

First records of the oriental prawn *Palaemon macrodactylus* (Decapoda: Caridea), an alien species in European waters, with a revised key to British Palaemonidae

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This paper details the first recorded instance of the prawn *Palaemon macrodactylus* in Europe, at the Orwell estuary, Suffolk. The species is native to north-east Asia, including Japan and Korea, and has previously been introduced to other areas outside its natural range. Records of the abundance of caridean species, obtained from routine benthic trawl samples in the Stour and Orwell estuaries, provide a summary of *P. macrodactylus*' habitat preference in reduced-salinity waters. Consistent catches and records of ovigerous females provide evidence for the stability of the Orwell population. A revised key to British Palaemonidae is also provided.

INTRODUCTION

Many exotic marine species have been introduced into Europe since the advent of regular intercontinental transport; a directory of marine introductions to British waters has been compiled (Eno et al., 1997) which records the 51 non-native species known up to 1997. Records of additional introductions continue to be reported in the scientific literature. Many of these introductions include species from East Asia (e.g. Smith et al., 1999; Nishikawa et al., 2000; Baldock & Bishop, 2001), some of which have been reviewed as economically important (Clark et al., 1998; Rainbow et al., 2003). Successful introductions generally involve species from similar latitudes (Eno et al., 1997). The possibility of further introductions should always be considered by those involved in biological monitoring.

This paper details the first recorded occurrence of the oriental prawn *Palaemon macrodactylus* Rathbun 1902 in Europe. The species was found at the Orwell estuary in Suffolk, eastern England, during a series of ecological surveys carried out on the Stour and Orwell estuaries by Unicomarine Ltd on behalf of Harwich Haven Authority. The fish and shrimp monitoring surveys undertaken are described. A benthos survey (Dyer, 2000) and a biotope mapping exercise (Worsfold, 2002) have also been conducted in the area: these found several other non-native species.

Another north-east Asian species, the ascidian *Styela clava* Herdman, believed to have been introduced to Plymouth in 1952 (Carlisle, 1954; Houghton & Millar, 1960), was found during the biotope mapping exercise, as well as during the present fish monitoring surveys. This species had already been recorded by the Marine Nature Conservation Review (Irving, 1998). Other non-native invertebrate species found during the above surveys include the molluscs *Ruditapes phillipinarum* (Adams &

Reeve), *Potamopyrgus antipodarum* (Gray), *Crepidula fornicata* (L.), *Crassostrea gigas* (Thunberg), *Mya arenaria* L., *Petricola pholadiformis* Lamarck, and *Ensis americanus* (Gould in Binney), and the barnacle *Elminius modestus* Darwin. The Chinese mitten crab (*Eriocheir sinensis* H. Milne-Edwards) has also been reported to occur in the Stour estuary (Rainbow et al., 2003), but has not been found there by the present authors. In addition, the sponge *Suberites massa* Nardo, found in the Orwell estuary during the biotope and trawl surveys, may be a cryptogenic species, as it has been recorded in British waters only near ports (Eno et al., 1997). A review of the physical and biological features of the Stour and Orwell estuaries is provided in Barne et al. (1988).

Palaemon macrodactylus is a large, edible palaemonid which is native to Japan, Korea and northern China (Rathbun, 1902; Newman, 1963). It was introduced into San Francisco Bay, California, prior to 1957 (Newman, 1963) and has since become well-established along most of the west coast of North America (Ricketts et al., 1968; Cohen, 1996; Williams, 1997; United States Geological Survey, 2002; California Resources Agency, 2002). Newman (1963) has discussed the possible means of introduction, and the expansion of the species' range has been documented by other authors (Ricketts et al., 1968; Cohen, 1996; Williams, 1997; United States Geological Survey, 2002; California Resources Agency, 2002). A number of papers and reports have been published which concern the species' ecology and physiology in American waters (Born, 1968; Sitts & Knight, 1979; Siegfried, 1980, 1982). Instances of the occurrence of the species in two Australian states have also been recorded (Pollard & Hutchings, 1990). However, the only confirmed instance is that recorded for an area near Newcastle, New South Wales (Buckworth, 1979; Holthuis, 1980). There is also an unsubstantiated record from South Australia (Williams et al., 1978, 1982; Carlton, 1985). In the United States,

Table 1. Caridean species composition and physicochemical data for trawls taken at all stations between December 2001 and November 2002. Figures in parentheses indicate the numbers of indigenous Palaemon macrodactylus. Target trawl positions are also shown.

