Quantitative morphological variation in *Sagitta setosa* Müller, 1847 (Chaetognatha) and two closely related taxa

Katja T.C.A. Peijnenburg[1] and Annelies C. Pierrot-Bults[2]

[1]*Institute for Biodiversity and Ecosystem Dynamics, Faculty of Science, University of Amsterdam, P.O. 94062, 1090 GB Amsterdam, The Netherlands, e-mail: peijnenburg@science.uva.nl;* [2]*Zoological Museum Amsterdam, University of Amsterdam, Mauritskade 57, 1092 AD Amsterdam, The Netherlands, e-mail: pierrot@science.uva.nl*

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Abstract

This paper reviews the quantitative morphological variation published for *Sagitta setosa* Müller, 1847 and two other species described within the *S. setosa*-complex, viz., *S. euxina* Moltschanoff, 1909 from the Black Sea, and *S. batava* Biersteker & Van der Spoel, 1966 from the Scheldt Estuary (Netherlands). Data on total (body) length, caudal length, numbers of teeth and hooks, ovary length, and dimensions of fins are compared between these three taxa. Additionally, samples from the North Sea, Mediterranean, and Black Sea are compared to look for geographic differences. Specimens from the Mediterranean were smallest with relatively long caudal segments, and few teeth and hooks, whereas specimens from the Black Sea were largest with relatively short caudal segments and many teeth and hooks. Specimens from the North Sea were intermediate with regards to these characters, but ranges overlapped and there were no obvious differences in allometry. These differences may be ecophenotypic, as the warm and salty Mediterranean Sea and cool and brackish Black Sea are at opposite ends of the environmental spectrum. The dimensions related to the fins showed clearer distinction between samples from different geographical areas, and slight differences in allometry. However, few data were available and little is known about the variance within each geographical area. We found more variation in quantitative characters within *S. setosa* from different parts of its range than between *S. setosa* and either *S. batava*, or *S. euxina*. *Sagitta batava* conformed to *S. setosa* in terms of all the morphological characters considered. The data for *S. setosa* derived from Biersteker & Van der Spoel (1966) were atypical and were found to be based on misidentifications of *S. elegans*. Therefore, we concluded that *S. batava* cannot be considered a separate taxon. For *S. euxina*, the data were inconclusive. Quantitative data completely overlapped between *S. setosa* from the Black Sea and *S. euxina*, but few data of *S. setosa* from the Black Sea were available. Because samples were either composed entirely of *S. setosa* or *S. euxina* (depending on sampling season and depth) and there was a large variation in body lengths and relative ovary lengths, we consider it possible that these samples represent seasonal variants of one and the same species.

Contents

Introduction

The first drawing of a chaetognath appears to be that of *Sagitta setosa* drawn by Martinus Slabber (1778) who had fished these so-called 'remarkable sea-worms' or '*Sagitta*' out of the inlet waters of Zeeland (Netherlands) on the 10th of July 1768. He could probably not have imagined that over 200 years later there would still be active discussion about the taxonomy of 'his' worms, both in relation to other animal phyla, as well as within the group itself.

Chaetognaths, arrow worms, comprise a small marine phylum of carnivorous invertebrates, ranging in size from 2-120 mm (Bone et al., 1991). About 80 planktonic and 20 benthic species are currently known (Pierrot-Bults, 1997). A striking feature of the phylum is the almost invariable body plan, even though extant species have a wide distribution and depth range. Chaetognaths appear to be morphologically constrained by their environment and mode

of life. This conservatism in body shape, however, may hide cryptic species, so that detailed analyses of morphological and genetic variation may uncover more species than are currently recognized (Pierrot-Bults & Van der Spoel, 2003). Particularly in the neritic environment, which is more heterogeneous than the oceanic environment and where species are more subject to geographic isolation, differentiation is expected to be greater (Pierrot-Bults, 1997).

