Running Head: The Manila clam in Britain

Introduction, dispersal and naturalisation of the Manila clam *Ruditapes philippinarum* in British estuaries, 1980-2010.

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The introduction of the Manila clam into British coastal waters in the 1980s was contested by conservation agencies. While recognising the value of the clam for aquaculture, the government decided that it posed no invasive risk, as British sea temperatures would prevent naturalisation. This proved incorrect. Here we establish the pattern of introduction and spread of the species over the first thirty years of its presence in Britain. We report archival research on the sequence of licensed introductions and examine their relationship in time and space to the appearance of wild populations as revealed in the literature and by field surveys. By 2010 the species had naturalised in at least eleven estuaries in southern England. These included estuaries with no history of licensed introduction. In these cases activities such as storage of catch before market or deliberate unlicensed introduction represent the probable mechanisms of dispersal. In any event naturalisation is not an inevitable consequence of introduction and the chances of establishment over the period in question were finely balanced. Consequently in Britain the species is not currently aggressively invasive and appears not to present significant risk to indigenous diversity or ecosystem function. However it is likely to gradually continue its spread should sea surface temperatures rise as predicted.

Key words: Manila clam, *Ruditapes philippinarum*, Invasion, Naturalisation, Non-indigenous species, British estuaries.

INTRODUCTION

The Manila clam, *Ruditapes philippinarum* (Adams & Reeve, 1850) is indigenous to sub-tropical and temperate coastal waters of the western Pacific and Indian oceans from the Sea of Okhotsk to the South China Sea and as far west as Pakistan (Humphreys *et al.*, 2014). While the adult clam lives buried in coastal sediments, natural dispersal is achieved during a planktonic larval stage. At metamorphosis the animal settles on the seabed from the intertidal to shallow sub-littoral zones. The species is euryhaline to the extent that even the more vulnerable larval stages can achieve growth in estuarine salinities as low as 12 (Lin *et al.,* 1983; Breber, 1996).

The Manila clam is a high value seafood species. Since the early 20th century, due to activities related to the aquaculture and fishing industries, the species has become established along the Pacific coast of North America, the Atlantic coast of Europe, the Mediterranean Sea and elsewhere. In the first such introduction, Japanese clams were taken to the Hawaiian Islands (Bryan, 1919; Yap, 1977). Other Japanese clams reached the North American Pacific coast in the 1930s, as an accidental introduction with stocks of Pacific oyster (Quayle, 1949). They now extend from California to British Columbia (Magoon & Vining, 1981). European introduction commenced in the 1960's when eastern Pacific clams were introduced to France where they are today cultivated on both Mediterranean and Atlantic coasts (Ifremer, 1988; Flassch & Leborgne, 1992). They have also been introduced for aquaculture into the Italian Adriatic and the coasts of Germany, Spain, Ireland and Norway (Humphreys *et al.*, 2014).

R. philippinarum was the latest of a number of commercially significant non indigenous bivalve species purposefully introduced into British waters, the others notably including the American hard-shelled clam *Mercenaria mercenaria* (Linnaeus, 1758) (Mitchell, 1974) and the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) (Humphreys, 2014). The Manila clam was first brought to Britain in 1980 by the then UK government's Ministry of Agriculture, Fisheries and Food (MAFF). Motivated by potential economic benefits from aquaculture, MAFF imported a consignment of Manila clams from the US Pacific coast. After quarantine procedures, experimental work and field trials, the species was made available to commercial growers (Humphreys, 2010). This ignited what was described in the national press as a "full scale row" between MAFF and the Nature Conservancy Council (the statutory conservation agency) concerning the introduction of an "alien monster" (Daily Telegraph 29th April, 1989). The first reported naturalised population in Britain occurred in Poole Harbour on the central south coast of England (Jensen *et al.,* 2004).

Here we report on the pattern of Manila clam dispersal from 1980 to 2010, its first 30 years in Britain. We relate this to collated information from various sources on licensed introductions and examine the implications of this relationship in terms of invasiveness, dispersal and future British distribution.

METHODS

Historic introductions

The pattern of licensed introductions since the initial importation of broodstock in 1980 has been established from: archived file materials held by the UK Joint Nature Conservation Committee (JNCC); aquaculture records provided by the British government's Centre for Environment, Fisheries and Aquaculture Science (Cefas); Parliamentary papers and Hansard (the record of proceedings of the British parliament); Government reports and aquaculture guidelines from the 1980's and journal papers reporting field experiments and trials.

Definition of wild clams

We define wild Manila clams as individuals which have not been introduced directly during aquaculture activity but which have settled naturally as spat from parents which have successfully reproduced in British waters. Therefore wild clams as we define them may or may not be feral, in the sense of deriving directly from anthropogenically introduced parents. Nevertheless, in line with Williamson, (1996), we apply the terms established and naturalised only to persistent self sustaining populations which are not dependent on seeding from aquaculture operations.

