, individually, allow a positive identification at the species level. Pooling characters into discriminant functions improved the usefulness of the individual characters. When only morphometric variables were used, pre-extrusion larvae mainly differed between species in L_S, eye diameter and head depth (Table IV); most of the classification power of this function relied on these three variables. None of the other morphometric traits increased the number of cases correctly classified. When only meristic and pigmentation variables were used, the resultant discriminant function included six useful variables (Table IV). The variables included characteristics of pigmentation patterns on the ventrum, dorsum and head; in *S. norvegicus* the ventral pigmentation was mainly represented by small expanded melanophores, whereas *S. mentella* had larger expanded and contracted melanophores on the ventrum (Table III). The third discriminant function, based on all variables combined, identified five useful variables (Table IV). Therefore, discriminant analysis described differences in morphological, meristic and pigmentation traits.

DISCUSSION

The results of this study are compatible with those of Magnússon (1981), who reported a definite size difference between larvae of *S. norvegicus* and *S. mentella* at the time of extrusion.

Additionally, this study reveals significant morphometric, meristic and pigmentation differences between pre-extrusion larvae of *S. mentella* and *S. norvegicus* in Icelandic waters (Table III). Morphologically, pre-extrusion larvae of *S. mentella* can be characterized as deeper bodied than those of *S. norvegicus*, as evidenced by their relatively greater L_S, body depth and head depth (Table II). The larvae of *Sebastes mentella* have larger eye diameters and greater pre-anal lengths than those of *S. norvegicus*. This observation, together with the findings of Magnússon & Magnússon (1977), suggests that larvae of *S. mentella* are larger at extrusion than those of *S. norvegicus*.

Table IV. Canonical discriminant functions, eigenvalues, % of variance, canonical correlation, Wilk's λ and χ^2 for the discriminant analysis of characteristics of pre-extruded larvae of *Sebastes mentella* and *Sebastes norvegicus*. Only largest coefficients for each function are shown.

	Discriminant function		
	Morphometrics	Meristic and pigmentation	All variables
L_S	0.781		0.585
H_D	0.366		0.372
D_E	0.348		
P_D		0.305	
P_V		-0.883	0.765
P_H		0.578	-0.367
$P_{D\text{-}B}$		-0.547	
$P_{V\text{-}T}$		0.413	-0.636
M_{POA}		0.398	
Eigenvalue	7.093	15.271	19.455
% of variance	100	100	100
Cannonical correlation	0.936	0.969	0.975
Wilk`s lambda	0.124	0.061	0.049
χ^{2*}	201.78	284.52	288.24

L_S, standard length; H_D, head depth; D_E, eye diameter; P_V, melanophore pattern located on the ventrum; P_D, melanophore pattern located on the dorsum; P_H, melanophore pattern located on top of the brain; $P_{D\text{-}B}$, postanal myomere on which the anteriormost melanophore on the dorsum begins; $P_{V\text{-}T}$, the ventral body melanophore line; M_{POA}, number of postanal myomeres.
*P <0,05.

In terms of meristics, Icelandic populations of *S. mentella* larvae have 29–32 total body myomeres, whereas *S. norvegicus* have 30–33. Despite overlap, the range of total myomeres found in this work for *S. mentella* and *S. norvegicus* is greater than the range reported by other authors (Table V). Evidently, there is geographic variation in these meristics, but this might also be compounded by differing methods of identification (Penney, 1985). On the other hand, the results of this study of frequency distribution of body myomeres of melanophore patterns on the dorsum and on the ventrum for *S. mentella* are compatible with those of Penney (1985) (see Fig. 3).

Pigmentation of *S. mentella* differs from that of *S. norvegicus* in several aspects. The dorsal and ventral body pigmentation tends to begin more posteriorly in *S. mentella* than in *S. norvegicus*; therefore, these pigmented areas tend to be longer overall in *S. norvegicus*. Moser *et al*. (1977) and Fahay (1983) reported for *S. norvegicus* the total number of melanophores in the dorsal and ventral row from 8 to 21 and 11 to 24, respectively; in samples of pre-extrusion larvae of *S. norvegicus*

from Icelandic waters, the frequency distributions of these characters have a shorter range (one melanophore per one myomere, Fig. 3).

