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The occurrence of *Sagartia elegans* (Dalyell, 1848) (Anthozoa: Actiniaria) in the Netherlands

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The occurrence of the sea anemone *Sagartia elegans* var. *miniata*, var. *nivea* and var. *venusta* in considerable numbers at three localities in the Netherlands is reported upon. Previous records of the species in Dutch coastal waters are reviewed. Most of these are considered as doubtful. Characters to distinguish *S. elegans* from *S. troglodytes* are discussed. Attempts are made to relate local occurrence of *S. elegans* with temperature data. *Sagartia elegans* is an autochthonous species in the Netherlands but its numbers vary considerably, and populations probably have no permanent character. In the past, populations presumably have been reduced and sometimes wiped out during relatively severe winters. Reinforcement of rest populations or recolonization is likely to happen through planktonic larvae from the Channel area and from off-shore populations. Recovery of populations in Dutch coastal waters apparently takes place after consecutive mild winters.

Introduction

During 1990 and subsequent years extensive populations of the acontiarian sea anemone *Sagartia elegans* (Dalyell, 1848) were found at different sites along the Dutch coast. This is remarkable, as the species was considered to be rare in the Netherlands. Although its occurrence in Dutch waters was reported upon from 1897 onwards, all records until 1950 were considered doubtful by Van Urk (1952). In the present paper the records of *S. elegans* in the Netherlands since 1950 are reviewed, and recent observations added.

In a paper on the distribution of Anthozoa in the south-west of the Netherlands Braber & Borghouts (1977) suggested that *Sagartia elegans* is sensitive to cold winters. After having been observed in 1962, the species disappeared during the severe winter of 1962/63. The observations of *S. elegans* from 1990 onwards were made after a series of mild winters. Therefore it was decided to relate all reliable autochthonous records of the species to the minimum seawater temperatures in the winter previous to each observation. For that purpose all post-1950 literature was scanned, as well as the so-called Central System (C.S.), a collection of record files of the Strandwerkgemeenschap (a Dutch society of marine naturalists) kept in the Nationaal Natuurhistorisch Museum at Leiden.

Records of *Sagartia elegans* in the Netherlands prior to 1990

Records of *Sagartia elegans* dating from before 1950 were reviewed and discussed by Van Urk (1952), who concluded that all records until then should be regarded as doubtful (including his own) and that the species could hardly be considered autochthonous in the Netherlands. And indeed, records available from this period are vague or altogether lacking descriptive notes, and not supported by voucher specimens.

Among the records discussed by Van Urk was an unpublished allochthonous one by D. van Nievelt from the files of the former Zoological Station of the Dutch Zoological Society. Van Nievelt (1953), in a written defence, questioned Van Urk's conclusion as to this record, and, although not claiming Van Urk to be definitely wrong, suggested it to have borne positively upon *S. elegans*. The record concerned two individuals, 13 and 2 mm in diameter, washed ashore on the beach of Domburg, province of Zeeland, among a cluster of egg-capsules of the Common Whelk *Buccinum undatum* Linnaeus, 1758. After they had been transferred to an aquarium, the largest anemone "produced a second juvenile". The large specimen had a brightly orange-brown column with white dots. When offered food it repeatedly emitted acontia through the column and sometimes through the mouth. These descriptive notes are indeed most suggestive of *S. elegans* except for the claim that the animal "produced a second juvenile". This suggests that Van Nievelt actually observed viviparity, which would not point at *S. elegans*. [It is true that viviparity has occasionally been suggested for this species, even quite recently (Ates, 1989: 25, explicitly for the var. *venusta*), but never beyond doubt]. On the other hand Van Nievelt's description does not match any of the manifestly viviparous acontiate species known from the Dutch coast and adjacent areas, viz.: *Sagartia ornata* (Holdsworth, 1858), *Cereus pedunculatus* (Pennant, 1777), and *Hormathia coronata* (Gosse, 1858). It therefore seems that the specimen was indeed *S. elegans*, and that Van Nievelt's statement that it "produced a living juvenile" was an interpretation rather than an actual observation, the juvenile concerned initially having been overlooked (cf. e.g. Stephenson, 1935: 323).

All records of *Sagartia elegans* from between 1950 and 1990 traced in the literature and the "Central System" are listed in table 1.

Table 1 (cf. fig. 1). Synopsis of the records of *Sagartia elegans* along the Dutch coast for the period 1950-1990. Reliable autochthonous records are marked with an asterisk (*). Autochthonous (Aut.) and allochthonous (All.) records are indicated. C.S. = Central System, the collection of record files of the Strandwerkgemeenschap; RMNH Coel. = Coelenterate collection of the former Rijksmuseum van Natuurlijke Historie, now National Museum of Natural History (NNM), at Leiden; Vlissingen = Flushing.