	Stour A	Stour 01	Stour 02	Stour 03	Stour 04	Stour 05	Stour 06	Orwell A	Orwell 01	Orwell 02	Orwell 03	Orwell 04	Orwell 05	Orwell 06	Harbour 1	Harbour 2
December 2001																
Trawl Start Position		51°36'0.92 01°13'0.92	51°56'0.96 01°11'0.29	51°57'0.18 01°11'0.41	51°57'0.20 01°11'0.40	51°57'0.02 01°10'0.04	51°57'0.10 01°08'0.20		51°57'0.37 01°17'0.26	51°38'0.64 01°16'0.50	51°59'0.52 01°16'0.12	51°59'0.43 01°16'0.04	51°59'0.93 01°13'0.71	52°00'0.36 01°11'0.57		
Trawl Finish Position		51°30'0.90 01°13'0.52	51°57'0.20 01°11'0.05	51°57'0.31 01°10'0.90	51°57'0.20 01°10'0.99	51°56'0.86 01°09'0.68	51°57'0.06 01°07'0.87		51°57'0.48 01°17'0.38	51°38'0.84 01°16'0.50	51°59'0.54 01°15'0.88	51°59'0.50 01°15'0.71	51°59'0.97 01°13'0.45	52°00'0.62 01°11'0.35		
Salinity (psu)		28.3	29.0	29.2	29.4	28.9	28.6		32.7	30.7	30.2	31.1	30.2	30.2		
Water Temperature (°C)		4.8	4.8	3.4	6.9	4.9	5.0		6.9	5.8	3.6	5.8	3.5	5.3		
Dissolved Oxygen (%)		97.3	90.0	93.0	98.0	96.6	97.5		101.0	95.0	95.2	97.2	96.6	96.6		
<i>Palaemon macrodactylus</i>																
<i>Palaemon elegans</i>																
<i>Pandulus montagu</i>																
<i>Crangon crangon</i>																
<i>Crangon alpinus</i>																
<i>Hippolyte varians</i>																
<i>Thonibia cranchii</i>																
January 2002																
Trawl Start Position		30.9	30.7	30.3	30.3	27.6	28.1		32.1	30.1	28.3	29.5	27.9	27.8		
Water Temperature (°C)		4.0	3.9	4.0	4.1	4.2	4.2		4.9	4.6	4.7	4.6	4.7	4.7		
Dissolved Oxygen (%)		127.5	108.0	116.8	119.8	116.7	121.1		114.1	105.3	100.7	118.5	115.4	113.1		
<i>Palaemon macrodactylus</i>																
<i>Palaemon elegans</i>																
<i>Palaemon serratus</i>																
<i>Pandulus montagu</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thonibia cranchii</i>																
February 2002																
Trawl Start Position		28.5	28.8	28.4	29.4	27.6	28.2		31.9	30.0	29.4	29.3	28.6	27.6		
Water Temperature (°C)		8.2	8.2	8.3	8.4	8.5	8.5		7.4	7.5	7.6	7.4	7.6	7.5		
Dissolved Oxygen (%)		95.4	97.3	95.6	93.0	94.0	93.5		96.4	95.1	96.1	92.2	91.5	86.6		
<i>Palaemon macrodactylus</i>																
<i>Palaemon elegans</i>																
<i>Palaemon serratus</i>																
<i>Pandulus montagu</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thonibia cranchii</i>																
March 2002																
Trawl Start Position		31.5	31.4	31.4	31.5	30.3	30.3		31.8	31.7	31.7	31.6	31.3	31.6		
Water Temperature (°C)		7.5	7.6	7.6	7.7	7.7	7.9		7.2	7.2	7.2	7.2	7.1	7.0		
Dissolved Oxygen (%)		92.0	96.0	96.1	95.6	94.2	94.8		97.3	96.0	95.8	95.6	96.2	95.5		
<i>Palaemon macrodactylus</i>																
<i>Palaemon elegans</i>																
<i>Palaemon serratus</i>																
<i>Pandulus montagu</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thonibia cranchii</i>																
April 2002																
Trawl Start Position		31.4	31.2	30.7	30.1	30.0	30.2		31.9	31.7	31.6	31.4	30.4	30.2		
Water Temperature (°C)		11.8	11.9	11.5	12.2	12.2	11.8		12.3	11.4	11.3	11.3	12.3	12.9		
Dissolved Oxygen (%)		98.3	101.7	99.4	97.6	98.9	99.2		98.2	98.8	99.2	101.6	99.5	95.2		
<i>Palaemon macrodactylus</i>																
<i>Palaemon elegans</i>																
<i>Palaemon serratus</i>																
<i>Pandulus montagu</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thonibia cranchii</i>																
May 2002																
Trawl Start Position		51°57'0.14 01°15'0.48	51°56'0.96 01°11'0.29	51°57'0.18 01°11'0.41	51°57'0.10 01°08'0.20	51°57'0.02 01°10'0.04	51°57'0.10 01°08'0.20		51°57'0.96 01°16'0.90	51°38'0.64 01°16'0.50	51°59'0.52 01°16'0.12	51°59'0.43 01°16'0.04	51°59'0.93 01°13'0.71	52°00'0.36 01°11'0.57	51°57'0.12 01°17'0.18	
Trawl Finish Position		51°57'0.14 01°15'0.16	51°57'0.20 01°11'0.05	51°57'0.31 01°10'0.90	51°57'0.06 01°07'0.87	51°56'0.86 01°09'0.68	51°57'0.06 01°07'0.87		51°56'0.02 01°16'0.73	51°38'0.84 01°16'0.50	51°59'0.54 01°15'0.88	51°59'0.50 01°15'0.71	51°59'0.97 01°13'0.45	52°00'0.62 01°11'0.35	51°17'0.19 01°17'0.19	51°57'0.06 01°16'0.57
Salinity (psu)		32.4	32.3	31.8	32.0	32.0	31.9		32.0	31.3	30.9	31.4	30.8	29.6	32.1	32.1
Water Temperature (°C)		14.6	14.8	14.9	14.9	14.9	15.1		14.5	14.2	14.6	14.5	14.8	15.2	14.3	14.4
Dissolved Oxygen (%)		91.7	94.8	89.4	95.2	94.5	95.2		86.8	86.2	86.4	86.5	86.4	78.4	88.0	93.8
<i>Palaemon macrodactylus</i>																
<i>Palaemon elegans</i>																
<i>Palaemon serratus</i>																