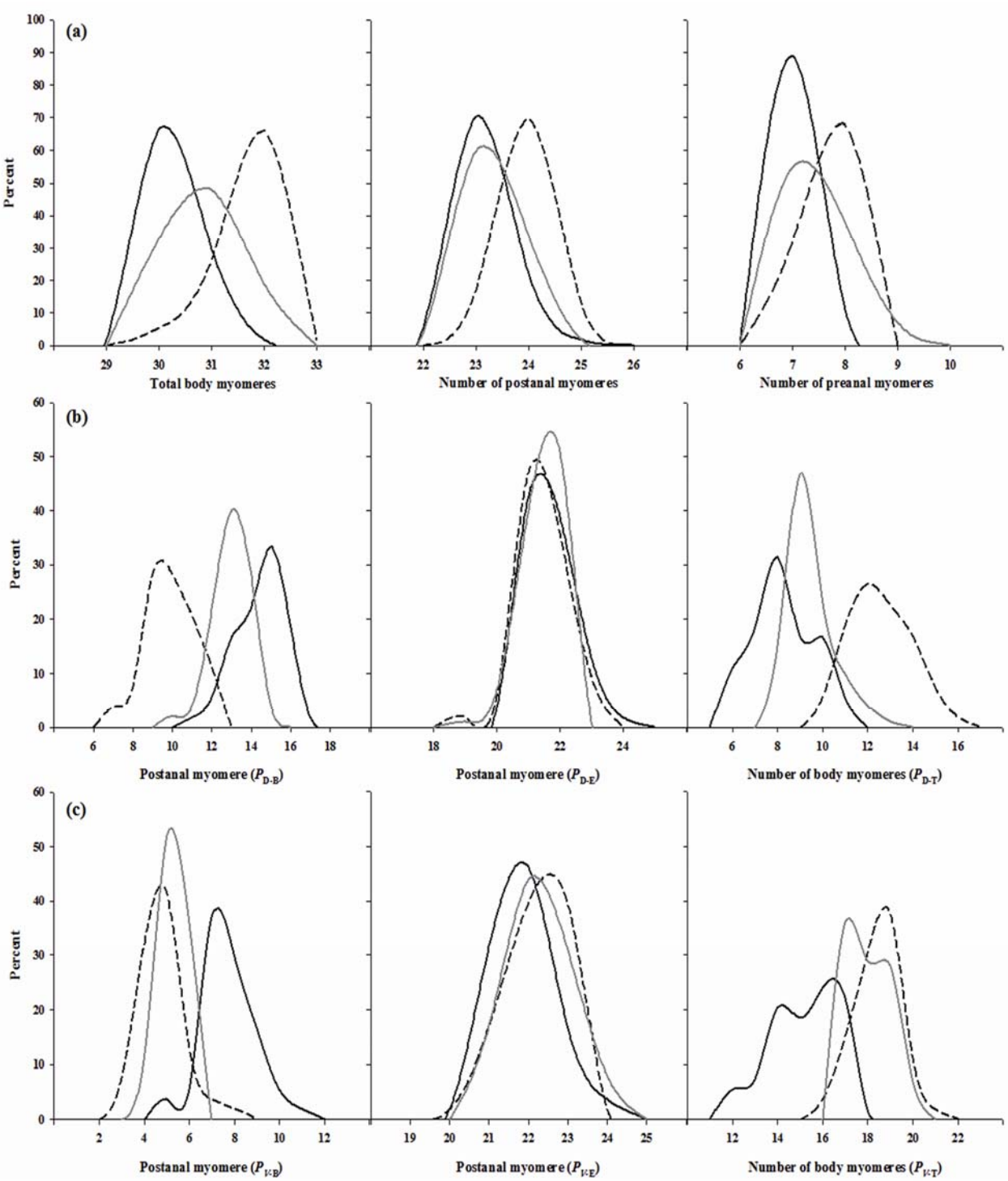

Fig. 3. Pre-extruded larvae of *Sebastes mentella* and *Sebastes norvegicus*. Frequency distributions of (a) body myomeres, (b) melanophore patterns on the dorsum and (c) melanophore patterns on the ventrum [---, *S. norvegicus*; ___, *S. mentella*; ___, *S. mentella* (Penney, 1985)].

