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Styela clava Herdman (Urochordata, Ascidiacea), a successful immigrant to North West Europe: ecology, propagation and chronology of spread

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ABSTRACT: Since its first occurrence at Plymouth, southern England, in 1952 the East Asiatic ascidian *Styela clava* has spread to many localities along the coasts of the south and west British Isles, Ireland, northern France, Belgium, the Netherlands, Denmark and Germany. While some dispersal may occur by natural means, spreading over long distances is probably due to transfer along with oysters when relaid elsewhere. Transport while attached to the hulls of ships or drifting *Sargassum* is also possible. *Styela clava* is a large, hardy and fast-growing species with a tough, leathery tunic, and has no recorded enemies or native analogues among the NW European ascidian fauna. At many sites it has established dense populations of 500–1000 specimens/m^2 and in some cases has nearly outcompeted some of the native ascidian species.

INTRODUCTION

The NW Pacific solitary ascidian *Styela clava* Herdman is indigenous to the Sea of Okhotsh, Sea of Japan and the coasts of Japan, Korea and northern China as far south as Shanghai (Abbott & Johnson, 1972). Over the past 70 years it has considerably extended its geographical range to include the coasts of California, the eastern United States, southern Australia and NW Europe. It is presumed in all these cases to have been unintentionally introduced by man. The present paper reviews the species' ecology and reproduction and updates its geographical distribution.

DESCRIPTION

The body is club-shaped and consists of an elongated oval body proper and a long tapering peduncle terminating in a discoid holdfast. Maximum length including the peduncle is 125 mm (in exceptional cases 160 mm), which makes *S. clava* the second largest ascidian in NW Europe. Small specimens, up to 30 mm long, have no distinct peduncle. Both apertures are four-lobed. The surface of the tunic on the peduncle and posterior part of the body is folded longitudinally, and on all other parts transversely wrinkled or irregularly grooved. The colour is chocolate-brown, darker on the peduncle. Smaller specimens are yellowish-brown. The apertures have alternately longitudinal yellow and brown stripes.

The surface of larger specimens forms a very suitable substrate for various epibionts. It is often overgrown with tufts of red or green algae, sponges, actinians, hydroids, bryozoans or smaller specimens of the same species. Other ascidians such as *Ascidiella aspersa* (O. F. Müller) or *Botrylloides schlosseri* (Pallas) are frequently attached to the tunic.

ECOLOGY AND LIFE CYCLE

Attachment, densities and depth of occurrence

S. clava is always attached to various objects such as rocks, stones, and shells of live or dead epifauna bivalves (*Mytilus edulis* L., *Modiolus modiolus* [L.] and species of oysters) and barnacles. Small individuals are sometimes attached to larger specimens. *S. clava* may fix itself to the haptera of *Laminaria saccharina* (L.) or, more often, to the main axis and lower primary laterals of *Sargassum muticum* (Yendo), but never to the thallus. Occassionally it attaches to peat (Buizer, 1980). It occurs in abundance on suitable artificial substrates such as pier piles, jetty walls, concrete structures, car tyres used as fender beams, and submerged ropes or iron chains and wires. It is also common on buoys and floating docks. The species is apparently a secondary settler as it seems to colonize only an already fouled substrate. It is mostly confined to sheltered localities free of strong wave action, such as inlets, bays, harbours and marinas.

On natural substrates such as rocks or oyster beds the species may attain densities of 50–100/m^2 (Minchin & Duggan, 1988; Lützen & Sørensen, 1993). Much higher densities, 500–1000/m^2, however, have been recorded from docks and sluice walls or test panels (Holmes, 1976; Sandee et al., 1980; Minchin & Duggan, 1988).

S. clava is a predominantly littoral species, which is especially abundant 10–200 cm below the sea surface in areas without tides or when attached to floating objects. When found under rocks, it is able to withstand some tidal emersion, as it may occur up to 30 cm above the level of extremely low water spring tides in southern England (Holmes & Coughlan, 1975). The species may extend to depths of 15–25 m (Abbott & Johnston, 1972; Buizer, 1980), but a record of 40 m by Dauvin et al. (1991) is probably exceptional.