Continued

Table 1 (Continued)

	Stour A	Stour 01	Stour 02	Stour 03	Stour 04	Stour 05	Stour 06	Orwell A	Orwell 01	Orwell 02	Orwell 03	Orwell 04	Orwell 05	Orwell 06	Harbour 1	Harbour 2
June 2002																
Salinity (psu)	33.0	32.9	33.1	33.2	33.1	33.1	33.0	33.2	33.0	33.0	nd	32.5	31.7	31.1	33.4	33.6
Water Temperature (°C)	18.5	19.2	18.6	18.5	19.2	23.1	20.2	18.6	19.8	21.6	21.6	21.8	22.1	22.1	20.6	20.2
Dissolved Oxygen (%)	98.8	99.4	96.8	97.8	103.9	94.6	102.1	97.4	111.4	111.4	nd	120.2	117.5	111.3	94.8	90.5
<i>Palaeomon macrodactylus</i>																
<i>Palaeomon elegans</i>																
<i>Palaeomon serratus</i>																
<i>Pandalus montagu</i>																
<i>Pandalus brevis</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thorulus cranchii</i>																
July 2002																
Salinity (psu)	33.4	33.1	33.5	33.2	33.1	33.1	33.0	33.2	33.0	33.0	33.0	32.5	31.7	31.1	33.4	33.6
Water Temperature (°C)	21.5	21.9	22.3	23.1	23.1	23.1	23.7	21.3	21.6	21.6	21.6	21.8	22.1	22.1	20.6	20.2
Dissolved Oxygen (%)	96.4	98.9	96.3	92.9	94.6	94.6	102.1	97.4	111.4	111.4	nd	120.2	117.5	111.3	94.8	90.5
<i>Palaeomon macrodactylus</i>																
<i>Palaeomon elegans</i>																
<i>Palaeomon serratus</i>																
<i>Pandalus montagu</i>																
<i>Pandalus brevis</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thorulus cranchii</i>																
August 2002																
Salinity (psu)	33.6	33.4	33.3	33.1	33.1	33.1	32.7	33.6	33.6	32.9	32.9	33.2	32.8	32.2	33.7	33.6
Water Temperature (°C)	19.3	19.5	19.6	19.5	19.5	19.7	19.8	19.7	19.8	20.0	19.8	19.9	20.0	20.0	19.8	18.9
Dissolved Oxygen (%)	85.5	79.5	79.5	77	79.1	79.1	82.5	87.6	87.6	75.8	73.6	76.8	72.7	71.2	89.5	87.6
<i>Palaeomon macrodactylus</i>																
<i>Palaeomon elegans</i>																
<i>Palaeomon serratus</i>																
<i>Pandalus montagu</i>																
<i>Pandalus brevis</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thorulus cranchii</i>																
September 2002																
Salinity (psu)	33.3	33.3	33.1	32.7	32.2	32.2	31.9	32.9	32.9	32.8	32.5	32.6	32.2	32.0	33.3	33.3
Water Temperature (°C)	16.1	16.1	15.7	15.0	14.5	14.5	13.9	15.6	15.6	13.6	13.6	13.5	13.4	13.5	16.2	13.8
Dissolved Oxygen (%)	83.2	83.1	82.3	81.6	82.9	82.9	85.0	86.9	86.9	87.9	85.3	85.2	83.1	81.7	83.2	92.7
<i>Palaeomon macrodactylus</i>																
<i>Palaeomon elegans</i>																
<i>Palaeomon serratus</i>																
<i>Pandalus montagu</i>																
<i>Pandalus brevis</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thorulus cranchii</i>																
October 2002																
Salinity (psu)	32.3	32.3	32.3	31.9	31.2	31.2	29.2	32.6	32.6	32.0	32.5	32.1	31.6	30.5	32.6	32.7
Water Temperature (°C)	10.9	10.9	10.9	10.9	10.9	10.9	10.8	11.4	11.4	11.6	11.5	11.7	11.6	11.8	11.5	11.4
Dissolved Oxygen (%)	88.4	91.3	91.3	87.6	86.5	86.5	85.8	91.0	91.0	96.9	94.4	95.0	88.2	85.3	91.7	92.8
<i>Palaeomon macrodactylus</i>																
<i>Palaeomon elegans</i>																
<i>Palaeomon serratus</i>																
<i>Pandalus montagu</i>																
<i>Pandalus brevis</i>																
<i>Crangon crangon</i>																
<i>Hippolyte varians</i>																
<i>Thorulus cranchii</i>																
November 2002																
Salinity (psu)																
Water Temperature (°C)																
Dissolved Oxygen (%)																
<i>Palaeomon macrodactylus</i>																
<i>Palaeomon elegans</i>																
<i>Palaeomon serratus</i>																
<i>Pandalus montagu</i>																
<i>Pandalus brevis</i>																
<i>Crangon crangon</i>																
<i>Philoceras fuscatus</i>																
<i>Hippolyte varians</i>																
<i>Thorulus cranchii</i>																

