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On the occurrence of the American jack-knife clam Ensis directus (Conrad, 1843) (Bivalvia, Cultellidae) in the Dutch Wadden Sea

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INTRODUCTION

The American jack-knife clam *Ensis directus* (Conrad, 1843) is a well known species of the east coast of North America (Abbott, 1974). In June 1979 the species turned up in Europe. The first specimens were found in the German Bight. Within a few years dense sublittoral populations had established themselves along the German North Sea coast (Von Cosel et al., 1982; Mühlenhardt-Siegel et al., 1983). A description and clues for identification have been supplied by Von Cosel et al. (1982) and De Boer (1984).

In the Netherlands empty shells of *E. directus* have been found washed ashore on the beaches of the islands Schiermonnikoog, Ameland and Terschelling for the first time in 1983 (De Boer & De Bruyne, 1983; De Bruyne & De Boer, 1983). This paper reports on findings of *E. directus* living in the Dutch Wadden Sea and on the possible mechanism of its westward dispersal into the Dutch Wadden Sea.

RESULTS

Regular sampling of the macrobenthic fauna at a number of fixed locations in the Dutch Wadden Sea revealed the presence of *Ensis directus* on several locations in 1983. Further inspection of samples collected previously showed that in 1981 this species had already been present in the sublittoral of the Ems estuary (Bocht van Watum). The identification of the specimens found was confirmed by Mr. R.M. van Urk, who prefers to call this species *Ensis americana* (Binney, 1870) (Van Urk, 1964, 1972).

Table 1 lists all known records of live *Ensis directus* in the Dutch Wadden Sea before October 1984. The locations are given in fig. 1. All records are from the intertidal zone, except for those from the Bocht van Watum and Molengat. Earlier records (1977) of two specimens of 2-3 cm length of *Ensis* sp. south of Terschelling by J.J. Beukema (personal communication) could not be identified as *E. directus* with certainty. Since 1983 *E. directus* is no longer a rare species, as can be seen from table 2. In the intertidal zone *E. directus* hardly occurs above Dutch Ordnance Level (N.A.P.). The species seems to prefer sandy sediments above muddy ones.

DISCUSSION

The occurrence of this American species in N.W. European waters is assumed to be the result of transport of larvae with tanker ballast water into the German Bight in early 1978 (Von Cosel et al., 1982). After its introduction into the German Bight the

Location	Date	Number	Length (mm)
1. Balgzand[1]	7-IX-1982	1	± 45
	VII-IX-1983	5	14; 16; 19; 19; 26
	II-III-1984	3	23; 29; 30
	VIII-IX-1984	14	11-30
2. Ballastplaat	31-VIII-1983	1	26
3. Piet Scheve Plaat	17-VIII-1983	1	± 90
	13-II-1984	2	40; ± 90
	6-IX-1984	2	4; 8
4. Schiermonnikoog[2]	21-VI-1983	5	25-30
5. Groninger Wad	14-IX-1983	1	23
	VIII-1984	21	10-19
6. Hond	VII-1984	5	34; 42; 43; 44; 52
7. Bocht van Watum	3-XII-1981	1	?
	11-XI-1982	2	25; 32
	24-II-1983	3	?; ?; 43
	7-XII-1983	1	12
	27-XII-1983	1	± 12
	9-VIII-1984	14	5-14
8. Molengat[3]	4-IV-1984	1	82

[1] J.J. Beukema, personal communication.
[2] J.B. Hulscher, personal communication.
[3] C. Swennen (1984).

Table 1. Records of *Ensis directus* in the Dutch Wadden Sea. For locations see fig. 1.