Sagitta setosa is a neritic species with a disjunct distribution over the continental shelf areas in the northeast Atlantic, Mediterranean, and Black Sea (reviewed in Furnestin, 1979). The species is typically associated with waters of reduced salinities in the respective areas (Furnestin, 1938; Fraser, 1949; Furnestin, 1958b; Hecq et al., 1975), but it can tolerate a wide range of environmental conditions (Table 1). Morphological variation has been reported within *S. setosa* from different areas (Ritter-Záhony, 1911a; Furnestin, 1958a; 1958b; Dallot, 1978; Andréu and Reira, 1990); even so, the species can be clearly distinguished from all other species (Pierrot-Bults & Chidgey, 1988; Fig. 1). Two other species, closely related to *S. setosa*, have been described, viz., *S. euxina* Moltschanoff, 1909 from the Black Sea and *S. batava* Biersteker and van der Spoel, 1966 from the Scheldt Estuary and the southern North Sea. The taxonomic status of these species remains unclear. Furnestin (1958b) considered *S. euxina* to be a larger variety of *S. setosa* while Winogradow (1933), Elian (1960), and Alvariño (1965) considered it a valid species. In the most recent revision of the phylum (Bieri, 1991), *S. euxina* is considered to be an intraspecific variety of *S. setosa*, but *S. batava* is placed into a different genus from *S. setosa*, namely *Mesosagitta* (*S. setosa* is placed in the new genus *Parasagitta*, however this nomenclature is not widely accepted and therefore not used here). A pilot study at the Zoological Museum in Amsterdam in 1969 revealed that the range of variation in caudal length of *S. batava*, the character most clearly distinguishing *S. setosa* from *S. batava* (Biersteker & Van der Spoel, 1966), falls within the known variation described for *S. setosa* (unpublished data). Consequently, *S. batava* was considered to be an intraspecific variant of *S. setosa* by Pierrot-Bults (1976) and Van der Spoel & Heyman (1983). Pierrot-Bults

Table 1. Ranges of salinity and average sea surface temperatures (for winter and summer, respectively) in the three major distribution areas of *Sagitta setosa* (based on data from Zenkevitch, 1963; Becker & Loewe, 2000; Walday & Kroglund, 2002; Zenetos et al., 2002, and Zaitsev et al., 2002), and maximum total length and minimum length of mature *S. setosa* as reported by Furnestin (1958b).

	Salinity (‰)	Temperature (°C)	Max. total length (mm)	Appearance of mature individuals (mm)
Mediterranean	36-39	14-23	12	8
North Sea	25-35	6-15	14	10
Black Sea	<10-24	7-14	19	13

(1976) suggested that *S. setosa*, *S. euxina*, and *S. batava* comprise a single complex that needs further study. This paper reviews the available literature to compare the variation in morphological characters (mostly quantitative) of these three taxa from different localities. The aims of this paper are to provide an overview of the morphological variation of *S. setosa* within its distribution range and to resolve the taxonomic status of *S. batava* and *S. euxina*.