Date	Locality	Status	N	Source	Remarks
viii.1950	Schouwen	Aut.	?	C. den Hartog et al., 1951: 100	Undocumented record
11.iv.1953	't Horntje, Texel	Aut.	2	C.S. (Stock & Swennen)	Undocumented record; specimens mislaid
17.iv.1954	Terschelling	All.	2	C.S. (Swennen)	RMNH Coel. 4869

8.x.1955	Noordwijk/ Noordwijkerhout	All.	3	C.S. (A.W.Lacourt); Spaink, 1957: 11	RMNH Coel. 17712 (3 specimens); *Sagartiogeton undatus*
26.iv.1958	Terschelling	Aut.	1	C.S. (Swennen)	Undocumented record; eastern mole of harbour.
18.x.1958	Huisduinen	All.	3-4	Den Hartog, 1959: 6	Misidentification; *Actinothoe sphyrodeta*
2.viii.1960	Den Helder	All.	3	Den Hartog, 1962a: 11	Idem.
24.viii.1960	Den Helder	All.	2	Den Hartog, 1962a: 11	Idem.
26.viii.1960	Den Helder	All.	4	Den Hartog, 1962a: 11	Idem.
*18.i.1961	Huisduinen	Aut.	1	Den Hartog, 1962b	Documented record.
23.iii.1961	Scheveningen	All.	1	C.S. (Swennen)	Undocumented record; from egg-capsules of Common Whelk.
Early 1962	Schouwen	Aut.	?	Braber & Borghouts, 1977: 19-20	Undocumented record.
Early 1962	Vlissingen	Aut.	?	Braber & Borghouts, 1977: 19-20	Idem.
*12.xi.1962.	Mole N of Beach-marker 3	Aut	ca 10	Den Hartog, unpubl.	Conclusive field notes; near low water mark.
*16.xi.1962	Nollepier, Vlissingen	Aut.	50-60	Den Hartog, unpubl.	Idem.
18.x.1977	Gorishoek/ Tholen	Aut.	1	Adema, 1978: 111	Undocumented record; probably *S. troglodytes*.
26.xii.1977	Flauwers	Aut.	5	Adema, 1978: 111.	Idem.
25.vii.1978	Noord-Beveland	Aut	many	W. Dekker: 114	Idem.
21.x.1978	Flauwers	Aut.	1	Adema, 1979: 99	Idem.
1.viii.1981	Kats	Aut.	1	Slager, 1982: 16-17	Idem.
1.viii.1981	Sas van Goes	Aut.	1	C.S. (Huysman).	Idem.
x.1981	Gorishoek	Aut.	?	Huysman, 1982: 33	Idem; purple variety.
x.1982	Terschelling	Aut.	?	Huysman, 1983: 19	Undocumented record of var. *aurantiaca*?; presumably *S. troglodytes*.
19.x.1982	West-Terschelling	Aut.	2	Slager, 1983: 150	Undocumented record.
*8.x.1983	Burghsluis	Aut.	3	Ates, 1989	Documented record.
17.ii.1988	Zoutelande	All.	2	Rappé, 1988: 129	In boring holes of *Barnea candida* (Linnaeus, 1758) in lump of peat; hence more likely to refer to *S. troglodytes* or *Sagartiogeton undatus*.

Most records listed were provided by non-specialists, and are insufficiently documented to allow identification afterwards (no voucher specimens and no relevant descriptive indications being available) and bear presumably upon brightly coloured specimens of *Sagartia troglodytes* (Price, 1847).

Some of these records may here be further elucidated and discussed:

— The allochthonous record by Swennen, RMNH Coel. 4869, concerns two very small rather poorly preserved specimens which are positively *S. elegans* [anatomy slightly asymmetrical; nematocysts in acontia: penicilli ca 49-57 × 5.3-5.8 μm; spirulae ca. 14-16 × 1.8 μm and 28.5-33 × 3.1-3.6 μm (cf. table 3)].

Fig. 1. Map of the coast of the Netherlands indicating all localities with reliable records of autochthonous *Sagartia elegans*. Open circles = pre-1990 records; black dots = post-1990-records.
1. West-Terschelling; 2. 't Horntje; 3. Huisduinen; 4. Beach-marker 3, near Den Helder; 5. Burghsluis; 6 Westbout; 7. Northern end of storm surge barrier, Schouwen; 8. Borrendamme; 9. Lokkersnol (near Cauwers-inlaag); 10. Weldamseweg; 11. Neeltje Jans; 12. Southern end of storm surge barrier, Noord-Beveland; 13. Jacobahaven; 14. Anna Friso; 15. Westkapelle; 16. Zoutelande; 17. Nollepier, Vlissingen; 18. Ritthem.
For topographic details and exact co-ordinates of these localities, see Topografische Dienst Nederland (TDN), 1995.