Osmoregulation

S. clava generally evades areas with estuarine conditions. Sims (1984) showed Californian specimens to have a limited osmoregulatory capability in hyposaline media. Three days' immersion in 26.5‰ saltwater resulted in poor vital functions and complete cessation of siphonal responses. This may explain why heavy rainfall during the winter of 1972/1973 was observed to drastically reduce the density of two monitored populations of *S. clava* in Newport Bay, California (Kelly, 1974). The species is nevertheless capable of surviving shorter temporary drops in salinity down to 8‰ and presumably does this by closing its siphons for extensive periods (Sims, 1984). The population in the Limfjord, Denmark, may tolerate salinities that are lethal to the species elsewhere. In the eastern part of the fjord the average salinity ranges between 26‰ and 28‰ with periodic drops to below 20‰ for several days. When subjected to a stepwise decrease in salinity from 31‰ to 18‰, 17 of 24 animals survived for 40 days (at 12 °C), while 6 of 12 specimens were still alive after 50 days when the salinity was further reduced to 16‰ (Lützen & Sørensen, 1993). This corresponds to the report by Kashenko (1996) that larvae of *S. clava* from the Sea of Japan are able to complete metamorphosis at salinities ranging from 32‰ to 20‰, but that a salinity below 18‰ was deleterious.

Reproduction, settling and growth

S. clava is hermaphroditic and oviparous with a pelagic lecithotrophic larval life of 24–28 h at 20 °C (Holmes, 1969). The morphology of the larva was described by Wallace (1961, as *S. mammiculata*). No data on reproduction are available from East Asia. Kelly (1974) found spawning to take place from June through September in Newport Bay, California. The annual cycle has been studied at Southampton 1964–1966 (Holmes, 1969) and in the Limfjord, Denmark, throughout 1991–1992 (Lützen & Sørensen, 1993). Ripe ova and sperm are present in the Limfjord population from mid-May, but settling hardly commences until late July. Reproduction and settling peak in August and September and continue until the end of October. The gonadal cycle in the English Channel follows the same course. Settlement also exhibits a similar pattern, as it takes place chiefly from ultimo July through September with a peak in August.

At the end of the breeding season there is a breakdown of ova and sperm that have not been spawned. This process starts in October or November and continues throughout late winter (Jørgensen & Lützen, 1997). In specimens which survive the winter there is reconstruction of the gonads during spring and early summer.

Growth of individual *S. clava* attached to fender beams or settlement panels was recorded both in the Limfjord and at Southampton, supplemented with size-frequency data of monthly samples over 2 years at the latter locality. Limfjord specimens which settle in mid-August grow to a length of 17–48 mm by the end of October. Growth rate decreases in November and growth is slow, if not completely arrested, during December through April (at temperatures of 0–5 °C). There is a considerable mortality, especially of smaller individuals, throughout winter. The 10-month-old survivors reach a length of 50–75 mm in June and become fully mature for the first time. When spawning starts in July and August they are 75–95 mm. During early and mid-summer there are also many 12 to 40-mm-long specimens, representing late settlers of the previous year. Such specimens, together with some of the larger ones, probably survive their second winter to attain a length of 110–120 mm and reproduce for the second time when 1.75–2 years old. The lifespan of Southampton *S. clava* is estimated to be shorter and only in exceptional cases does it exceed 15 months (Holmes, 1969). Thus, the year class that settled between July and early September 1964 had largely disappeared between September and October of the next year.

Competition

Wherever *S. clava* has appeared it has succeeded in establishing populations that have either consolidated or expanded slowly (Berman et al., 1992) or rapidly (Buizer, 1980). At many places its success is due to the fact that it has no native analogues (Berman, 1990). Compared to most indigenous solitary ascidians, because of its tough tunic it is better protected against desiccation if exposed. All 20 specimens of different sizes survived 3 days' stay above water when kept moist at 10 °C (Lützen & Sørensen, 1993). The tunic also offers effective protection against predators, of which none have been recorded so far. Svane (1983) correlated a thick leathery tunic with a slow generation turnover, but growth in *S. clava* is comparatively fast. The species is able to withstand temperatures ranging from subzero to at least 23 °C (Holmes, 1976; Buizer, 1980) corresponding to the natural regime in NW European coastal waters. Even in the severe winter of 1979 no increased mortality was observed in the eastern Scheldt population (Buizer, 1980). Due to its considerable body length, even medium-sized specimens stand clear of almost all other sessile organisms on a surface. This not only makes it more competitive as a filtrator, but may also allow it to eliminate larvae of co-inhabiting species from the plankton. Osman et al. (1989) have shown that *S. clava* is capable of ingesting large numbers of oyster larvae [*Crassostrea virginica* (Gmelin)] and that it may reduce their settlement on adjacent surfaces.