Material and methods

Quantitative morphological data from three taxa and three European basins, using morphological characteristics depicted in Figure 1, were obtained from ten different studies (Table 2). Total length (T.L.) and length of the caudal segment (C.L.) were recorded in all studies. However, data on ovary length (O.L.), relative positions of the fins (distance between ventral ganglion and anterior fin, V.G-A.F., and seminal vesicles and caudal fin, S.V.-C.F.) and numbers of teeth and hooks were not always recorded (Table 2). All lengths of morphological structures were expressed as percentages of total length for a certain length class. Therefore, two interdependent variables are being compared and correlations may consequently be exaggerated or spurious (Bookstein et al., 1985). Other studies on morphological variation within *S. setosa* (Dallot, 1978; Andréu & Riera, 1990) reported only summary
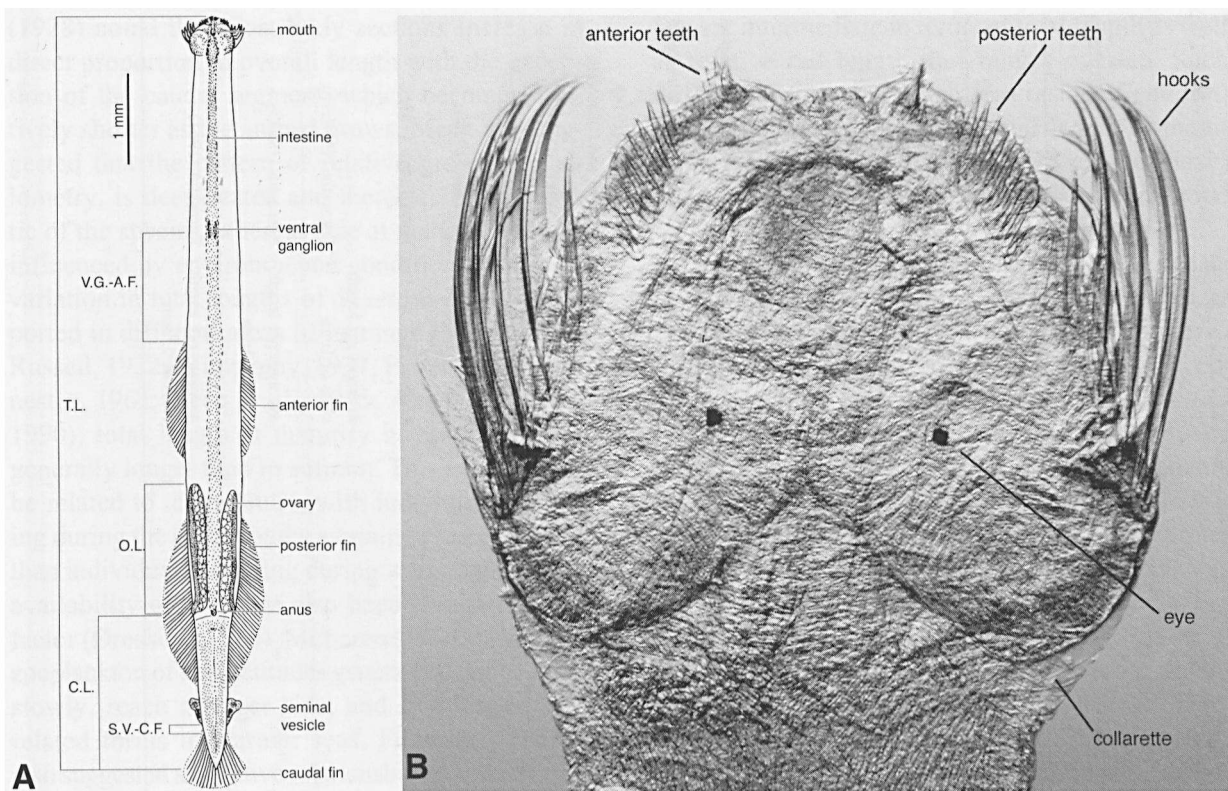
Fig. 1. Morphology of *Sagitta setosa.* (A) Ventral view of the body with recorded morphological measurements indicated as T.L. (total length), C.L. (caudal length), O.L. (ovary length), V.G.-A.F. (distance between ventral ganglion and anterior fin), and S.V.-C.F. (distance between seminal vesicles and caudal fin; drawing from Pierrot-Bults & Chidgey 1988). (B) Dorsal view of a head of *S. setosa* from the Celtic Sea (northeast Atlantic), with different types of head armature and other characters indicated.

statistics and could therefore not be included herein. Different data formats were used: ranges per length class, averages per length class, and individual data (Table 2). The individual data format is the most accurate, but unfortunately original datasets could not be retrieved. Therefore, it was not possible to carry out any statistical tests on the data. Instead, we plotted all available data for a certain taxon or geographical area and connected the extreme data points to represent the range of morphological variation reported. For compárison, individual data or averages per length class of specific studies not included in the ranges, were plotted on top of these ranges. Preservation methods of the samples were not always reported. Ritter-Záhony (1911a) used alcohol-preserved specimens for his measurements and Baldasseroni (1914), Scaccini & Ghirardelli

(1941), and Ghirardelli (1952) used formalin-preserved samples and/ or living material. Different preservation techniques may result in different levels of shrinkage of chaetognaths (Conway & Robins 1991) and may therefore be a source of error in this comparative study. Additional information on sampling localities, dates, and numbers of specimens analysed (if reported) are indicated in Table 2.

Results and discussion

Total length and caudal length

An increase in length with progressing stages of maturity is generally observed in chaetognaths. Meek

Table 2. Sources of quantitative morphological data for the three taxa *Sagitta setosa*, *S. batava*, and *S. euxina* that were summarized in the figures of this paper. + indicates a character that was recorded for most specimens and - indicates a character that was not recorded (for abbreviations see Material and Methods and Fig. 1).