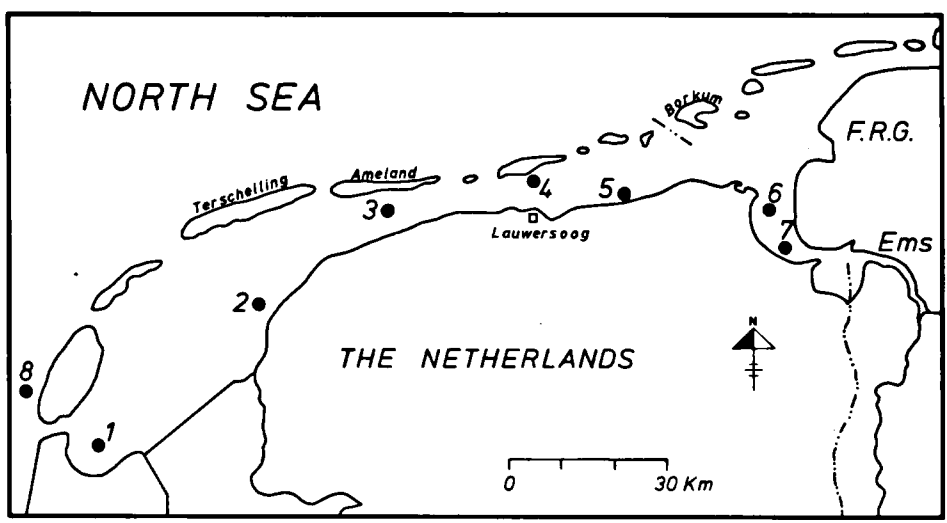

Fig. 1. Locations in the Dutch Wadden Sea area where *Ensis directus* was found. For explanation see table 1.

species dispersed rapidly along the coasts. Already in 1981 juvenile specimens were found in Danish waters off Rømø (Von Cosel et al., 1982) as well as in the Danish Wadden Sea near Rømø (P.B. Madsen, personal communication). In September 1985 some shells were found washed ashore near Hirtshals, N. Denmark (K. Reise and U. Mühlenhardt-Siegel, personal communication). According to length frequency analysis of specimens washed ashore at Blåvandshuk-Skallingen (Denmark) in May 1983 Mühlenhardt-Siegel et al. (1983) conclude that already in the spring of 1979 larvae must have been present in the adjacent Danish coastal waters.

The first specimens in the Dutch Wadden Sea were found in the Ems estuary in 1981. A specimen of 45 mm length found at Balgzand in September 1982 may indicate the presence of *E. directus* in the westernmost part of the Dutch Wadden Sea even in 1981. In any case the species had spread over the entire Dutch Wadden Sea by 1982 (table 1).

In the sublittoral along the German coast *E. directus* has established dense populations which regularly show massive mortality (Mühlenhardt-Siegel et al., 1983). Since densities of *E. directus* in the intertidal zone reach values of a few specimens per square meter, it has become a significant component in the Wadden Sea ecosystem. Even oystercatchers (*Haematopus ostralegus*) have adapted to preying on these bivalves (C. Swennen, personal communication).

The spreading of *E. directus* along the coasts of the North Sea took place rapidly. A rapid dispersion of larvae in a northerly direction is very well possible because of the existence of a northerly directed residual current in the eastern part of the German Bight (Goedecke, 1968). A fast dispersion in southwesterly direction, however, is less likely because in this case the larvae should be able to move against a northeasterly directed residual current. Such a counter-current dispersion is nevertheless possible. It was demonstrated for the mussel parasite *Mytilicola intestinalis* Steuer, 1902 (Crustacea, Copepoda), which has spread from Borkum to Ameland in the years 1950-1959 (Havinga, 1960; Korringa, 1952, 1953, 1954). Larvae of *M. intestinalis* are pelagic for ca. 40 hours (Grainger, 1951). Therefore, the observed fast dispersion of *E. directus* can be explained only by a long lasting pelagic occurrence. Transport of postlarval bivalves by tidal currents is known to exist in *Cerastoderma edule* (L., 1758) (Baggerman, 1953) and *Macoma balthica* (L., 1758) (De Vlas, 1973; Beukema, 1973). Observations by Williams & Porter (1971) make it very likely that such transport does occur in *E. directus*. They found *E. directus* abundantly in plankton samples from January to June, the length of

Location	1983	1984
1. Balgzand[1]	0.6	1.2
2. Ballastplaat	1	—
3. Piet Scheve Plaat	2	1.3
4. Groninger Wad	0.6	9
5. Bocht van Watum	0.2	1.6

[1] J.J. Beukema, personal communication.

Table 2. Density (N/m²) of *Ensis directus* in autumn at some locations in the Dutch Wadden Sea. For locations see fig. 1.

the specimens ranging from 2 to 46 mm. Similar observations were made in the German Wadden Sea, where specimens of *E. directus*, ranging from 25 to 55 mm, were found in plankton samples in February and the summer of 1982. Juvenile *Ensis* sp. (1-2 mm) were found from June to November 1982 (W. Heiber, personal communication). Experiments by Sigurdsson et al. (1976) with 20 bivalve species, among which *Ensis* sp., indicate that byssus drifting constitutes an effective means of transport for young postlarval bivalves.

Transport of pelagic larvae and postlarvae in the opposite direction of the northeasterly residual current is possible only when the animals are transported preferentially by the westerly directed ebb component of the residual current, or when inversions of the residual current pattern occur.