S. clava is at a disadvantage as it spawns weeks or months after the most common native species with which it competes for space. On floating docks and pier walls of Limfjord harbours and marinas, successful settling of mussel spat may totally prevent *S. clava* from recolonizing a surface previously heavily populated by the species. On the other hand, late *S. clava* settlers may colonize surfaces left bare after the death of previously settled *Ascidiella aspersa* (Holmes, 1969).

Since the introduction of *S. clava* to the south coast of England, the increase in its number seems to have been paralleled by a decline in the population of another ascidian, *Ciona intestinalis* (L.) (M. Thorndyke, personal communication). In southern California *S. clava* and other immigrant ascidians are now the dominant ascidians and have largely replaced the indigenous *Pyura haustor* (Stimpson) and *Ascidia ceratodes* (Huntsman) which were the most abundant species years ago (Lambert & Lambert, 1998). At many sites in New England, the species has slowly built up its populations, occurring in dense monocultural stands containing thousands of individuals (Berman, 1990).

DISTRIBUTION AND SPREAD

Chronology of spread

Spread to regions other than Europe

S. clava was probably introduced to California in the late 1920s (Abbott & Johnson, 1972). The species, sometimes known as *S. barnharti* Ritter & Forsyth, is now distributed from San Francisco Bay to Mission Bay, San Diego (Fay & Johnson, 1971; Abbott & Johnson, 1972; Sims, 1984). A small isolated population at Nanaimo, Vancouver Island, British Columbia, Canada, was discovered in the 1990s (Lambert & Lambert, 1998).

S. clava was first found off Massachusetts in 1970 (Berman et al., 1992). Presently, the species has extended its range from Long Island, New York to Portsmouth, New Hampshire (Carlton, 1989; Osman et al., 1989).

In southern Australia Holmes (1976) reported *S. clava* in 1972 from fouling panels in Hobson's Bay, Victoria, from where it has apparently not spread further.

Spread to and within Europe (Fig. 1)

1952–1969: *S. clava* was first discovered in Europe in Plymouth Sound in the summer of 1953 by Carlisle (1954), who considered it to be a new species, *S. mammiculata*. The specimens were so large (54–111 mm) that they must have settled in 1952. Tokioka (1955) and Millar (1960) showed that *S. mammiculata* and *S. clava* were one and the same species. There are no further records until 1957–1958, when it was found in the harbours of both Portsmouth and Southampton (Coughlan, 1969; 1985). In 1959 numerous specimens were discovered in Langstone Harbour (Houghton & Millar, 1960). By 1962 the species had become very abundant in Southampton Waters and had spread to the harbours of Shoreham, Poole and Chichester (Stubbings & Houghton, 1964; Holmes, 1969; Coughlan, 1985; Wells, 1987). The first find from outside the south coast of England was made in September 1968, when Coughlan (1969) collected many specimens on Pwllcrochan Flats, Milford Haven, south Wales. The size of the specimens (63–