Identification

A degree of taxonomic volatility has led to a number of synonyms for *Ruditapes philippinarum*, some of which are still used by biologists and which are commonly found in the literature on the species. Notable among these are the genus synonyms *Tapes* and *Venerupis.* Here we refer to all species in line with the accepted binomials as specified in the World Register of Marine Species (WoRMS, 2014).

As a non-indigenous species the Manila clam is not yet included in widely used British identification keys and can consequently be mistaken for related native species with which it can be sympatric: notably another venerid bivalve *Ruditapes deccusatus* (Linnaeus 1758). Wimbledon (2003) has provided a useful photographic guide comparing the gross shell morphology and coloration of the two species, but phenotypic shell variation is such that these features alone are not always sufficient to definitively separate them. Therefore we have based our identifications also on siphon anatomy. In particular we distinguish the separate inhalant and exhalent siphons of *R. deccusatus* from those of *R. philippinarum* which are joined for most of their length (see Humphreys, 2010). A third native clam *Venerupis corrugata* (Gmelin, 1791), which can be sympatric with *R. philippinarum* towards the seaward end of British estuaries also has fused siphons, but can be distinguished on the basis of shell shape and much larger pallial sinus, a feature of the inside of the shell.

Distribution and abundance

The progress of dispersal of the species was determined from a number of sources. Malacological Society of London records, grey literature searches and informal reports and specimens provided by colleagues from universities and government fishery agencies all provided useful information over the period in question. In all cases, such initial reports were followed up and substantiated in terms of both species and location by our own field visits and observations. In addition opportunities presented by our own funded research and commissioned surveys have also been useful in tracking the clam's dispersal (Jensen *et al.,* 2004; Humphreys *et al.,* 2007; Caldow *et al.,* 2007; Herbert *et al.,* 2010).

Dates of first arrival of wild populations have been determined where possible on the basis of our own field monitoring, if necessary extrapolating from the oldest age group in a recently established population when first discovered. Occasionally unpublished reports have also proved useful in this respect.

While this paper is primarily about dispersal and gross distribution we have also made some attempt to report abundance in such a way to allow comparisons over time and between locations. Although all reported occurrences were substantiated by us, our information on abundance is derived from many different sources, surveys and projects over the thirty year period. Our own methods for example ranged from shore based sediment sampling, boat based core, hand dredge and grab sampling, to using commercial dredges from larger fishing and research vessels. In one case our historic evidence consists of records (by R.H.) of shell fragments resulting from predation by gulls and crows. Since these approaches varied by locality and time we cannot with confidence provide comparative information on abundance in terms of population densities, but as an alternative we have presented approximate comparative abundance estimations according to the SACFOR scale (Hiscock, 1996).

Names and locations of coastal sites

The names and numbers of coastal sites referred to in this paper are in accordance with the estuaries review conducted by the Nature Conservancy Council (NCC) and published in Davidson *et al.*, (1991). That report includes a comprehensive list of British estuaries defined broadly enough to include extensive areas of soft tidal sediment at the marine end of the estuarine continuum, but located outside river mouths. Davidson's report therefore provides a useful catalogue of coastal locations within which Manila clam habitat types would be present. As well as providing exact site locations and names, Davidson's catalogue has proved useful in provoking us to confirm the apparent absence of the species from ostensibly compatible estuaries.

RESULTS

Earliest British introductions

The initial consignment of imported Manila clams reached the MAFF Fisheries Laboratory at Conwy, North Wales in 1980. The near-by Menai Strait provided the location for the first documented introduction into UK coastal waters in 1983. In 1984 the Conwy laboratory provided broodstock to the Seasalter Shellfish Company which operated hatchery sites in Reculver (outer Thames estuary) and Walney Island (Morecambe Bay). The earliest record of a commercial licence to deposit Manila clams (under mesh) in British waters was given to the Walney Island hatchery for the purpose of on-growing clams for sale as a part-grown alternative to smaller and more vulnerable hatchery spat. These and Guernsey Sea Farms, a third hatchery in the Channel Islands, commenced the supply of juvenile Manila clams for aquaculture enterprises, both in the UK and abroad. Between 1984 and 2010 the Manila clam was introduced under licence into 18 further British coastal locations from the west of Scotland to southern England. Table 1 provides a chronological record of earliest licensed introduction by estuary. The locations of these sites are shown in Figure 1.

Distribution

For the period 1980-2010, Malacological Society of London records contained no suggestion of the existence of wild Manila clam populations north of the southern and south east coasts of England. Moreover although we know of licensed introductions further north of these areas (Figure 1), our own searches on both the east and west coasts of Britain corroborated this absence.