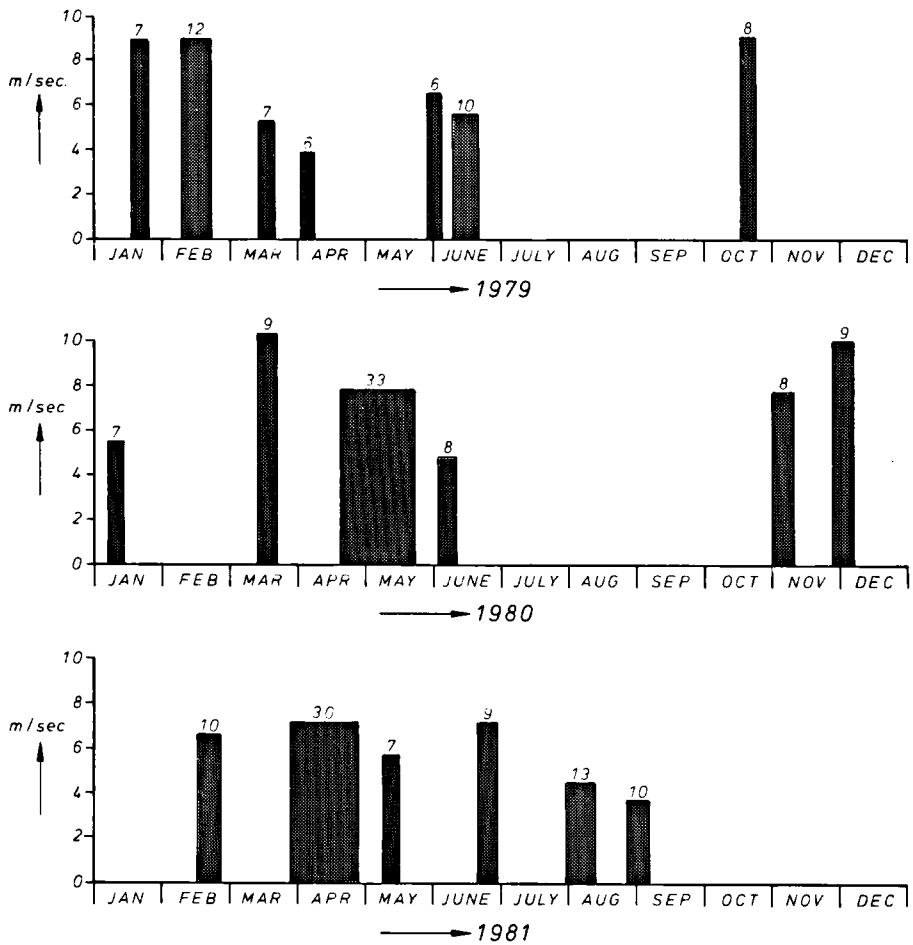

Fig. 2. Periods with northeasterly winds (340°-110°), recorded at Lauwersoog, and mean wind velocity (m/sec). Figures above the bars indicate the length of the periods (days).

Selective tidal migration as has been demonstrated to occur in *Macoma balthica* (see De Vlas, 1973; Beukema, 1973), larvae of *Pleuronectes platessa* (L., 1758) (Creutzberg, et al., 1978; Rijnsdorp & Van Stralen, 1982) and *Macropipus holsatus* (Fabricius, 1798) (Venema & Creutzberg, 1973) is not known to exist in *Ensis directus*.

In an analysis of 27 years of current measurements carried out at Dutch light vessels Van de Kamp (1983) shows that at LV "Terschellingerbank" inversions of the residual current pattern do occur. Even over a period of a month westerly (SW-NW) directed residual currents have been found. Under the influence of persistent northeasterly winds the water circulation pattern in the North Sea changes in such a way that north of the Wadden Sea a westerly directed residual current develops (Riepma, 1980; Backhaus, 1984). Such northeasterly winds proved to have been present for periods of at least seven days in the months with a net westerly water movement at LV Terschellingerbank. Wind data, recorded at Lauwersoog by the Royal Netherlands Meteorological Institute, show that such northeasterly winds were present during several periods in 1979-1981 (fig. 2). Therefore, the conclusion is drawn that in those years there have been several periods with water circulation conditions favourable for a dispersal of *E. directus* from the German Bight to the Dutch Wadden Sea. This conclusion is further corroborated by the results of a simulation kindly carried out by Dr. J.O. Backhaus with his North Sea water circulation model. In this simulation arbitrary matter was continuously introduced near the mouth of the Elbe from 1 October 1979 to 31 May 1980. In April and May 1980, months with prevailing northeasterly winds (cf. fig. 2), the matter was dispersed in a westerly direction, reaching as far as Texel (fig. 3). Another simulation in which matter was introduced near Texel, showed a significant southwesterly dispersal along the Dutch coast during April 1981 (cf. fig. 2).