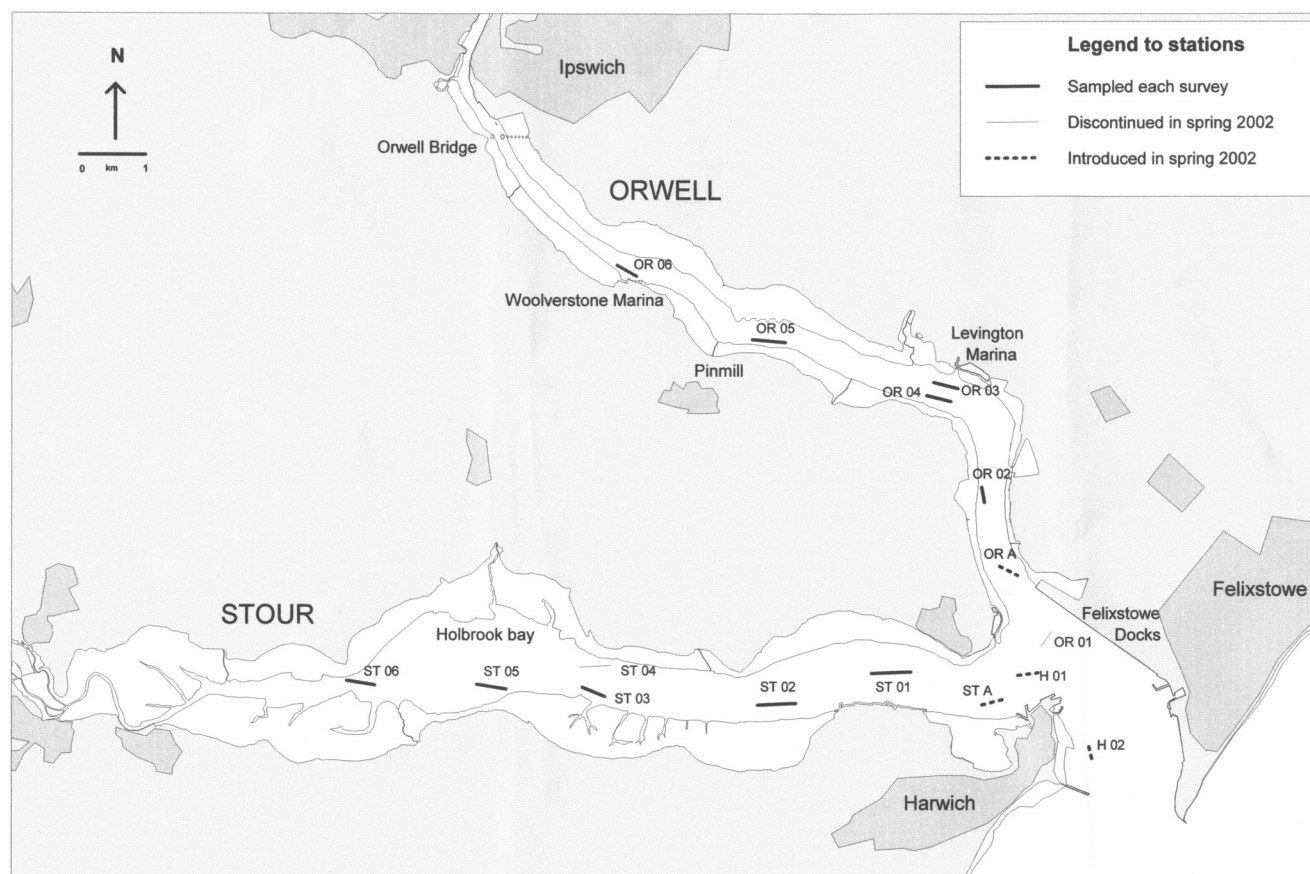


Figure 1. Map of target trawl positions in the Stour and Orwell estuaries, Essex and Suffolk, UK.

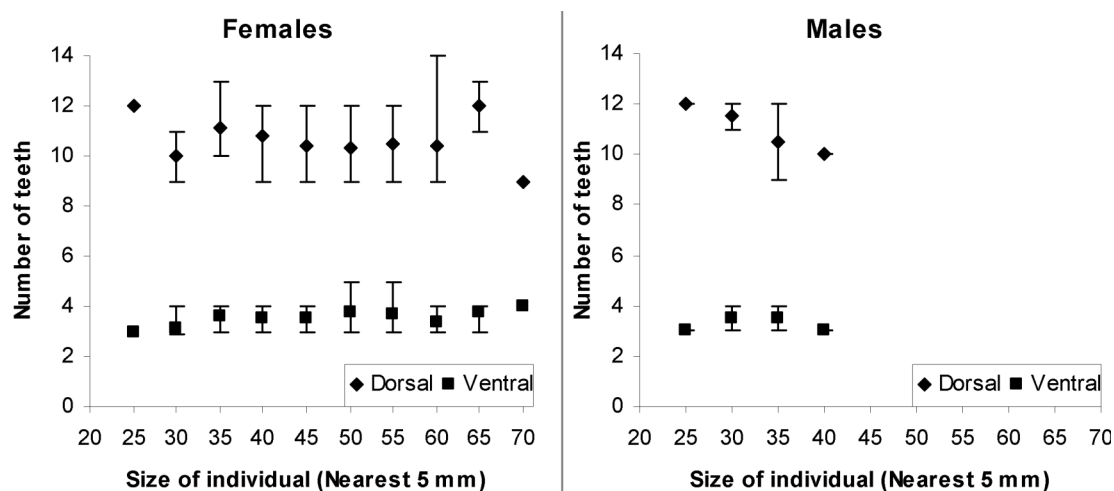


Figure 2. Average number of rostral teeth (dorsal and ventral) in relation to body length for female and male *Palaemon macrodactylus* from the Orwell estuary. Error bars represent the range.

P. macrodactylus has become an intrinsic part of the shrimp fishery and is known as ‘oriental shrimp’.

The opportunity is taken here to revise the current standard identification guide to British Palaemonidae (Smaldon et al., 1993) to include *P. macrodactylus*. Another species, *Leander tenuicornis* (Say), which has been recorded from British waters and which is listed in Howson & Picton’s (1997) Species Directory, but which is missing