— The record published by Spaink (1957: 11; communicated by A.W. Lacourt) of thousands of sea anemones, mostly *S. elegans* and *S. troglodytes*, found washed up on the beach at Noordwijk-Noordwijkerhout on 8.x.1955, represents a misidentification as far as *S. elegans* is concerned. A sample from the collection of the late Mr A.W. Lacourt, labelled *Sagartia elegans*, Noordwijkerhout, 8.x.1955, A.W. Lacourt, VII C6, now in the RMNH collection (RMNH Coel. 17712), actually contains 3 specimens of *Sagartiogeton undatus* (re-identification J.C. den Hartog, 1987).
This phenomenon of massive strandings of sea anemones, predominantly *S. troglodytes*, usually mixed with much smaller numbers of *Metridium senile* (Linnaeus, 1761) and *Sagartiogeton undatus* (O.F. Müller, 1788), has been known for a long time from the sandy beaches of the provinces of North and South Holland and still occurs regularly. So far these strandings have never yielded any *S. elegans*.
— Four records of allochthonous specimens by J.C. den Hartog (1959: 6; 1962a: 11-12), claimed to belong to *Sagartia elegans* var. *venusta*, were based on misidentifications and actually bore upon *Actinothoe sphyrodeta* (Gosse, 1858). They constitute the first records of that species in the Netherlands.
— The record by J.C. den Hartog (1962b) of an autochthonous individual of *S. elegans* var. *miniata* found just below low water mark on the sea-dike at Huisduinen near Den Helder on 18.i.1961, is provided with clear descriptive notes and leaves no doubt about the identity of the specimen. It is the first authentic autochthonous record of *Sagartia elegans* in the Netherlands.
— Unpublished finds by J.C. den Hartog of ca 10 specimens on a jetty near beach-marker 3 (close to Den Helder) on 12.xi.1962, and of 50-60 large specimens (measuring up to at least 3 cm across the base) on the Nollepier at Vlissingen on 16.xi.1962, leave no doubt either.
— The records by Braber & Borghouts (1977) are unfortunately undocumented. Their sea anemone collection, donated by the Delta Institute, Yerseke, to the Nationaal Natuurhistorisch Museum, Leiden, contained no samples of *Sagartia elegans*.

Records of *Sagartia elegans* in the Netherlands since 1990

In 1990, populations of *Sagartia elegans* were discovered at three localities along the Dutch coast, viz. near Zoutelande and Westkapelle in the province of Zeeland, and near 't Horntje on the Island of Texel (fig. 1). The records of the species since 1990 are summarized in table 2.

Table 2 (cf. fig. 1). Synopsis of autochthonous records of *Sagartia elegans* along the Dutch coast since 1990. All records refer to the var. *miniata*, unless stated otherwise.

Date	Locality	N	Observer/ collector	Remarks
30.iii.1990	Zoutelande	100s	Faasse	Attached to stones at MLWS-level. Bases of some anemones surrounded by freshly accumulated sand. Some anemones with shell debris attached to column. A few

				specimens of the varieties *nivea* and *venusta* among predominating var. *miniata*.
29.iv.1990	Zoutelande	100s	Faasse	Intertidal, among stones of breakwater near low water mark. Including specimens of var. *nivea* and var. *venusta*; 10 specimens collected (RMNH Coel. 18794).
1.v.1990	Zoutelande	100s	Den Hartog & Faasse	Idem. Including 1 specimen of var. *nivea*; 8 specimens collected (RMNH Coel. 18501).
16.ix.1990	W-Terschelling	1	Dekker	Depth 10 m (RMNH Coel. 18508).
15.x.1990	't Horntje	1	Dekker	MLWS-level (RMNH Coel. 18507).
19.x.1990	't Horntje	1	Dekker	MLWS-level.
21.xi.1990	't Horntje	6	Dekker	MLWS-level.
14.xii.1990	't Horntje	2	Dekker	Intertidal? One specimen of var. *nivea*.
19.xii.1990	't Horntje	18	Dekker & Ates	Var. *miniata* and var. *nivea*.
15.i.1991	't Horntje	30-40	Dekker & Ates	MLWS-level. Including var. *nivea*; var. *miniata* predominating.
29.i.1991	't Horntje	5	Dekker	MLWS-level. Including var. *nivea*.
2.iii.1991	Vlissingen	5	Faasse	—
25.i.1992	Zoutelande	100s	Faasse	Especially below low water mark.
22.ii.1992	Schouwen	10	Faasse	Near northern end of storm surge barrier in Oosterschelde.
7.iii.1992	Ritthem	1	Faasse	—
1.x.1992	Zoutelande	30	Ates & Faasse	Subtidal (SCUBA dive). Dramatic decline of population in this locality caused by supply of sand for coastal protection. Including var. *nivea*.
10.x.1992	Neeltje Jans	1	Faasse	On a pontoon.
11.iii.1993	't Horntje	2	Dekker	MLWS-level.
29.vi.1993	Neeltje Jans	15	Faasse	On a pontoon, var. *venusta*.
20.xi.1993	Westkapelle	10s	Faasse	—
29.xi.1993	't Horntje	2	Dekker	Under stones, 0.5 m below low water mark (RMNH Coel. 18795).
12.ii.1994	Westkapelle	10s	Faasse	—
11.vi.1994	Borrendamme	1	Faasse	Subtidal (SCUBA dive).
6.viii.1994	Lokkersnol	1	Faasse	Idem.
3.ix.1994	Wissenkerke	1	Faasse	Idem. Depth 35 m.
15.x.1994	Zoutelande	10s	Faasse	Subtidal (SCUBA dive). Varieties *miniata*, *nivea*, and *venusta*.
5.xi.1994	Weldamseweg	1	Ates & Faasse	Subtidal (SCUBA dive).
12.xi.1994	Westbout	28	Faasse	Idem; including 8 specimens var. *nivea* and 1 specimen var. *venusta*.
3.ii.1995	Jacobahaven	ca 20	Faasse	Intertidal.
3.ii.1995	Noord-Beveland	100s	Faasse	Including 6 specimens of var. *nivea*. Near southern end of storm surge barrier in Oosterschelde.
3.v.1995	Westbout	ca 40	Faasse	incl. var. *nivea*.
5.v.1995	Weldamseweg	2	Ates & Faasse	Subtidal (SCUBA dive). Including 1 sp. of var. *nivea* and 1 var. *rosea*.
20.v.1995	Weldamseweg	22	Faasse	Subtidal (SCUBA dive). Including 20 specimens of var. *nivea*.
1.vii.1995	Neeltje Jans	10s	Faasse	On a pontoon. Including ca 5 specimens of var. *venusta*