Basin	Taxon	Sampling area	Sampling season	Number analysed	T.L.	C.L.	O.L.	V.G.-A.F.	S.V.-C.F.	Teeth	Hooks	Data format	Reference
N.E. Atlantic	'setosa'	North Sea (throughout)	Nov.-Feb.-March	?	+	+	-	-	-	+	+	ranges	Ritter-Záhony (1911a)
	'setosa'	North Sea (throughout)	?	?	+	+	-	-	-	+	+	ranges	Ritter-Záhony (1911b)
	'setosa'	S. North Sea (English Channel)	Oct.-Nov.	121	+	+	+	+	+	-	.	averages per length class of 1mm	Furnestin (1958b)
	'setosa'	Central North Sea (Flamborough)	Oct.	17	+	+	-	-	-	+	+	individual data	Biersteker and Van der Spoel (1966)
	'batava'	Scheldt Estuary and S. North Sea	all year	16	+	+	-	-	-	+	+	individual data	Biersteker and Van der Spoel (1966)
Mediterranean	'setosa'	Adriatic Sea	all year	?	+	+	-	-	-	+	+	ranges	Baldasseroni (1914)
	'setosa'	Adriatic Sea	July-Aug.	?	+	+	-	-	-	+	+	ranges	Scaccini and Ghirardelli (1941)
	'setosa'	Tyrrhenian Sea (Gulf of Naples)	July-Sept.	?	+	+	-	-	-	+	+	ranges	Ghirardelli (1952)
	'setosa'	Ligurian Sea and Gulf of Lyon	July	~100	+	+	+	+	+	-	-	averages per length class of 1mm	Furnestin (1958b)
Black Sea	'euxina'	Black Sea	?	?	+	+	-	-	-	+	+	ranges	Winogradow (1933)
	'setosa'	S.W. Black Sea (near Bosporus)	July	47	+	+	+	+	+	-	-	averages per length class of 1mm	Furnestin (1958a+b)
	'euxina'	W. Black Sea (Rumanian coast)	May	?	+	+	+	+	+	-	-	averages per length class of 1mm	Furnestin (1958b)
	'euxina'	S.E. Black Sea (Trebizond region)	all year	100	+	+	+	+	+	+	+	averages per length class of 0.5mm	Furnestin (1961)

(1928) noted that most body sections increase in direct proportion to overall length with the exception of the caudal segment, which becomes relatively shorter as the animal grows. Meek also suggested that the pattern of relative growth, or allometry, is deep-seated and therefore characteristic of the species, whereas size at maturity is often influenced by environmental conditions. Seasonal variation in total lengths of *S. setosa* has been reported in different areas of its range (Meek, 1928; Russell, 1932; Wimpenny, 1937; Pierce, 1941; Furnestin, 1961; Hecq et al., 1975; Andréu & Riera, 1990); total length at maturity in early spring is generally longer than in autumn. This is thought to be related to temperature, with individuals maturing during the cold months attaining greater lengths than individuals maturing during warm months, but availability of food has also been mentioned as a factor (Øresland, 1986). McLaren (1966) stated that zooplankton of high latitudes generally develop more slowly, reach a larger size, and live longer than related forms in warmer seas. Furnestin (1958b) also suggested a negative relationship between length of *S. setosa* and temperature, based on her data from three different basins (Table 1). Development of chaetognaths is continuous without abrupt changes, although the term 'larva' is used for the very early stages (Pierrot-Bults & Chidgey, 1988). Several maturity classification schemes for chaetognaths exist (reviewed in Pearre, 1991) but maturity stages of the specimens used in this study were seldomly reported. There is little concensus about the number of annual breeding cycles of *S. setosa* in different parts of its range. For the North Sea, between one and six generations per year have been suggested (reviewed in Pearre, 1991), for the Black Sea, Besiktepe & Unsal (2000) proposed a single breeding season in which two broods are produced, and for the Mediterranean Sea, the number of breeding cycles is unknown. However, Dallot (1968) found that *S. setosa* in captivity under optimal conditions matured rapidly, in one to three days.

A negative correlation between percentage tail length of total length and total length can be observed in Figure 2. Specimens from the Mediterranean are generally the smallest, with relatively long tails, whereas those from the Black Sea are the largest with relatively short tails; specimens from the North

Sea are intermediate in terms of total length as well as relative tail length, but ranges overlap. Such differences may well arise as a result of environmental differences, because total length at maturity is affected by temperature (as discussed above) and tail length is negatively correlated with total length.

Comparing Biersteker & Van der Spoel's data (1966) with the ranges plotted in Figure 2, it is clear that the data of relative caudal length for *S. batava* fall within the range reported for *S. setosa* from the North Sea. However, their data for *S. setosa* include some very large specimens (>14mm), and these specimens have an allometric relationship atypical of *S. setosa*, namely, that the slope is less steep (Fig. 2). Our re-examination of the samples that were used in the study of Biersteker & Van der Spoel (1966) showed: 1) that their specimens of *S. setosa* were misidentifications of (juvenile) *S. elegans*, and 2) that their *S. batava* specimens corresponded to *S. setosa*. Furnestin (1958a; 1958b; 1961) reported a lot of overlap between average caudal lengths per size class of *S. euxina* and *S. setosa* from the Black Sea, and considered this character unfit for discriminating between the two taxa. Indeed, her data for *S. setosa* from the Black Sea (plotted in Fig. 2) all fall within the range reported for *S. euxina*.