The presence of one or more subcaudal melanophores in some of the larvae of *S. mentella* from the Labrador and Newfoundland areas distinguishes them in this respect from the basic *S. mentella* stocks off the region extending from south-west Iceland and south of Greenland to north of Flemish

Cap, whose larvae were reported to have no subcaudal melanophores (Kotthaus, 1961; Henderson, 1965; Bainbridge & Cooper, 1971; Templeman, 1980; Serebryakov, 1982). In this study, pre-extrusion larvae of both *S. mentella* and *S. norvegicus* lack subcaudal melanophores. It is possible that the presence of melanophores in some of the larvae of *S. mentella* from the North American shelf and slope areas indicates interbreeding, presumably with *Sebastes fasciatus* Storer 1854 (Templeman, 1980). The larvae of *S. norvegicus* in some samples from the North American shelf areas possess more subcaudal melanophores than those from other North Atlantic Ocean regions (Templeman, 1980).

Table V. Standard length (L_S) and number of body myomeres found in pre-extrusion larvae of *Sebastes mentella* and *Sebastes norvegicus.*

	Hatching (L_S mm)	Number of body myomeres	Locality	Reference
S. mentella	7-9			Barsukov *et al*. (1985)
	7.0-11	28-31	Northern part of the north-west Atlantic Ocean	Serebryakov (1982)
		30-32	Western North Atlantic Ocean	Fahay (1983)
		30-32	South coast of Newfoundland	Penney (1985)
	6.8-8.1	29-32	Iceland	This work
S. norvegicus	6-8			Barsukov *et al.* (1985)
	6.5-7.3			Colton & Marak (1969)
	6.7-7.2			Moser *et al.* (1977)
		28-30	Northern part of the north-west Atlantic Ocean	Serebryakov (1982)
		30-32	Western North Atlantic Ocean	Fahay (1983)
	5.8-6.6	30-33	Iceland	This work

The presence, in Icelandic waters and other parts of the North Atlantic Ocean, of three species of *Sebastes* (*S. mentella, S. norvegicus* and *S. fasciatus*), of which the two sharp-beaked *mentella*-type species (*S. mentella* and *S. norvegicus*) are similar in appearance and usually more numerous, offers obvious challenges for management, as these species are now treated as a single group for management purposes. Consequently, the diagnosis of the species is still very difficult (Barsukov *et al*., 1985; Sévigny *et al*., 2000). Nevertheless, identifications of any specimens may be possible with genetic methods (*e.g*. DNA sequence data; Rocha-Olivares, 1998; Sakuma *et al*., 2005). *Sebastes mentella* and *S. norvegicus* tend to live at different depths, release larvae at different times, differ in size at first reproduction and presumably differ in growth rates, with potential differences in the nursery areas inhabited by the juveniles. The larvae are affected differently by currents, temperature conditions and plankton blooms, with consequent effects on larval growth and mortality (Templeman, 1980). The differences observed in this study, between pre-extruded larvae of *S. mentella* and *S. norvegicus*, could be owing to spatial population differences in pigment expression at the genetic level, or spatial differences in environmental factors, such as temperature, affecting larval development. Such variability in environmental conditions could also possibly affect larval fish development, which might be expressed in pigment variability (Sakuma *et al*., 2005).

The resultant 98,9–100% correct classification according to morphometric, meristic and pigmentation variables reported in this study, of pre-extruded larvae, is encouraging, particularly in its potential applicability to new research on early life history of these species. Development of discriminant functions based on characteristics of pre-extrusion larvae of known species, and subsequent extrapolation to young planktonic larvae may finally prove to be an effective identification tool for larval *Sebastes* in the North Atlantic Ocean.

Accurate identification of larval and pelagic juvenile *Sebastes* is important for their use in biomass estimates and recruitment studies. Very few *Sebastes* species, however, can be accurately identified throughout their entire early life history based on morphological, meristic and pigment characters alone. Spatial variability in pigment patterns is difficult to account for because of the lack of complete descriptions of early life history for many species of *Sebastes* (Kendall, 1991; Moser, 1996), and should be taken into consideration when examining larvae from different geographic locations. The results presented in this article are a first step to demonstrate a new approach to determining the differences between pre-extruded larvae of *S. norvegicus* and *S. mentella* in Icelandic waters and help to complete the descriptions of their early life history. Despite the potential constraints noted above, the type of analysis presented here seems promising.

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