from Smaldon et al.’s (1993) standard work, has also been added to the key given here.

MATERIALS AND METHODS

The data considered here were collected as part of a regular monitoring programme (of the fish and shrimp populations of the Stour and Orwell estuaries) conducted

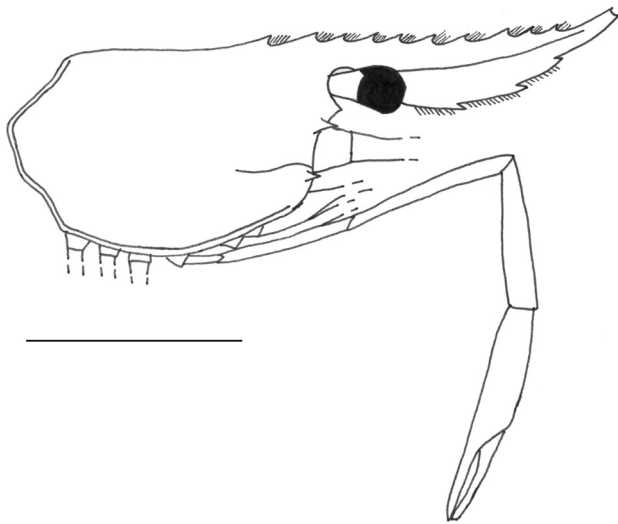


Figure 3. *Palaemon macrodactylus* Rathbun from the Orwell estuary. Lateral view of cephalothorax and pereopod 2. Scale bar: 10 mm.

by Unicomarine Ltd. on behalf of Harwich Haven Authority. The methods used and the results obtained have already been reported in a summary of the data for 2001–2002 (Ashelby et al., 2002). Those methods relevant to the present paper are briefly summarized, below.