Meristics

The number of teeth and hooks increases with age until maturity and then decreases, since some are lost in older animals (Ritter-Záhony, 1911b; Kapp, 1991). Temperature may also affect the numbers (Ritter-Záhony, 1911a; Tokioka, 1974). Data on the numbers of posterior teeth and anterior teeth are summarized in Figures 3A and 3B, respectively. There is a positive relationship between the numbers of teeth and total length, which is steeper in the case of posterior teeth. There is little overlap between the ranges of Mediterranean and Black Sea specimens, while those from the North Sea are intermediate and overlapping with both. However, the separation of these ranges is mainly the effect of differences in total length. The data for North Sea '*S. setosa*' reported by Biersteker & Van der
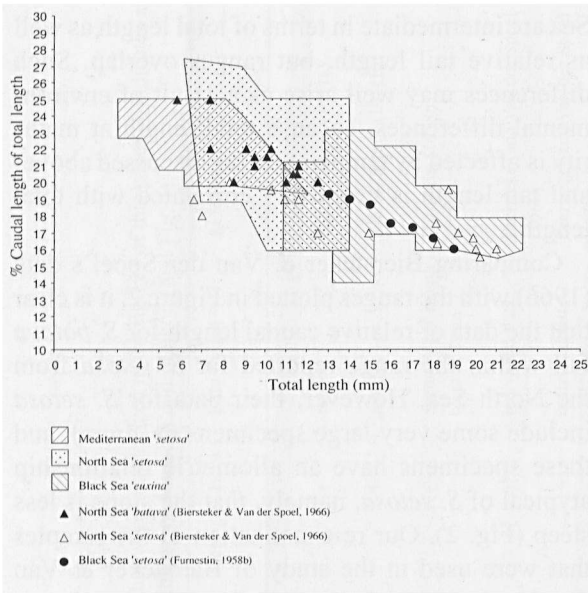
Fig. 2. Percentage caudal length of total length plotted against total length for different taxa from the *S. setosa*-complex from three different basins (for data sources see Table 2). Individual data for '*S. batava*' and '*S. setosa*' are from Biersteker & Van der Spoel (1966). Datapoints for *S. setosa* from the Black Sea are averages per size class (from Furnestin 1958b).

Fig. 3. Number of posterior (A) and anterior (B) teeth plotted against total length for different taxa from the *S. setosa*-complex from three different basins (for data sources see Table 2). Individual datapoints for '*S. batava*' and '*S. setosa*' are from Biersteker & Van der Spoel (1966).

Spoel (1966) are typical of *S. elegans* (as discussed above). Winogradow (1933) and Elian (1960) considered the difference in numbers of posterior and anterior teeth between *S. setosa* and *S. euxina* from the Black Sea important (anterior teeth: 3-8 and 8-10, posterior teeth: 6-12 and 15-20 for *S. setosa* and *S. euxina*, respectively). However, according to Furnestin (1958b) these differences were mainly the result of length differences, because the *S. euxina* specimens were larger and consequently had more teeth. The numbers of hooks do not, or hardly change in relation to total length, and do not separate specimens or taxa from different localities (Fig. 4)