Wild Manila clam populations were found to be present in two regions of England: The central south coast from the Exe Estuary in the west to Chichester Harbour in the East, and the Kent and Essex coasts from the Thames estuary northwards to the Stour estuary.

Patterns of introduction and spread

SOUTH COAST

The English coastline extending from The Exe estuary east to Pagham Harbour includes 18 estuaries, five of which are on the Isle of Wight (Table 2a). Poole Harbour, one of the mainland estuaries, contains the UK's first reported naturalised Manila clam population (Jensen *et al.*, 2004). Here wild clams appeared about two years after the initial (1988) licensed introduction for aquaculture by Othniel Oysters Ltd. Subsequently the population extended its distribution within the Harbour and, between 2002 and 2009, increased its mean intertidal population density from 5 to 12 individuals per m^2 (Herbert *et al.*, 2010). By 2010 wild Manila clams had also naturalised in six other south coast estuaries (Table 2a).

The earliest and currently most extensive of these new populations is in Southampton Water which lies about 48 km east of Poole Harbour. We estimate that the species arrived in Southampton Water in 2002: By 2004 relatively small specimens (length up to 21mm.) were found ranging from the Itchen and Test rivers of the upper estuary to the lower reaches of the north shore of Southampton Water proper. By 2005 larger specimens of up to 45mm. were commonplace on both north and south sides of the estuary.

Opposite Southampton Water on the north coast of the Isle of Wight, observations of bird-predated shells indicated that wild Manila clams arrived in the Medina Estuary in 2003. Naturalisation here has resulted in a persistent population which has occasionally been exploited by clam boats from other Solent harbours and by hand gathering at low tide (Herbert, 2009).

Immediately to the east of Southampton Water are Portsmouth, Langstone and Chichester harbours which are connected by tidal creeks in their upper reaches. Despite anecdotal reports of clams in Portsmouth Harbour around 2005, an extensive benthic survey in 2006 revealed none. Nevertheless by 2010 our dredging of the upper reaches of the Harbour confirmed the presence of a population with length up to 52 mm. and age up to five years, which now attracts a local fishing effort.

Continuing east to Langstone Harbour, an anecdotal report of Manila clams in 2005 was followed by a single specimen report to the Malacological Society of London in 2006. The estuary now contains a persistent wild population with densities sufficient to attract a fishing effort including clam boats from adjacent estuaries. In the neighbouring Chichester Harbour our searches in 2004 and 2005 failed to find any Manila clams. In 2006 however a systematic survey turned up a single clam of age 3-4 years (Emu, 2007). Further searches in the vicinity of the find again failed to reveal more clams although a small number of shells were recovered. It appears that although the species could be found occasionally the evidence suggests no significant naturalised population there before 2010. The next estuary to the east, Pagham Harbour has its entrance about 12km to the east of Chichester Harbour with the headland of Selsey Bill lying between. We found no documentary or field evidence of the Manila clam.

Taking Poole Harbour as the site of the pioneer Manila clam population, the above timescales indicate an inferred average rate of spread eastwards of approximately 4.5 km per year

Approximately 45 km to the west of Poole Harbour is the next estuarine system of Portland Harbour and The Fleet. The Harbour and the adjacent Weymouth Bay are protected from prevailing south westerly winds by the limestone outcrop of Portland. Consequently the area is popular with SCUBA divers and snorkelers who by 2003 were known to be collecting Manila clams (McTaggart *et al.,* 2004). This population does not yet extend significantly into The Fleet although a single Manila clam was found there in a thorough 2010 survey by one of our students (Short, 2010). Although the Manila clam has been introduced at three south coast sites further west we only found Manila clams in one of these sites, namely the Exe estuary, were it was first introduced in 1984 and was considered naturalised by 1995 by local fishermen. However the exact status of the clam in the Exe remains uncertain.

EAST COAST

Davidson (1991) identifies 17 estuaries from the north Kent coast, north to Felixstowe, four of which flow into the outer Thames area. For simplicity on Table 2 and Figure 2 we conflate these into a single reference to the Thames Estuary, the outer reaches of which contain various Manila clam populations as detailed below.

The south shore of the outer Thames Estuary around Whitstable has a long tradition of bivalve production and was a significant site in the history of British Manila clam introduction, due to the presence of the commercial bivalve hatchery at Reculver. Having received broodstock for the production and distribution of spat the hatchery company subsequently established two local aquaculture sites, at Reculver in 1988 and Seasalter in 1992. These sites remained licensed for deposition of Manila clams for every year up to (and beyond) 2010. A third site on the Isle of Sheppy has been licensed since 2003. By 2010 wild clams could be found from The Swale (which separates Sheppy from the Kent mainland) to Reculver and evidence of dead shells suggests a wider distribution along this coast.