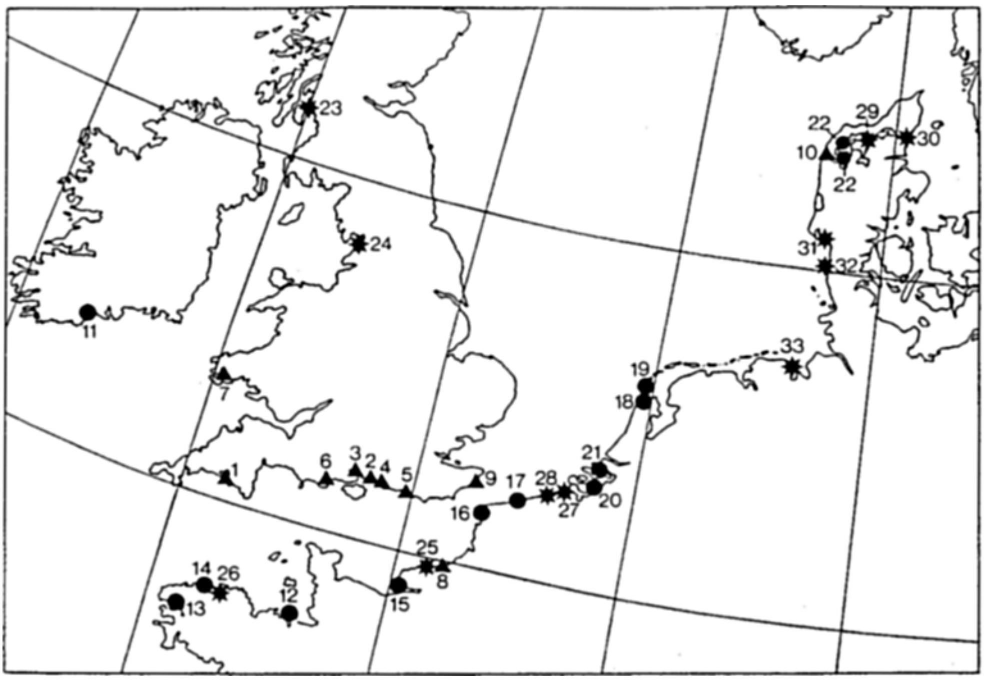

Fig. 1. Distribution of *Styela clava* in NW Europe. Triangles, 1952–69; circles, 1970–80; asterisks, 1981–97. 1 Plymouth Sound; 2 Portsmouth Harbour; 3 Southampton Harbour; 4 Langstone and Chichester Harbours; 5 Shoreham Harbour; 6 Poole Harbour; 7 Milford Haven; 8 Dieppe; 9 Dover Harbour; 10 Nissum Bredning; 11 Cork Harbour; 12 Dinard; 13 Brest; 14 Roscoff; 15 Le Havre; 16 Ambleteuse; 17 Dunkerque; 18 Den Helder; 19 Harbours of 't Horntje and Oudeschild, Texel; 20 Eastern Scheldt; 21 Grevelingen; 22 Island of Mors; 23 Isle of Cumbrae; 24 Heysham Harbour; 25 Paluel Power Station; 26 Morlaix; 27 Knokke-Heist and Zeebrugge; 28 Oostende; 29 Central broad, Limfjord; 30 Eastern Limfjord; 31 Esbjerg Harbour; 32 List Harbour, Sylt, and Havneby Ferry Harbour, Rømø; 33 Wilhelmshaven

125 mm) indicated that they were of the 1967 year class. By the late 1960s *S. clava* had crossed the English Channel, as a small population was discovered at Dieppe, in 1968 and 1969 (Monniot, 1970). From 1969 there is an unconfirmed report of *S. clava* from Dover Harbour (Coughlan, 1985). In the mid-1960s the species was presumably introduced to Nissum Bredning, western Limfjord, Denmark (Lützen & Sørensen, 1993).

1970–1980: The early 1970s saw a further spread of *S. clava* to Cork Harbour, Ireland, in 1971/1972 (Guiry & Guiry, 1973; Minchin & Duggan, 1988), to the present day the only known Irish population, and to a number of French localities: Dinard in 1971 (Huwae & Lavaleye, 1975); Brest and Roscoff, Bretagne, both in 1973 (Minchin & Duggan, 1988); and Le Havre harbour in 1977 (Breton & Dupont, 1978). By 1980 the species had extended its range further northwards along the French coast to Ambleteuse (Buizer, 1980) and Dunkerque in 1980 (Davoult et al., 1993).

The first Dutch populations of *S. clava* were discovered in Den Helder harbour in March 1974 and a few months later the species had settled at the harbour of 't Horntje on Texel (Huwae, 1974; Huwae & Lavaleye, 1975). By 1976 the species had been firmly established on pontoons in the naval harbour of Den Helder. In the autumn of 1974 a few specimens were found for the first time in the eastern Scheldt, SW Netherlands (Westerwil, 1975). In the following years *S. clava* became abundant all over this area and (from 1980) invaded the nearby Grevelingen area (Buizer, 1980).

A small population of *S. clava* that had presumably been present from the mid-1960s in the westernmost part of the Limfjord, Denmark, was recorded with certainty in 1978 (Christiansen & Thomsen, 1981a,b). By 1980, the species had extended its range further eastwards into the fjord to the east and west of the island of Mors.