Ovary length

Only Furnestin (1958a; 1958b; 1961) recorded ovary length per size class (averages), depicted in Figure 5, noting a positive relationship between ovary length and total length in most samples, but not for the sample of *S. setosa* from the Black Sea. Furnestin (1958b) noted that the variation within a single size
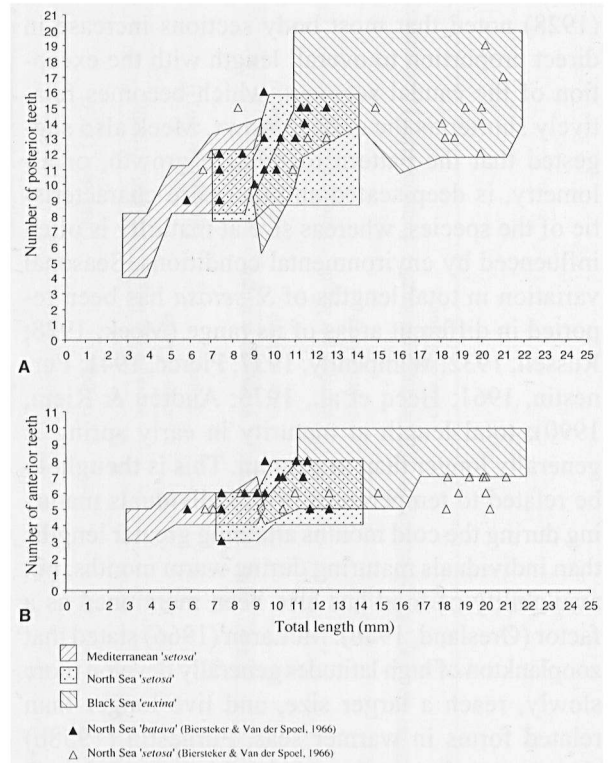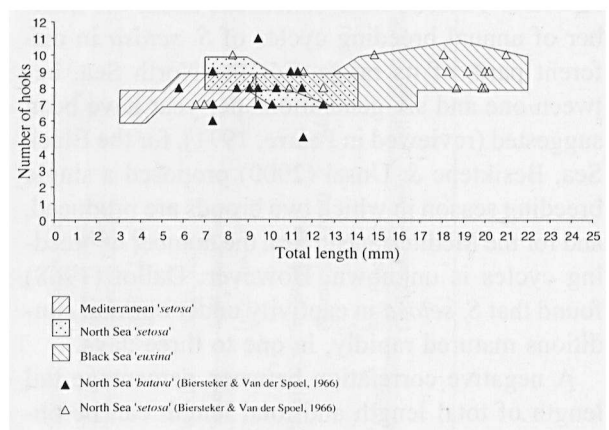

Fig. 4. Number of hooks plotted against total length for different taxa from the *S. setosa*-complex from three different basins (for data sources see Table 2). Individual datapoints for '*S. batava*' and '*S. setosa*' are from Biersteker & Van der Spoel (1966).
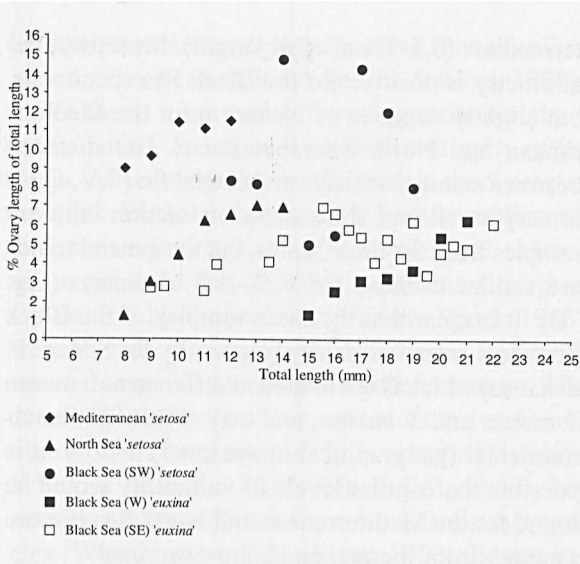
Fig. 5. Percentage ovary length of total length (averages per size class) plotted against total length for different taxa from the *S. setosa*-complex from three different basins (data from Furnestin, 1958a; 1958b; 1961, see Table 2).

Fig. 6. Posterior ends of the body showing variation in ovary size, and number and sizes of the ova from species (re)descriptions of (A) *S. batäva* from the Scheldt Estuary (redrawn from Biersteker & Van der Spoel, 1966), (B) *S. euxina* from the Black Sea (redrawn from Elian, 1960), and (C) *S. setosa* from the Black Sea (redrawn from Elian, 1960).

class could be very large, especially for samples from the North Sea and Black Sea. However, generally, specimens from the North Sea had relatively shorter ovaries than specimens from the Mediterranean Sea. The 1969 pilot study reported highly variable ovary lengths for specimens from the Scheldt Estuary, varying between 2.1 and 17.4% of total length (unpublished data). In addition, the holotype of *S. batava* has ovaries extending past the anterior end of the posterior fins (~17.5% of total length, Fig. 6A), indicating that specimens from the North Sea may also possess (very) long ovaries.