North of the Outer Thames area is the Crouch-Roach estuary whose complex system of tidal channels separates Foulness Island from the Essex mainland. This estuary system was licensed for Manila clam deposits off Paglesham for nine of the years between 1996 and 2009. Although we did not find wild Manila clams in the Crouch estuary system (prior to 2010) they were found on the large area of sediment seaward of Foulness known as Maplin Sands. This area can also be thought of as the seaward limit of the outer Thames Estuary: An estuary in which wild Manila clams are now extensively distributed and well established.

Further north again is the Blackwater Estuary which shares its outer reaches with the smaller Colne Estuary. Since 1992 Manila clam deposition has been licensed at five sites and the species has become naturalised. However it appears not to support a commercial fishery here, although it is caught and sold in small numbers as by-catch from a Pacific oyster fishery.

Hamford Water and the estuaries of the Stour and Orwell rivers discharge into a bay lying approximately between the towns of Walton-on-the-Naze and Felixstowe. Wild Manila clams can be found in this area from the shore off Walton to the upper reaches of the Stour by Mistley. Here the species density is sufficient to support a local fishing effort with techniques ranging from raking sediment approached from the shore to dredging from boats. Although there have been licensed deposits of Manila clams further north on this coast we found no evidence or reports of wild clams.

In the 26 years since the Manila clam was first introduced on the east coast, it has established wild populations from Whitstable to Felixstowe, a direct north-south distance of around 80 km.

Relationship between licensed introductions and wild clam presence

In order to reflect on the relative importance of natural and anthropogenic means of dispersal in Britain, we have in Table 2 categorised the south and east coast estuaries considered above according to the relationship they demonstrated between licensed introduction and wild Manila clam presence between 1980 and 2010. These relationship types are provided below:

Type 0. Sites with no history of licensed introduction and no wild clam presence.

Type 1. Sites with a history of licensed introduction but no wild clam presence.

Type 2. Sites which combine a history of licensed introduction with a wild clam presence.

Type 3. Sites with no history of licensed introduction but with wild clams present.

Between 1980 and 2010 the Manila clam became naturalised in eleven British estuaries. Figure 2 provides a map on which the estuaries from Table 2 along with other south and south-east coast estuaries are marked according to our type categories. It is clear from this map that there is no simple relationship between licensed introduction and the presence of wild Manila clams. Type 1 and 2 sites demonstrate that while naturalisation could follow licensed introduction (e g Poole Harbour and the Thames Estuary), this result was not inevitable. (e.g. the Crouch-Roach Estuary) at least within the timescale we are considering. Type 3 sites such as Portsmouth Harbour and the Stour Estuary demonstrate effective dispersal other than through licensed introduction for aquaculture. Ostensibly this suggests natural larval dispersal however anthropogenic explanations other than licensed introduction are also possible as discussed below.

DISCUSSION

Climate compatibility

In the 1980's MAFF scientists believed that the British coastal environment, while favorable for the rapid growth of small but matured clams, was too cold to support breeding and recruitment (Spencer *et al.,* 1991). Their opinion on the incompatibility of British sea temperatures and Manila clam naturalisation was informed by evidence from experimental work in the Menai Strait, Wales during 1983 and 1984. Despite unusually warm summer sea temperatures spawning did not occur (Millican & Williams, 1985). Nevertheless this opinion was contentious. In particular the UK's statutory agency for conservation was concerned about the possibility of the clams successfully spawning to produce self sustaining wild populations, with implications for indigenous ecology and biodiversity. This controversy has been detailed elsewhere (Humphreys, 2010).

The discovery of naturalised Manila clams in Poole Harbour on the British south coast demonstrated the erroneous nature of the Ministry's position. However, Poole Harbour is a unique marine environment by virtue of the extent to which it combines large size, micro-tidal regime, lagoonal character (due to a double high water effect) and relatively warm southern position (Humphreys & May, 2005). Consequently it remained uncertain whether naturalisation there was a peculiar event or whether a further extension of the clam's British distribution might be expected (Jensen *et al.,* 2005a). We must now recognise a more general compatibility between British estuarine habitats, including sea temperature regimes, and the requirements of the Manila clam, at least on the south and south east coasts of England.

Nevertheless it remains unlikely that the species can naturalise in currently colder British waters significantly north of our reported wild populations. In Morecambe Bay for example, despite annual licensed deposits throughout the 1990's, there are no wild Manila clams. This absence of established wild populations in northern Type 1 sites suggests that the government's original position was only valid for northern coasts.