1981–1997: During this period there were only a few new British records of *S. clava*. There was an unconfirmed report of the species from the Isle of Cumbrae, western Scotland, in 1981, and a find of several specimens, all probably from the summer of 1982 settlement, in April 1983 in Heysham Harbour, Lancashire (Coughlan, 1985). Slager (1982a,b) reported additional finds from the eastern Scheldt and from the harbour of Oudeschild, Texel, The Netherlands. New French records included a mussel bed near the power station at Paluel, west of Dieppe, from 1983 (Davoult et al., 1993) and Morlaix, Bretagne, from 1990 (Dauvin et al., 1991). Two finds in 1986-88 from the Belgian harbours of Knokke-Heist and Zeebrugge (d'Udekem d'Acoz, 1986; Dumoulin, 1987; Rappé, 1990) and a third find from Ostend in 1995 (Eneman, 1995) filled the gap in distribution between the northern French and the southern Dutch populations. Lützen & Sørensen (1993) described the steady eastward expansion of *S. clava* through the Limfjord, Denmark. By 1986 the species had entered the fjord's central broad, but not until 1991 did it reach the eastern mouth of the fjord into the Kattegat.

Apart from the 1974 finds from Den Helder and Texel, The Netherlands, there were no further records of *S. clava* from the North Sea proper until a few specimens (settled in 1994) were identified in March 1995 in the Esbjerg yacht harbour, SW Jutland, Denmark. It had probably arrived there some years before (A. Andersen, personal communication). Surveys by the author in 1995 established that the species was probably absent from the following German localities at that time: Cuxhaven, Wilhelmshaven, Helgoland and Langeroog yacht harbour. The first specimens from the German North Sea coast were collected from floats in the harbour of List, island of Sylt, in the autumn of 1997, and in June 1998 the pilings in the ferry harbour of Havneby on Rømø, Denmark (a few nautical miles from List), were found to be massively covered by the species (K. Reise, personal communication). When Wilhelmshaven was revisited in June 1998 *S. clava* was observed to be rather abundant in the Nassauhafen basin.

Means of spreading

The spread of *S. clava* along the Limfjord, within the Zeeland province of The Netherlands, and perhaps along part of the south coast of England probably occurred through dispersal of planktonic eggs and larvae. The species' overall discontinuous distribution must, however, be explained otherwise. Circumstantial evidence suggests that *S. clava* was first introduced to Europe by vessels returning in 1952 to Devonport (at Plymouth) and Portsmouth from the Korean War (Coughlan, 1969). Coughlan (1985) and Minchin & Duggan (1988) presumed the isolated populations in Ireland, western England and Bretagne to have been introduced on hulls of coastal tankers and ferries from southern England. Being a rather rheophobic species, it remains a question, though, whether *S. clava* can survive on ships in continuous service. The only record from a ship's hull is that of a vessel moored for almost a year in Cork Harbour (Minchin & Duggan, 1988).

It is significant that the initial record of *S. clava* from the Limfjord, Denmark, was from an oyster bed where spat from the English Channel had been relaid previously. Probably also many of the French and some Dutch populations originated with spat of the Japanese oyster (*Crassostrea gigas* Thunberg) introduced from Japan, an import which started in the early 1970s, or with oysters transferred within the Channel region.

Still another possibility is distribution of specimens on drifting *Sargassum muticum*, introduced to Europe early in the 1970s (Critchley et al., 1983). The primary laterals of this seaweed, to which *S. clava* frequently attaches, become detached from the holdfast toward the end of the growth cycle and can float for some considerable distance. *Sargassum* fronds with *S. clava* are often cast ashore in the Limfjord. This means of transportation is probably merely of local importance, as *S. clava* arrived at most NW European sites 5–15 years before *S. muticum*, but this may be how the isolated SE North Sea populations became established.

CONCLUSIONS

Over the last 45 years, the immigrant *S. clava* has become a conspicuous member of benthic and fouling communities in NW European waters. Its impact on the native communities is generally little known. At some places it seems to have competitively excluded some other ascidians, but in most habitats has been added to the community without any demonstrable effects. The species is tolerant of a wide range of temperatures and some populations are adaptable to changing salinity. It is a likely prediction that in the not too distant future the species will spread further along the coasts of NW Europe and that its distribution will finally include most parts of the British Isles and western Scandinavia.

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