Clearly, ovary length is highly variable and in the past *S. euxina* and *S. batava* have been associated with the occurrence of multiple maturity cycles (Furnestin, 1961). Especially the case of *S. euxina* and *S. setosa* from the Black Sea is interesting. Elian (1960) stated that *S. euxina* is the larger species in the Black Sea with relatively long ovaries that contain many small eggs (20-30) whereas *S. setosa*, the smaller species, has relatively short ovaries with fewer and larger eggs (6-10, Fig. 6B and 6C, respectively). Moreover, ecological differences between the two species have been noted, namely that *S. euxina* is characteristic of the cold period of the year (November-May) and occurs in deeper layers
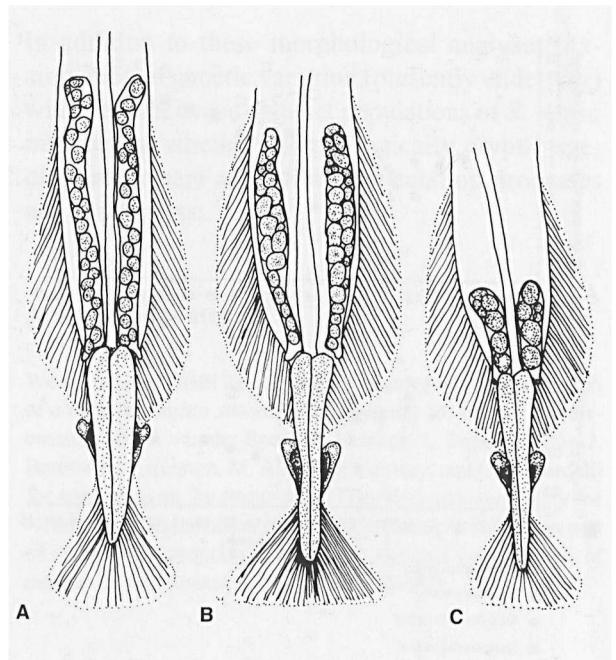
and more at open sea, whereas *S. setosa* is characteristic of the warm period of the year (June-August) and occurs closer inshore and in the upper layers (Winogradow, 1933; Elian, 1960). Interestingly, we found no reports of records from the Black Sea of the two species co-occurring. However, Furnestin (1961) suggested the presence of two maturity cycles based on her data from the Trebizond region (SE Black Sea) in which *S. setosa* may represent the first cycle of this species (individuals <17mm total length), and *S. euxina* the following cycles (individuals >17mm total length, see Figure 5, open square symbols).

Fins and dimensions

Fins are delicate structures which are often damaged during preservation. However, fin remains are usually enough to distinguish the beginnings and ends of the fins. Herein, only the distances between ventral ganglion and anterior edge of anterior fins
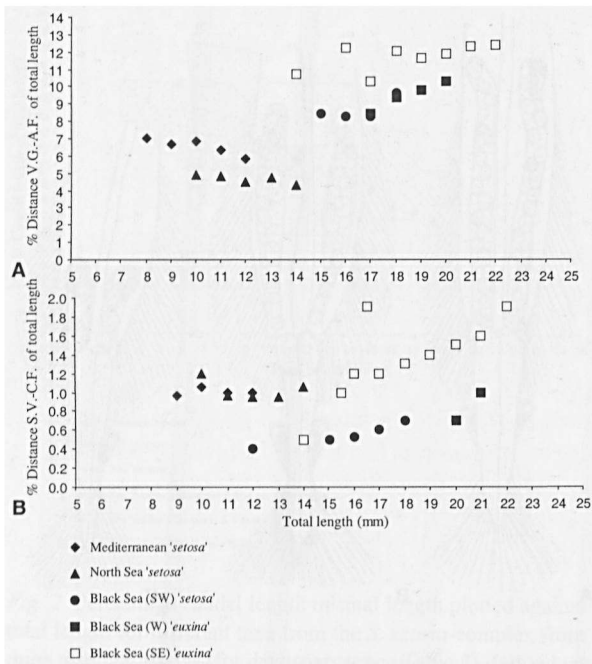
Fig. 7. Average percentage distance between ventral ganglion and anterior fin (A) and average percentage distance between seminal vesicles and caudal fin (B) of total length, plotted against total length for different taxa from the *S. setosa*-complex from three different basins (data are from Furnestin, 1958a; 1958b; 1961, see Table 2).

(Fig. 7A) and between seminal vesicle and caudal fin (Fig. 7B) are compared (other data were not available). Ritter-Záhony (1911a) described varieties of *S. setosa* from the North Sea with considerable differences in anterior fin length and distance between the ventral ganglion and anterior fin. According to Meek (1928), fins are secondary structures that appear late in life (especially the anterior pair), and so are subject to environmentally induced variability, which is apparent not only between regions but also seasonally and annually within the same region (Ritter-Záhony, 1911a; Meek, 1928; Russell, 1932).