Invasiveness and the dynamics of naturalisation

The naturalisation of non-indigenous species requires more that just their introduction into physically compatible habitats. In this respect it is informative to focus on the south and east coast locations where our evidence demonstrates that temperature is not a limiting factor.

In the context of efforts to discriminate relatively benign arrivals from serious ecological threats, the concept of biological invasion has been refined over recent years. Once defined simply as a case of “any sort of organism arriving somewhere beyond its previous range” (Williamson, 1996), not all non-indigenous species are now regarded as invasive and the term is often restricted to alien arrivals with the ability to “spread aggressively” (Maynard & Nowell, 2009), by which is meant causing serious ecological change such as the decline or extinction of endemic species and altering the structure of communities (Clout & Williams, 2009).

A readily dispersed life cycle stage and high fecundity are regarded as adaptations associated with species invasiveness. These characteristics can exert a combined effect referred to as “propagule pressure”, defined as the number of individuals released into a region to which they are not native (Lockwood *et al.*, 2005). In addition to having a planktonic larval stage, Manila clams have considerable reproductive potential: Large clams in good condition can spawn up to 8 million eggs (Spencer 2002). Such reproductive effort will increase the probability of success by improving the chances of sufficient numbers finding suitable habitat and surviving predation. Consequently propagule pressure is regarded as of fundamental importance to invasive population growth and range expansion, both generally (Grice, 2009) and in the particular case of marine molluscs in estuarine ecosystems (Miller *et al*., 2007).

Conversely both abiotic and biotic factors, collectively referred to as invasion or environmental resistance (Williamson, 1996), will tend to limit the success of the potentially invasive population. For example, fecundity in bivalves can be significantly affected by food supply, temperature, salinity, parasites and water contamination. Moreover mortality, especially in the early stages of the life cycle can be prodigious. During their planktonic larval stages both active predators and non-selective filter feeders contribute to bivalve larval mortality rates as high as 99% (Gosling, 2003). Manila clams are no exception, and even settled specimens as large as 10 mm. length can be consumed by the indigenous shore crab *Carcinus maenas* (Linnaeus, 1758) at rates up to 50 clams per crab per day (Spencer, 2002). In Poole Harbour, Caldow *e. al.*, (2007) have recorded oystercatchers (*Haematopus ostralegus* Linnaeus 1758) consuming Manila clams at rates typical of their consumption of native bivalves.

In stable ecosystems environmental resistance will provide a relatively consistent challenge to potential invader species. However estuaries are recognised as challenging environments prone to wide fluctuations in the abundance of many constituent species (e.g. Boasch, 1967; Kaiser *et al.*, 2005; McLusky & Elliot, 2004). In a meta-analysis of invasibility, Colautti (2006) found a significant positive association with community disturbance. This suggests that natural volatility in the benthic communities of temperate estuaries must from time to time present opportunities to alien species. The suggestion by Spencer (2002) that harsh winters can lead to good years for Manila clam settlement by suppressing the abundance of the predator *C. maenas* (a phenomenon which has been demonstrated for bivalves in the Wadden Sea (Beukema & Dekker, 2014)), exemplifies this possibility, In Poole Harbour the naturalisation of the Manila clam in the 1980s followed an earlier decline in the abundance of the bivalves *Scrobicularia plana* (da Costa 1778) and *Macoma baltica* (Linnaeus, 1758) attributed to tri-butyl tin pollution (Caldow *et al.,* 2005; Humphreys *et al.,* 2007).

The existence of Type 1 sites in climate compatible areas suggests that even in southern Britain propagule pressure and environmental resistance was finely balanced, sometimes favouring establishment such as in Poole Harbour and the Stour Estuary, sometimes preventing it, and occasionally, such as in The Fleet and Chichester Harbour, leaving isolated individuals as relics of otherwise unsuccessful spatfalls. Moreover even when naturalisation does occur, reported population densities are far below that recorded in some more southerly European sites such as on the Italian Adriatic coast (Humphreys *et al*., 2007, Breber, 2002).

Moderate population densities may also explain the current lack of evidence that naturalised Manila clam populations cause the decline or local extinction of indigenous species, even with regard to *Ruditapes decussatus*, the closest native relative with which it is sympatric, and which therefore might be the best candidate for competitive exclusion effects. Indeed in the Bay of Santander on the Atlantic coast of Spain where the two co-exist (a phenomenon we have also observed in Poole Harbour), their respective abundances do not show any significant negative correlation. Consequently it has been concluded that interspecific competition for space or resource between the two species is not intense (Juanes *et al.,* 2012) and it appears that predation rather than competition limits the density of both (Bidegain & Juanes, 2013).