12.vii.1995	Westkapelle	10s	Faasse	Subtidal (SCUBA dive).
16.ix.1995	Weldamseweg	2	Ates & Faasse	Subtidal (SCUBA dive).
29.xi.1995	Burghsluis	11	Faasse	Intertidal.
29.xi.1995	Schouwen	ca 30	Faasse	Near northern end of storm surge barrier in Oosterschelde. Including 1 specimen var. *nivea*.
9.iii.1996	Neeltje Jans	ca 20	Faasse	Intertidal.
26.vi.1996	Westbout	4	Faasse	Subtidal (SCUBA dive).
26.vii.1996	Anna Friso	10	Faasse	Including 6 specimens of var. *venusta*.
14.xii.1996	Westbout	6	Faasse	Intertidal.
11.iii.1997	Westkapelle	ca 30	Faasse	Intertidal.

The locality near Zoutelande was visited numerous times. Therefore only some key data are listed in the table. Although the population at this locality seemed on the decline ever since it was discovered on 30 March 1990, considerable numbers (hundreds) were still present until at least January 1992, especially concentrated subtidally. However, in the summer of 1992 a thick layer of sand was supplied to the beach of this locality for coastal protection. This had a devastating effect on the population as revealed by a SCUBA dive on 1 October, when no more than approximately 30 surviving specimens were found. Since, the population survived up to at least 15 April 1995 (when twenty specimens were observed subtidally (Faasse; SCUBA dive).

At the locality near 't Horntje, Texel, the species was frequently observed up to 29 January 1991. Following an icy spell in February 1991, no specimens were found despite intensive search, both intertidally and subtidally. After an absence of more than two years the species re-appeared in March 1993.

It is worth mentioning that the var. *nivea* (oral disc and tentacles white; Zoutelande, Westbout, 't Horntje) and the var. *venusta* (oral disc plain orange, tentacles white; Zoutelande, Westbout) were not previously recorded in the Netherlands.

Characters distinguishing *Sagartia elegans* and *S. troglodytes*

Sagartia elegans and *S. troglodytes* are hard to confuse by specialists and by those who by experience have learned to distinguish between both species in the field. In spite of this, most of the autochthonous Dutch records of *S. elegans* undoubtedly bear upon *S. troglodytes*. This is due to the fact that these records were provided by non-specialists and amateur naturalists of the 'Strandwerkgemeenschap' who possibly had never seen the species, but who apparently knew from the literature or by hearsay that both species occur in the North Sea and were to be expected on the Dutch coast. Thus, lacking both sufficient field experience and knowledge (and equipment!) to take into account relevant anatomical and microscopical characters, they generally seem to have based their identifications on a combination of vague indications and wishful thinking.

Notably for this reason it may here be useful to present and discuss once more the differences between the two species (table 3). These were previously summarized, but not fully so, by Stephenson (1935: 338-340) and Manuel (1981: 142, table 1).

Table 3. Differences between *Sagartia elegans* and *S. troglodytes*.