Each month, from June 1999 to June 2000, beam trawl samples were taken from six locations on the Stour estuary (Essex and Suffolk), and six on the Orwell estuary (Suffolk). The fish and shrimp in the catch were identified, counted, and measured. Simultaneous records were made of the salinity, temperature and dissolved oxygen content of the water; zooplankton samples were also taken (Dyer, 2001). The sampling positions are shown in Figure 1. The trawls were taken mostly from the seabed, at a depth of 5–6 m below chart datum. The surveys recommenced in December 2001, and now include estimates of the abundance of benthic biota. For each taxon recorded, reference specimens were fixed in a neutral formaldehyde solution and stored in 70% industrial methylated spirits.

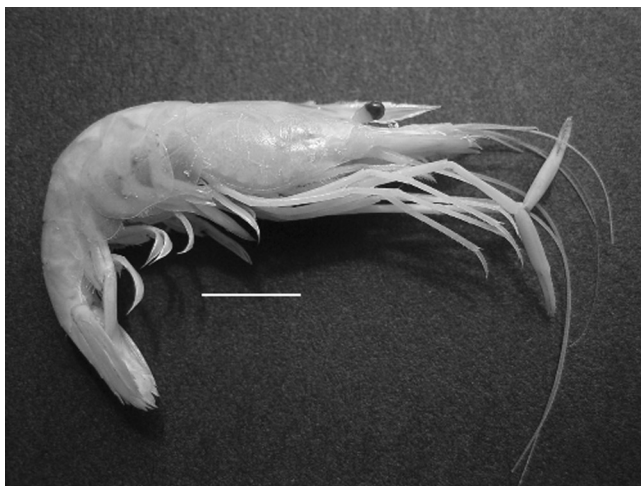


Figure 4. General body form of *Palaemon macrodactylus* Rathbun from the Orwell estuary. Scale bar: 10 mm.

Some of the palaemonid prawns found in the survey of December 2001 were seen to be distinct both from those found previously and from any described in the standard identification guide (Smaldon et al., 1993). Specimens were sent to C. Fransen at the Nationaal Natuurhistorisch Museum, Leiden, for examination. They were subsequently passed on to L.B. Holthuis, who made the initial, tentative identification of *Palaemon macrodactylus*. The identification was confirmed using the description given by Newman (1963) and by the examination of, and comparison with, American material from San Francisco, California (RMNH D 18677), Japanese material from Honshu (RMNH D 32098), and Korean material from Tusan (RMNH D 8985), all of which is held in the collection of the Nationaal Natuurhistorisch Museum, Leiden. Material from the Orwell estuary has been lodged at the Nationaal Natuurhistorisch Museum, Leiden (RMNH D 49812) and at the Natural History Museum, London (NHM 2004.2581–2589).

RESULTS

Distribution

Palaemon macrodactylus was found in the mid reaches of the Orwell estuary, Suffolk. The species was found to the east of Pinmill, Station 5, and close to Woolverstone Marina, Station 6 (Figure 1). Catches of *P. macrodactylus* at these stations have remained consistent. A single specimen was also found at Station 3, close to Levington Marina, in May 2002. The species is noted as being absent from the lower reaches of the Orwell. Two specimens captured by the authors in Holbrook Bay in September 2002, represent the only current recorded instances of the species in the Stour estuary. Salinity at the sites from which *P. macrodactylus* has been recorded ranges from 27.6 to 32.2 ppt. Records of salinity, dissolved oxygen and temperature for stations at which *P. macrodactylus* has been found, or noted as absent, are shown in Table 1, but are unavailable for November 2002. These provide an indication of habitat preference.

Numbers of individuals of all caridean species recorded from the routine surveys in 2001 and 2002, including other Palaemonidae, are also shown in Table 1, highlighting both the identities and the abundance of species that co-occur with *P. macrodactylus*.

Records of ovigerous females

The *P. macrodactylus* population in the Orwell estuary mostly comprises females. Few males have been found. Ovigerous females ranging from 35 mm to 65 mm in length have been encountered. A small proportion of the females caught in December 2001 and January 2002 were seen to be ovigerous. In December ovigerous individuals comprised 11.8% of the total number of females. January showed a slight increase, with 13.3% of captured females bearing eggs. A particularly large ovigerous female, measuring 65 mm, was collected from Station 6 in January 2002. No further ovigerous females were then encountered until June 2002; however, such females were then collected every month from June through to September, inclusive. The proportion of egg-bearing

females encountered in these months was higher than the proportion encountered during the winter. In both June and July, 83.3% of captured females were ovigerous, rising to 100% in August. September saw a marked drop in the number of ovigerous females, with 44.4% of the females caught bearing eggs; none were caught in October. Females carrying very small numbers of eggs (less than 5) were not scored as 'ovigerous'.