In summary our evidence suggests that the Manila clam is not currently an aggressively invasive species in British waters and appears not to present a significant direct risk to indigenous ecosystem diversity or function.

Mechanisms of dispersal

Using hydrodynamic and larval behaviour modeling we have (with colleagues) demonstrated a correspondence between predicted larval dispersal and wild clam densities within Poole Harbour (Herbert *et al.,* 2012). However the spread between estuaries represents a more challenging phenomenon as pelagic larvae must drift on coastal currents to the next suitable estuarine habitat, overcoming natural barriers such as headlands and off-shore currents. In modeling this phenomenon on the south coast we found high levels of predicted larval retention within Poole Harbour and increasing hydrodynamic depletion of larval density with increasing distance from the harbour mouth (Herbert *et al.*, 2012). The implication of this effect in terms of propagule pressure in an adjacent estuary makes it questionable that natural dispersal can account for wild clams in all British estuaries with no history of licensed introduction (Type 3 sites, Figure 2). Consequently, notwithstanding the assertion by Breber (2002) that natural larval dispersal explains the clam's spread along the Italian Adriatic coast, we are sceptical that this fully accounts for dispersal in Britain's northern European waters. In seeking alternative explanations we have looked more closely into anthropogenic mechanisms of dispersal.

The combination of high value and volatile supply of estuarine bivalves generates a repertoire of responses from necessarily versatile and opportunistic fishers. As the supply of a species declines in one area fishers will switch to other species or areas. Despite the size of in-shore bivalve boats (generally less that 10m length), neighbouring estuaries at least 50 km away from the home port can and will be fished (Jensen *et al.*, 2005b).

In this context various fishing practices can lead to the seeding of new estuaries. Commonly selling-on the catch involves periodic sale to wholesalers on the quayside, or transport by the fisher to a wholesale operation. Either way, sales are not typically conducted daily and accumulating catch may therefore be stored, commonly by suspension under a boat or floating platform. Spawning at this time can add prodigious numbers of larvae to the few adults that maybe lost overboard by accident. Such events represent anthropogenic mechanisms in which licensed fishers inadvertently create connectivity between estuaries.

Furthermore the relatively low capital costs of Manila clam fishing also attracts unlicensed fishers from outside the legitimate fishing community. Despite the efforts of regulatory authorities such informal enterprises can be a major problem (Jensen *et al.*, 2005b). In this competitive and lucrative context anecdotal evidence suggests that the illegal introduction of Manila clams for the purpose of establishing new fisheries represents a further dispersal mechanism.

In any event we postulate that, through these various mechanisms of dispersal, in combination with warming sea temperatures, it must be expected that the species will continue its spread in British waters, thereby further extending the northern boundary of its European distribution.

Policy, naturalisation and climate change

In Poole Harbour the assertion in 1980 that the Manila clam posed no risk by virtue of its inability to naturalise at British water temperatures proved incorrect within two years of its introduction. This and the subsequent spread we have reported here makes the case of the Manila clam instructive in considering various aspects of the relationship between science and policy, not least when conflicting scientific opinions are available. We have elsewhere begun to examine how the case of the Manila clam elucidates the role of science in the policy process (Humphreys, 2010). However in the context of this paper the most significant ecological question stems from our prediction that the spread that we have reported will continue: What will be the long term impact of the species in British waters?

It is possible, given current climate change predictions (UKCPO9) that the Manila clam could significantly threaten native community function. Conversely however, in the same context of warming seas, the species will become an important asset if boreal species of similar niche retreat northwards. Elsewhere we have reported a benefit of the Manila clam in terms of a reduction of predicted overwintering oystercatcher (*Haematopus ostralegus* Linnaeus 1758) mortality (Caldow *et al.*, 2007); a finding which suggests the clam could help reduce the negative effect of habitat loss as a consequence of sea level rise (Durell *et al.*, 2006). Such considerations illustrate the complexity of the issues that climate change presents for conventional conservation approaches.

In any event the current status of the Manila clam in British and other northern European waters is unlikely to remain constant. In this context continued monitoring is necessary, along with further research on its dispersal and interactions within indigenous European estuarine communities.

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Note

The authors would be interested to receive both historic and contemporary information from readers on the distribution of wild Manila clam populations in British and northern European waters. Please contact the corresponding author.

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Tables

Table 1. Industry-related Manila clam introductions in Britain, 1980-2010. In chronological order of initial introduction to site.