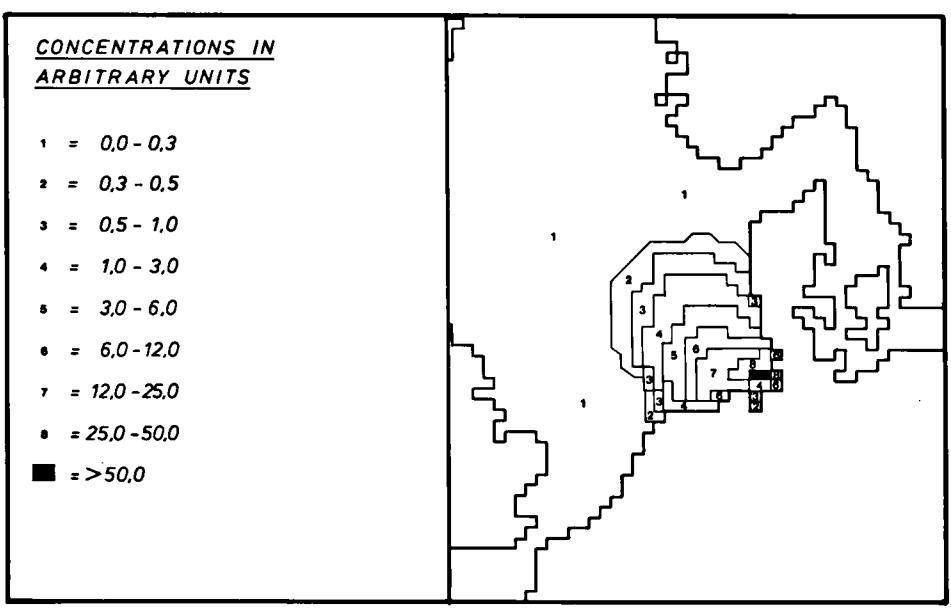

Fig. 3. Simulation of dispersion of matter introduced near the mouth of the river Elbe. Distribution patttern on 31-V-1980 (courtesy of Dr. J.O. Backhaus).

Another possible mechanism for a westward transport of larvae and postlarvae of *E. directus* is the existence of residual counter-currents. These counter-currents were found to exist in the coastal area of the German Bight by Göhren (1970). They develop along gently sloping coasts in shallow water. So even under conditions of the "normal" northeasterly residual current in the German Bight a westward dispersal of *E. directus* would have been possible through these counter-currents. These counter-currents may very well have contributed to the westward dispersal of *Mytilicola intestinalis* cited above.

CONCLUSIONS

After first appearing in the German Bight in June 1979 *Ensis directus* has spread out towards Danish and Dutch coastal waters. In 1981 it was first found in the Ems estuary and in 1982 it was found living in intertidal flats over the entire Dutch Wadden Sea. The fast dispersion of this species is supposed to be due to a long lasting pelagic occurrence of larvae and postlarvae. Furthermore, the dispersal in a westerly direction towards the Dutch Wadden Sea is likely to have been caused by the occurrence of residual counter-currents due to periodic northeasterly windfield stress as well as deformation of rotational tidal currents in shallow waters.

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SAMENVATTING

De Amerikaanse zwaardschede *Ensis directus* (Conrad, 1843) werd voor het eerst in 1979 in Europa aangetroffen in de Duitse Bocht (Noordzee). Sindsdien heeft deze Oostamerikaanse soort zich zowel in noordelijke als westelijke richting verspreid. In 1982 kwam de soort over de gehele (internationale) Waddenzee voor. De verspreiding in noordelijke richting laat zich gemakelijk verklaren door de richting van de reststromen in het oostelijk deel van de Noordzee. De verspreiding in westelijke richting, d.w.z. tegen de reststroom in, kon worden verklaard uit (1) het pelagisch voorkomen van larven en postlarven gedurende een groot deel van het jaar, (2) het bestaan van westwaarts gerichte tegenstromen in ondiepe wateren van de Duitse Bocht, en (3) het periodiek omkeren van de reststroompatronen in de Noordzee onder invloed van wind uit het Noordoosten.