Description

The species has been adequately re-described by Newman (1963). However, it is necessary to describe the European specimens in relation to other species likely to be found in similar environments. To this end, a revised key to the British Palaemonidae is presented below. A summary of morphological features (lengths to the nearest 5 mm, counts of rostral teeth and sex) for the Orwell specimens is provided in Figure 2. The cephalothorax is illustrated in Figure 3 and a photograph showing general body form is given (Figure 4). The most useful features, with regard to their ability to aid identification, are summarized below.

Palaemon macrodactylus is a large species, and has been recorded as attaining 51 mm (Newman, 1963), 55 mm Siegfried (1980) and 73 mm (California Resources Agency, 2002) in the United States. Orwell specimens ranged from about 25 to 70 mm (Figure 2). Females are relatively large, ranging from 25 to 70 mm (Figure 2), and averaging 45 mm, in size. The males found in the Orwell population were smaller on average, ranging from 25 to 35 mm in size. There may be up to 15 dorsal rostral teeth (9 to 14 in Orwell specimens, Figures 2 & 3), a greater number than is found in other British species of *Palaemon*. Of these teeth, three (occasionally four) lie behind the orbit. The most posterior tooth is somewhat removed from the others. Females from the Orwell had an average of 11 dorsal rostral teeth. Despite their smaller size, males from the Orwell displayed a greater number of dorsal rostral teeth (9 to 12 in Orwell specimens, Figure 2). The ventral margin has three to five, but usually four, teeth (Figures 2 & 3). The shorter ramus of outer antennular flagellum is fused to the longer ramus for a quarter of its length. The palm of the second pereopod is broad. The body is greenish brown, with brown chromatophores and dull orange joints in a living specimen. The chromatophores are scattered over the body and generally do not form streaks or lines of pigment, as they do in the *Palaemon elegans* Rathke and *Palaemon serratus* (Pennant) found at the same sites. The latter two species also have more reddish brown chromatophores. Similarly, the rostrum of *P. macrodactylus* is translucent in life, lacking the pigment spots found on the rostrum of the other palaemonids found at the same sites. The body is uniformly pale orange after storage in alcohol.

In many respects, *P. macrodactylus* is similar to *Palaemon longirostris* H. Milne-Edwards, and has therefore been placed alongside it in the key. Differences can be found in the numbers and positions of rostral teeth, the density of setae on the rostrum, the breadth of the propodus and the ratio of the fused and free parts of the shorter ramus of the inner antennular flagellum. *Palaemon serratus* is also similar to *P. macrodactylus* but the distal third of the rostrum lacks

teeth and streaks of pigment are present on the body. It should be noted that specimens of *P. longirostris* have been found with up to 12 dorsal rostral teeth (de Man, 1915), and that, during the course of the surveys considered here, specimens of *P. serratus* were found in the Orwell which possessed up to nine dorsal rostral teeth.

Key to palaemonid species in British waters

The following key is based on that written by Smaldon (1979) and revised by Holthuis & Franssen (1993). To this, the diagnostic features of *Palaemon macrodactylus* have been added. A further species, *Leander tenuicornis*, which was not included in the original key, has also been included using published descriptions (Squires, 1990; Jayachandran, 2001). Habitat and pigmentation notes have also been added.

1. Rostrum very short, unarmed. Carapace with strong supraorbital spines which are more than half as long as the rostrum; without branchiostegal or hepatic spine. Second pereopods asymmetrical, with swollen chela. Living in sponges *Typton spongicola* Costa, 1844
- Rostrum well developed with teeth on dorsal and ventral borders. Carapace without supraorbital spines; with branchiostegal or hepatic spine. Second pereopods symmetrical, chelae slender. 2
2. Carapace with branchiostegal spine; without hepatic spine 3
- Carapace without branchiostegal spine; with hepatic spine, far behind anterior margin *Periclimenes sagittifer* (Norman, 1861)
3. Carapace without branchiostegal suture. First pleopod of male with well developed appendix interna on endopod. Rostrum sexually dimorphic: broad and arched in females, slender and upturned in males, with 11–13 dorsal teeth (two of which lie behind the orbit); and 4–7 ventral teeth. Dactylus of pereopod 2 longer than propodus. Warm water species (western in Britain), found among *Sargassum* spp. in the open sea or in shallow water benthic vegetation. *Leander tenuicornis* (Say, 1818)
- Carapace with branchiostegal suture extending posteriorly from a point on the anterior margin, dorsal to the branchiostegal spine. First pleopod of male without appendix interna on endopod. Rostrum shape variable, with 4–15 dorsal teeth. Dactylus of pereopod 2 equal to or shorter than propodus. Predominantly benthic species. 4
4. Mandible with palp. Rostrum straight or curved, with five or more dorsal teeth and three or more (in exceptional cases two) ventral teeth. Up to four dorsal teeth lie behind edge of orbit. Brackish or marine 5
- Mandible without palp. Rostrum straight, 4–6 dorsal teeth, two ventral teeth. One dorsal tooth behind edge of orbit. Brackish water species common in saltmarsh pools *Palaemonetes varians* (Leach, 1814)