Year of introduction	Location	County	Purpose	Source	Key to site locations as shown in Fig. 1
1983	Menai Strait	Gwynedd	Experimental	Millican & Williams (1985)	1
1984	Exe Estuary	Devon	Commercial trial with gametogenesis monitoring	JNCC archive	2
1984	Morecambe Bay	Cumbria	On-growing from hatchery	Cefas (2010)	3
1985 or before	Poole Harbour	Dorset	Informal commercial trial	Humphreys (2010)	4
1985 or before	Helford Estuary	Cornwall	Commercial trial	Hansard (1985)	5
1985 or before	Teign Estuary	Devon	Commercial trial	Hansard (1985)	6
1985 or before	Chichester	Hampshire	Commercial trial	Hansard (1985)	7

	Harbour				
1985 or before	Blackwater Estuary	Essex	Commercial trial	Hansard (1985)	8
1985 or before	Blythe Estuary	Suffolk	Commercial trial	Hansard (1985)	9
1985 or before	Loch Creran	Argyll	Commercial trial	Hansard (1985)	10
1986	Walton-on-the-Naze	Essex	Commercial trial	MAFF 1987	11
1988	Reculver (Thames estuary)	Kent	Aquaculture from hatchery	Cefas (2010)	12
1988	Lochs Miodart & Ceann Traigh	Argyll	Experimental	Lake (1992)	13
1991 or before	Beaulieu Estuary	Hampshire	Commercial trial	Spencer *et al.* (1991)	14
1992	Seasalter (Thames estuary)	Kent	Aquaculture	Cefas (2010)	15
1996	Crouch Estuary	Essex	Aquaculture	Cefas (2010)	16
2001	Fowey Estuary	Cornwall	Aquaculture	Cefas (2010)	17
2003	Sheppy (Thames estuary)	Kent	Aquaculture	Cefas (2010)	18
2004	Colne Estuary	Essex	Aquaculture	Cefas (2010)	19

Table 2. UK distribution of Manila clams by 2010, showing estuaries of a. the south and b. the south east coasts of England. Estuaries are numbered in line with Davidson *et al.*, (1991). Key: Types 0-3 estuaries are as defined in the text. DSW signifies an estuary containing a government designated shellfish water; * signifies an Isle of Wight estuary, all others being on the mainland. N A. signifies not applicable. The words rare and common are defined in terms of the SACFOR scale (Hiscock, 1996).

2a

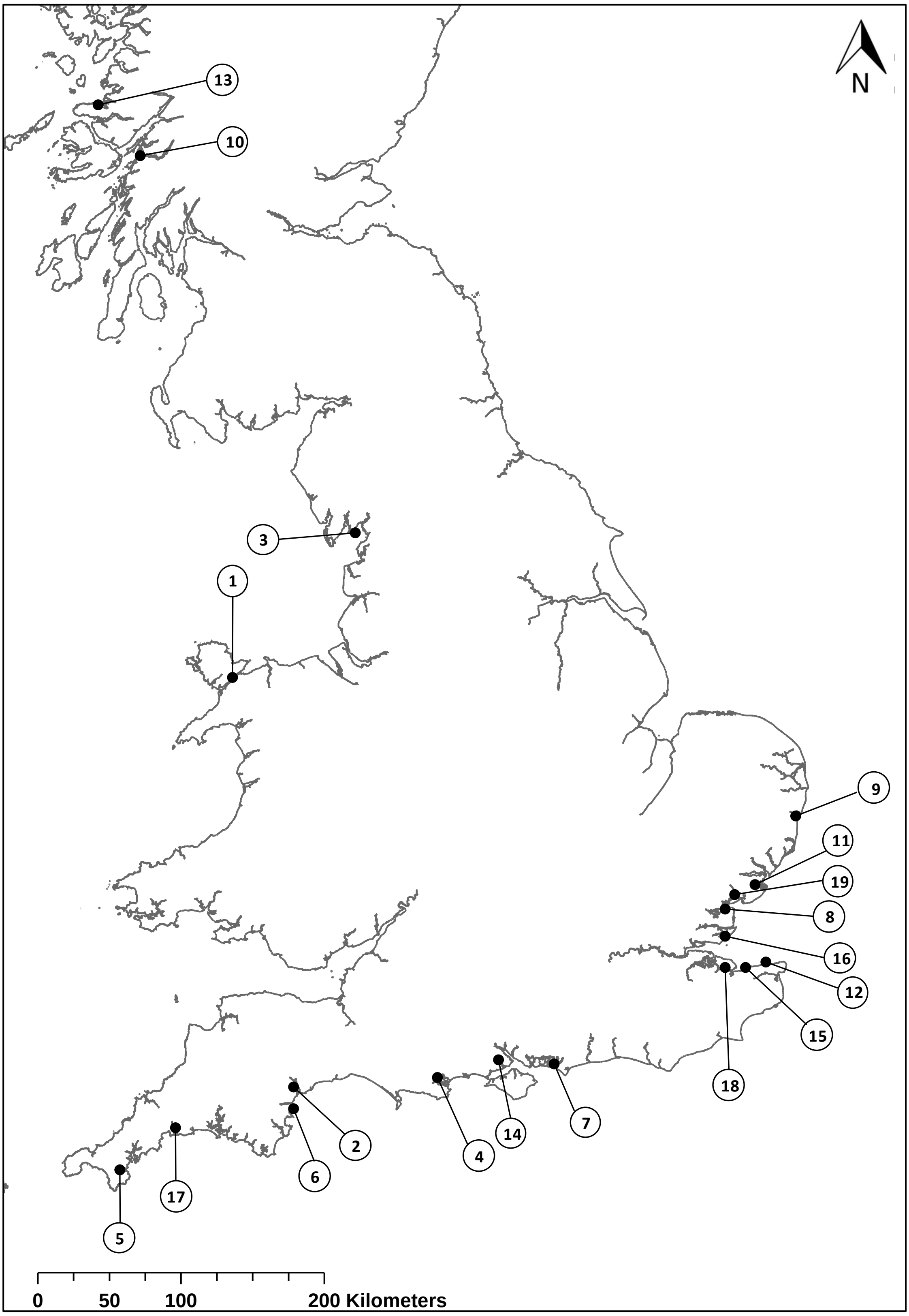
Estuary number	**Estuary name**	**Earliest aquaculture introduction**	**Current wild clam status and local abundance**	**Notes**
144	Exe Estuary	1984	Present Rare	Type 2 & DSW
143	Otter Estuary	NA	Absent	Type 0
142	Axe Estuary	NA	Absent	Type 0
141	The Fleet (& Portland Harbour)	NA	Naturalised in Portland Harbour only Common	Type 3 & DSW
140	Poole Harbour	1988	Naturalised Common	Type 2 & DSW
139	Christchurch Harbour	NA	Absent	Type 0 & DSW
133	Lymington Estuary	NA	Absent	Type 0 &DSW
138	Yar Estuary*	NA	Absent	Type 0 & DSW
137	Newtown Estuary*	NA	Absent	Type 0
132	Beaulieu River	1991	Absent	Type 1 & DSW
131	Southampton Water	NA	Naturalised Common	Type 3 & DSW
136	Medina Estuary*	NA	Naturalised Common	Type 3 & DSW
135	Wootton Creek*	NA	Absent	Type 0
130	Portsmouth Harbour	NA	Naturalised Common	Type 3 & DSW
134	Bembridge Harbour*	NA	Absent	Type 0
129	Langstone Harbour	NA	Naturalised Common	Type 3 & DSW
128	Chichester	1985 or before	Occasional	Type 2 & DSW