	Sagartia elegans	*Sagartia troglodytes*
1. Habitat	Usually on hard substrata in localities without, or with only little sedimentation.	Often in mud or sand, the base fixed to submerged solid substrata such as stones, shells, etc.
2. Columnar suckers	Suckers usually conspicuous, visible as distinct pale dots, very weakly adherent and only rarely with attached fine debris or shellfragments.	Suckers rather inconspicuous, strongly adherent, often attaching course shell gravel, etc.
3. Colour and pattern	Pattern of the oral disc and tentacles in bright tints and relatively uniform. Insertions of mesenteries usually obscure.	Pattern and colour of oral disc and tentacles extremely variable, often in dull colours, but specimens with a predominantly brightly orange, purple or opaquely white oral discs are not uncommon. Insertions of mesenteries usually distinct in at least the lowest part of the column.
4. Asexual reproduction	Frequent pedal laceration, often giving rise to smaller or larger groups of identically coloured individuals.	Absent. Never occurring in groups of identically coloured specimens.
5. Symmetry	Often somewhat irregular due to asexual reproduction.	Hexamerous.
6. Texture	Relatively soft and easily damaged when detached from its substratum.	Relatively tough and less vulnerable to damage.
7. Acontia	Relatively thick, usually present in profusion and emitted freely upon irritation.	Very thin and relatively inconspicuous. Only emitted by highly stressed or damaged specimens.
8. Cnidom of acontia (cf. fig. 2)	Spirulae: 34.9(32.0-37.8) × 3.6(3.6-4.0) [Spirulae: 15.8(14.2-17.8) × 2.0(1.8-2.2)] Penicilli: 60.2(56.1-65.8) × 5.8(5.3-6.2)	Spirulae: 15.4(13.4-16.5) × 2.6(2.4-2.7) [Spirulae: 15.1(13.4-16.0) × 1.4(1.3-1.6)] Penicilli: 24.9(22.7-26.7) × 3.8(3.6-4.0)

Ad. 1 and 2. Habitat and colour.— There are no absolute differences in the habitat of the two species. *Sagartia troglodytes* is most frequently found buried in mud or sand, the base fixed to submerged hard substrata such as stones and empty bivalve shells, both intertidally and subtidally. Such forms usually have opaque, greyish to flesh-coloured columns. However, the species may also occur in cleaner habitats, e.g. among exposed beds of juvenile mussels (*Mytilus edulis* Linnaeus, 1758) between granitic boulders high in the tidal zone. Here one often finds individuals with more brightly coloured, often striped columns.

Ad. 2. Adherence of gravel to the column.— The upper part of the column of *S. troglodytes* is often covered with attached coarse shell gravel. *Sagartia elegans* is definitely much less inclined to cover its column with foreign material, but modest cover with fine gravel has occasionally been observed by us in the var. *miniata*, both in situ and under aquarium conditions.

Ad 4. Asexual reproduction.— *Sagartia elegans* var. *miniata* frequently reproduces asexually by pedal laceration, which gives rise to the formation of clones of identically coloured specimens. This phenomenon is not found in *S. troglodytes*, where it is

usually hard to find even two specimens with identical coloration close together.

Both Stephenson (1935: 338) and Manuel (1981: 148) claimed that *S. troglodytes* may reproduce by viviparity. However, records of viviparity, also in the Netherlands, relate exclusively to *Sagartia ornata* (Holdsworth 1855) (cf. Den Hartog, 1970: 96-97; Faasse, 1991), formerly regarded as a variety of *S. troglodytes* but suggested to be at least a different subspecies by Den Hartog (1970) and currently shown to be a separate species (Shaw et al., 1987).

Ad. 7. Acontia.— In *S. elegans* the acontia are longer, thicker and more conspicuous than in *S. troglodytes*. Upon irritation, e.g. by detaching a specimen from its substratum or by simply touching it, *S. elegans* generally readily emits acontia through its mouth and/or through cinclides in the column wall, often in profusion. *Sagartia troglodytes* has a tougher texture and is far less inclined to emit its thinner, less developed acontia, unless the internal structures are forced out of the gastric cavity by severe damage. If it proves difficult to trace any acontia, the species concerned is definitely not *S. elegans*.

Ad. 8. Cnidom of acontia.— Acontia of members of the genus *Sagartia* and of the family Sagartiidae are heavily laden with nematocysts of two kinds, here referred to as spirulae (= basitrichs) and penicilli (= p-mastigophores or p-rhabdoids). As shown in the table and in fig. 2, the dimensions of both types differ profoundly in *S. elegans* and *S. troglodytes*.

The means and ranges presented in the table are in μm, based on 20 measurements each. They were taken from a well developed specimen of *S. elegans* from Westkapelle (RMNH Coel. 18794) and an about equally large specimen of *S. troglodytes* from Katwijk (RMNH Coel. 11549). The second size-class of spirulae is generally relatively uncommon and inconspicuous, and therefore easily overlooked; hence being of no practical importance for identification this category is placed in brackets and not depicted in fig. 2.