The data concerning relative distance between ventral ganglion and anterior fin (V.G.-A.F.) from Furnestin (1958a; 1958b; 1961, Fig. 7A) show greater distinction between samples from the three basins than the other characters mentioned so far. Average V.G.-A.F. distances of Black Sea samples are >8% of total length, of North Sea samples <5% of total length, and of Mediterranean samples in-

termediate (5.8-7% of total length). Moreover, the allometry is positive for the Black Sea specimens, but slightly negative or isometric for the Mediterranean and North Sea specimens. The distance between seminal vesicles and caudal fin (S.V.-C.F.) is very small and shows less distinction between samples from the three basins, but the general trends are similar to those for V.G.-A.F. distances (Fig. 7B). It is clear that the three samples of the Black Sea show more variability (especially for S.V.-C.F. distance) which is not related to differences between *S. setosa* and *S. euxina*, and may result from environmental (geographical or seasonal) factors. It is possible that similar levels of variability would be found for the Mediterranean and North Sea if more samples from these regions are examined.

Conclusions

Many of the characters discussed here would appear to be influenced by environmental conditions. A wide range of conditions prevail from the warm and salty waters of the Mediterranean Sea on one hand, to the cold and brackish waters of the Black Sea on the other, with the North Sea exhibiting intermediate conditions. This disparity is reflected in morphological differences between samples of *S. setosa*, namely in total length, relative tail length, and numbers of teeth and hooks, though the measured ranges of these characters overlap and there are no obvious differences in allometry. This may indicate that these morphological differences are under ecophenotypic control. Our genetic data differentiate between *S. setosa* populations from the different basins, and show that populations of the Mediterranean and Black Sea are more closely related to each other than to the North Sea (Peijnenburg *et al.*, 2004). This supports the idea that the morphological differences observed between populations from the three different basins are mainly the result of environmental factors. Andréu & Riera (1990) also concluded that most of the morphological characters they examined were more variable between seasons within a region than between regions (one Mediterranean and two North Sea localities were considered). Only the allometric relationships of caudal length and the distance

between anterior and posterior fins showed more variation between regions (Andréu & Riera, 1990).

We found more variability in quantitative characters within *S. setosa* from different parts of its range, than between the nominal taxa in the *S. setosa*-complex. We have shown that *S. batava* conformed to *S. setosa* in terms of all morphological characters considered and that the specimens attributed to *S. setosa* by Biersteker & Van der Spoel (1966) were in fact *S. elegans*. On this basis, *S. batava* can no longer be considered a different taxon. The data for *S. euxina*, however, are inconclusive. Quantitative characters completely overlapped between *S. setosa* from the Black Sea and *S. euxina*, but authors who considered *S. euxina* as a distinct species (Winogradow, 1933; Elian, 1960) did not include morphological measurements of *S. setosa*. The only qualitative morphological difference they mentioned is the presence of a (small) collarette in *S. euxina*, which is absent in *S. setosa*. However, Furnestin (1958b) observed that a small collarette is present in *S. setosa* (see also Fig. 1B) and may sometimes be absent in *S. euxina*. Winogradow (1933) and Elian (1960) further considered the ecological differences between the two taxa very important, and it is noteworthy that Elian (1960) reported samples from the same region in the western Black Sea that are either entirely composed of *S. euxina* and sampled in winter, or entirely composed of *S. setosa* and sampled in summer. This, together with the large variation in total lengths and relative ovary lengths, strengthens the likelihood of a seasonal succession of maturity cycles in the Black Sea corresponding to either *S. setosa* or *S. euxina*, as suggested by Furnestin (1961). However, more data are needed relevant to the life history of the species in the different geographical areas.

This study shows that a lot of morphological variation exists within *S. setosa*. However, we consider this variation insufficient to separate the species. More conclusive data about subtle morphological differences require powerful morphometric methods, e.g., multivariate and shape analyses, and should avoid the use of percentages and other derived measures. Moreover, more detailed examination of morphological structures using electron microscopy may reveal species-specific differences, e.g., in the surface structure of teeth and hooks (Kapp 1991).

In addition to these morphological analyses, examination of genetic variation (presently underway) within and between disjunct populations of *S. setosa* may reveal whether morphologically cryptic species are present and whether speciation processes are in progress.

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