	Harbour		Rare	
127	Pagham Harbour	NA	Absent	Type 0

2b				
Estuary number	**Estuary name**	**Earliest Aquaculture introduction**	**Current wild clam status and local abundance**	**Notes**
106	Ore/Alde/Butley Estuary	NA	Absent	Type 0 & DSW
107	Deben Estuary	NA	Absent	Type 0
108	Orwell Estuary	NA	Absent	Type 0
109	Stour Estuary	NA	Naturalised Common	Type 3
110	Hamford Water (& Walton Backwaters)	1986	Absent	Type 1 & DSW
111	Colne Estuary	2004	Naturalised Common	Type 2 & DSW
112	Blackwater Estuary	1985 or before	Naturalised Common	Type 2 & DSW
113	Dengie Flat	NA	Absent	Type 0 & DSW
114	Crouch-Roach Estuary	1996	Absent	Type 1 & DSW
115	Maplin Sands	NA	Naturalised Common	Type 3 & DSW
116	Southend-on Sea	NA	Absent	Type 0 & DSW
117-120	Thames Estuary	1988	Naturalised Common (at various locations)	Type 2 & DSW
121	Pegwell Bay	NA	Absent	Type 0 & DSW
122	Rother Estuary	NA	Absent	Type 0

Figures

Fig. 1. Map of Britain showing the approximate positions of sites of licensed Manila clam introduction for aquaculture between 1980 and 2010 (see also Table 1).



N
13
10
3
1
9
11
19
8
16
12
15
18
7
14
4
2
6
17
5
0
50
100
200 Kilometers

Fig. 2. South and south east coasts of Britain showing sites of introduction and 2010 wild clam distribution (information from Table 2). Circles represent the relationship between licensed introductions and the presence of wild populations up to 2010 (see discussion).

Key to circle shading.

Un-shaded. Type 0 estuary: no introduction and no wild population.

Left shaded. Type 1 estuary: introduction but no wild population.

Fully shaded. Type 2 estuary: introduction and wild population present.

Right shaded. Type 3 estuary: no introduction but wild population present.