The dimensions given here for *S. elegans* are in accordance with those found in specimens from the British Isles, the Faroes and the Atlantic coasts of France and Spain, and those presented for *S. troglodytes* are in accordance with British specimens (unpublished data J.C. den Hartog). The considerably wider ranges given for both species by Stephenson (1935: 337, 339) and especially Manuel (1981: 144, 148) are misleading, and apparently based on unusual extremes;

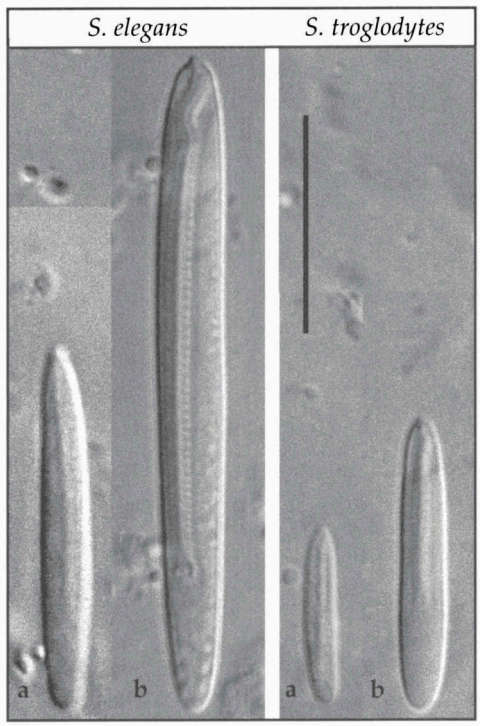

Fig. 2. (cf. table 3.8). Nematocysts of acontia of *Sagartia elegans* (RMNH Coel. 18794; Westkapelle) and *S. troglodytes* (RMNH Coel. 11549; Katwijk aan Zee); a = spirulae, b = penicilli. Scale bar = 20 μm.

these ranges further indicate that the authors did not distinguish the inconspicuous, small spirulae as a separate category.

The relatively small nematocysts found in the acontia of the very small allochthonous specimens found by Swennen (cf. p. 265) are in accordance with a common tendency that nematocyst size in species of Actiniaria correlates with body size (large specimens usually having larger nematocysts than smaller specimens).

The difference in size of the acontian nematocysts provides a conclusive character to distinguish between *S. elegans* and *S. troglodytes*. However, using this character, notably when dealing with preserved material, care should be taken not to confuse small *S. elegans* with *Sagartiogeton undatus* (cf. table 4). It should further be emphasized that the cnidoms of *S. troglodytes* and *S. ornata* cannot be differentiated by light microscopy.

Table 4. *Sagartiogeton undatus*, survey of the cnidom of acontia of two well developed Dutch specimens from Katse Hoek, Noord-Beveland (RMNH Coel. 11227) and from Noordwijkerhout (RMNH Coel. 17712). For comparison with *Sagartia elegans* and *S. troglodytes*, see table 3.

Specimen	Nematocyst type	Dimensions in μm	N
RMNH Coel. 11227	Spirulae	23.8(20.5 - 26.6) × 2.7(2.7 - 2.9)	20
	[Spirulae	13.2(11.6 - 14.2) × 1.6(1.4 - 1.8)	20]
	Penicilli	40.8(35.6 - 43.6) × 5.1(4.5 - 5.4)	20
RMNH Coel. 17712	Spirulae	26.6(24.0 - 28.5) × 2.7	20
	[Spirulae	14.2(12.9 - 15.6) × 1.9(1.8-2.2)	20]
	Penicilli	47.0(42.7 - 50.7) × 5.4(5.3 - 6.2)	20

Dutch autochthonous records of *Sagartia elegans* in relation to sea-water temperatures

For an analysis of the possible relation between autochthonous records of *Sagartia elegans* in the Netherlands and sea-water temperatures only fully reliable records were taken into account, i.e. those listed in table 2 and those marked with an asterisk in table 1. Sea-water temperature data were taken for this purpose from a long-term series of measurements from 't Horntje, Texel (Van der Hoeven, 1982, and supplementary data up to 1993 from the files of the Netherlands Institute for Sea Research, NIOZ).

It appears that most reliable observations of *S. elegans* were made in periods following one or more mild winters with relatively high minimum monthly mean sea-water temperatures (fig. 3a).

It is interesting to note that the species disappeared from 't Horntje in the winter of 1991 (February), whereas the population at Zoutelande (near Vlissingen) survived this winter. For a comparison of the minimum monthly mean temperatures at these localities for the years 1988-1991, see table 5.

Temperatures during the summer months do not seem to have influenced the occurrence of *Sagartia elegans* (cf. fig. 3b).

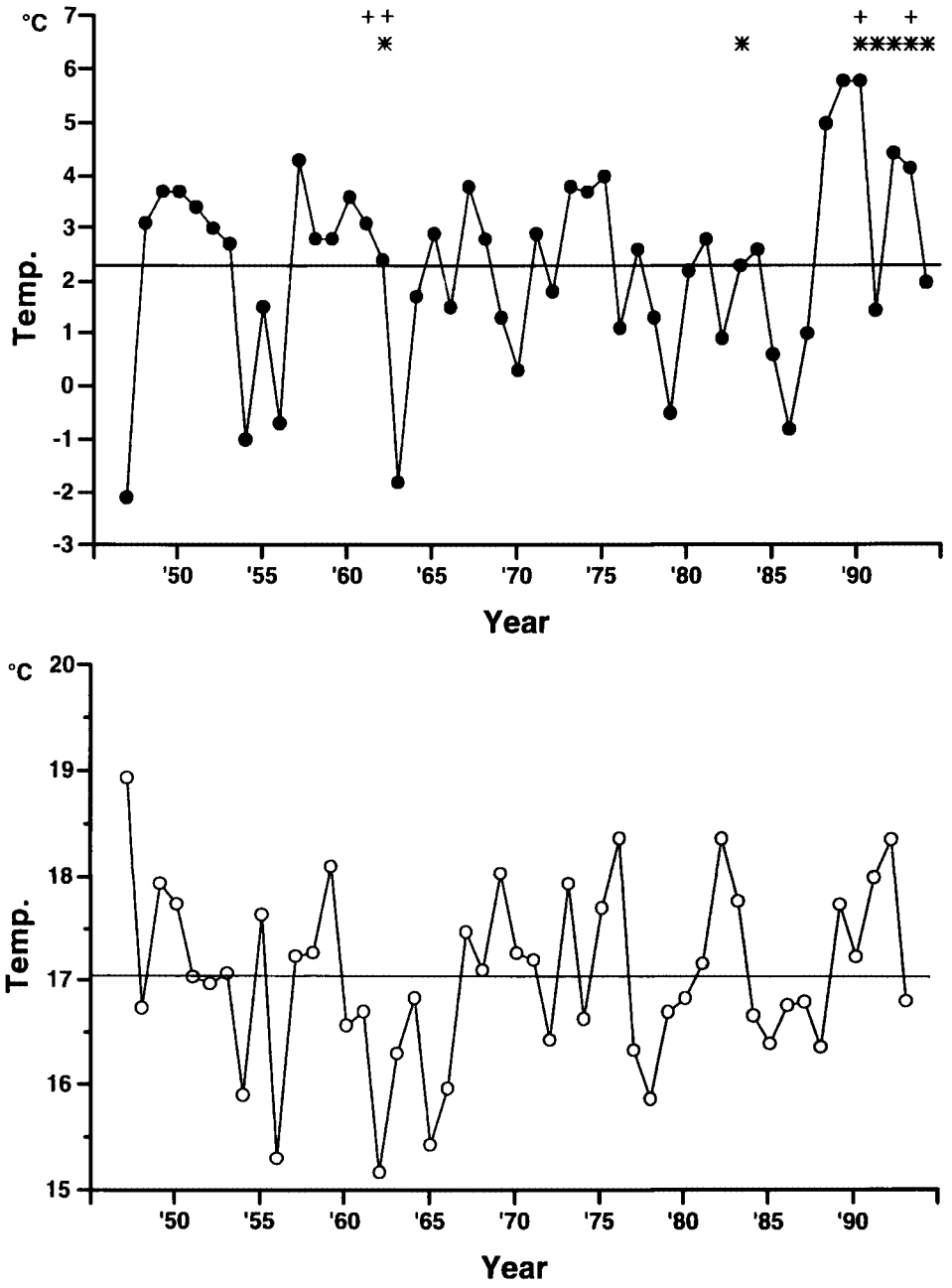

Fig. 3. Sea-water temperatures (in °C) at 't Horntje, Texel; 3a, minimum monthly mean temperatures from 1947 to 1994; 3b, mean summer temperatures (July, August, September) from 1947 to 1993. The horizontal lines denote the long term means.
Years with reliable observations of *Sagartia elegans* indicated for the southwestern (*) and northern (+) part of the Dutch coast.

Table 5. Comparison of the minimum monthly mean sea-water temperature at 't Horntje (Wadden Sea) and Vlissingen (Westerschelde) in the period 1988-1991. Data from 't Horntje from files of NIOZ, those from Vlissingen made available by Rijkswaterstaat.

Locality/Year	1988	1989	1990	1991
't Horntje	5.1°C	5.8°C	5.8°C	1.4°C
Vlissingen	5.6°C	5.7°C	6.2°C	1.9°C

Discussion

The Dutch coast is characterized by sandy shores and estuaries. Originally, hard substrata were barely present, but since some centuries dikes have been reinforced with limestone, basalt cobbles, granite boulders and more recently concrete blocks and asphalt. At several sites, mainly at the entrances of the estuaries, these dikes flank deep tidal channels. At three such sites populations of *S. elegans* have become established beyond doubt, viz. the northern part of the entrance of the Westerschelde, the entrance of the Oosterschelde and the Marsdiep region (Huisduinen and Texel) (tables 1, 2; fig. 1). At all locations the species was found at and below MLWS-level. The species is usually found on hard substrata, and does not thrive in estuarine conditions with sedimentation and reduced salinities.

Braber & Borghouts (1977) suggested a susceptibility of *S. elegans* to low winter temperatures. As mentioned above, the species disappeared during the winter of 1991 from 't Horntje, Texel (minimum monthly mean sea-water temperature 1.4°C) and not from Zoutelande. The minimum for Vlissingen (near Zoutelande, cf. fig. 1) in this winter was 0.5°C higher than at Texel (table 5). True enough, this is not a striking difference, but more detailed data might have revealed more extreme short-term differences between the minima for Texel and Vlissingen (note also that use of the 'minimum monthly mean' implicates that a possible lower minimum for any significant period ranging over end and beginning of two subsequent months goes unnoticed). Unfortunately such detailed data were not available to us. However, if we assume that a minimum monthly mean of slightly below 2°C is unfavourable for *S. elegans*, it should be emphasized that this minimum was not reached in the majority (28 out of 46) of Dutch winters between 1947 and 1993 (fig. 3a). Noting this, considerably more records of the species in this period would be expected than are actually available. There may be several reasons why the number of reliable records is much lower than expected. For instance, the quantity and quality of (potential) observers and their methods may be significant. Thus, for plausible reasons, most of the older observations are from the tidal zone or just below it, whereas our own search for Anthozoa from the 1980s on was also extended into the subtidal area, by snorkeling and SCUBA diving

During low tide, specimens in the tidal zone face exposure to more extreme air temperatures. As a consequence intertidal individuals or populations are likely to be the first to disappear. Actually, since the cold winters of 1995/1996 and 1996/1997, numbers of *S. elegans* have decreased significantly, intertidally but also subtidally, and we only succeeded in finding the species at localities near the entrances of the

estuaries in the southwestern part of the Netherlands (table 2, fig. 1). In captivity *S. elegans* was found to tolerate incidental temperature drops to as low as 0°C (pers. observ. R.M.L. Ates). Nevertheless, our findings, although offering no conclusive proof, definitely suggest that Braber & Borghouts (1977) rightly assumed the disappearance of *S. elegans* to be due to the severe winter of 1962/1963. During that winter the minimum monthly mean sea-water temperature dropped some 3°C below the minimum registered at Texel in 1991 (see fig. 3a), which coincided with the disappearance of the species.

From the data in fig. 3a it follows that the Dutch population of *S. elegans* may have suffered decimation due to low temperatures during 18 out of 46 winters since 1947. In six winters the minimum monthly mean dropped below 0°C (which implicates the incidence of even lower short term minima). Therefore, even in the absence of more detailed data, it seems obvious that populations of *S. elegans* in the Netherlands have no permanent character, and that periods of decimation or extinction alternate with periods of recolonization and/or recovery.

Having determined where and in which periods *S. elegans* was definitely present, or is likely to have been present on the Dutch coast, some of the undocumented records listed in table 1 could refer to *S. elegans* after all, viz.: 11.iv.1953, Texel (Stock & Swennen); 26.iv.1958, Terschelling (Swennen); beginning of 1962, Schouwen and Vlissingen (Braber & Borghouts, 1977) (cf. table 1 and fig 2a).

Sagartia elegans forms stable, permanent populations in the Channel area, and the species also occurs occasionally in off-shore waters along the Dutch coast, where it has been recorded on ship's wrecks, etc. (Van Moorsel et al., 1991; Van Moorsel & Waardenburg, 1992), and in trawl catches of a benthic survey by NIOZ (RMNH Coel. 18648, 18649). Therefore, recolonization of the Dutch coast after relatively extreme winters is likely to take place by planktonic larvae from these populations. It may take some time for settled larvae to grow up and develop significant populations by subsequent sexual and asexual reproduction. Obviously the development of such "self-sustaining" populations will be favoured by a number of consecutive mild winters, and it may therefore be more than mere chance that the records of manifest numbers of the species coincide with such periods (cf. table 1, 2 and fig. 2a). It may further be observed that, provided suitable temperatures and substrata, such populations once established will reproduce sexually, thus increasing the numbers of planktonic larvae and hence the chance of settlement in less typical habitats and deeper penetration into the sea arms of the Dutch delta area.

Conclusion

There is no conclusive evidence for the occurrence of *Sagartia elegans* in the Netherlands prior to 1952 (Van Urk, 1952) but at present it is unquestionably an autochthonous species. It is most likely to be found on dikes in the most seaward parts of the Westerschelde, Oosterschelde and Wadden Sea. As the species appears to be sensitive to relatively low winter temperatures, it can only develop significant populations after several consecutive mild winters. Due to its estuarine character and the frequency of relatively cold winters, the Dutch coast is a marginal area for *S. elegans*.

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