5. Mandibular palp of three segments. Dactyl of pereopod 2 about 0.5 length of propodus. Rostrum variable. Variously pigmented or pigment lacking. . .6
 — Mandibular palp of two segments. Rostrum straight or very slightly upcurved; 7–9 dorsal teeth, three (rarely two or four) ventral teeth. Three (occasionally two) of the dorsal teeth behind posterior edge of orbit. Dactyl of pereopod 2=0.33 times length of propodus. Chromatophores form vertical pigment streaks on abdomen. Marine or estuarine.
 *Palaemon elegans* Rathke, 1837
6. Rostrum straight, or nearly so, with dorsal teeth extending into distal third. 7
 — Rostrum with distinct upward curve, dorsal teeth not extending into distal third. Six or seven (exceptionally up to nine) dorsal teeth, excluding subdistal tooth, four or five ventral teeth. Two of the dorsal teeth lie behind posterior edge of orbit. Merus of pereopod 2=1.25 times length of carpus. Vertical pigment streaks on abdomen. Marine or estuarine; common in rocky areas *Palaemon serratus* (Pennant, 1777)
7. Rostrum with seven to 15 dorsal rostral teeth (excluding subdistal tooth), of which two to four lie behind the posterior edge of the orbit; most posterior tooth about 1.5 times more distant from first than from next distally 8
 — Rostrum with five or six dorsal teeth (excluding subdistal tooth) and three (rarely two or four) ventral teeth. One dorsal tooth behind posterior edge of orbit, second tooth often directly above edge. Lower half of rostrum with scattered red pigment spots. Carpus of pereopod 2 about 1.2×length of merus. Brackish water species. *Palaemon adspersus* Rathke, 1837
8. Rostrum with seven or eight (up to 12 in exceptional cases) dorsal rostral teeth (excluding subdistal tooth), of which two lie behind the posterior edge of the orbit, and with three or four (rarely five) ventral teeth. Few setae between dorsal rostral teeth. Shorter ramus of antennular flagellum fused for third of its length to longer ramus. Carpus of pereopod 2 equal or slightly longer than merus; palm slender. Brackish water species found in upper reaches of estuaries
 *Palaemon longirostris* H. Milne Edwards, 1837
 — Rostrum with nine to 15 (usually ten to 12) dorsal rostral teeth (excluding subdistal teeth), of which three (seldom four) behind posterior edge of orbit, and with three to five (usually four) ventral teeth. Rostrum strongly setose between rostral teeth. Shorter ramus of antennular flagellum fused for a quarter of its length to longer ramus. Carpus of pereopod 2 equal or slightly shorter than merus; palm broad. Commonly estuarine
 *Palaemon macrodactylus* Rathbun, 1902

DISCUSSION

A large species of north-east Asian prawn has been introduced to British waters. The first records of the species in Europe are documented here; but, it is also known to have been previously introduced to San

Francisco Bay, western North America (Newman, 1963) and to have spread successfully there (Ricketts et al., 1968; Cohen, 1996; Williams, 1997; United States Geological Survey, 2002; California Resources Agency, 2002). It is tentatively assumed that the species first arrived in the vicinity of the Orwell Estuary some time between June 2000 and December 2001; however, as Carlton (1985) noted, the date of first collection is not necessarily, and indeed is rarely, coincident with the date of introduction.

The species has been found at three locations in the mid reaches of the Orwell estuary, where it was the third most common caridean in December 2001, and at one location in the Stour estuary. It currently lives at salinities of 27.6 to 32.2 ppt in the Orwell estuary. Material from other locations must be examined, in order to confirm that the Orwell was the point of introduction to Europe. The prawns are readily identifiable, once suspected, and can now be searched for in other areas.

The possible means by which marine species may be introduced are summarized by Eno et al. (1997). It is thought that the release of eggs or larvae contained in the ballast water or seawater-intake pipes of large vessels is one of the most common means by which exotic marine species are introduced into waters to which they are not native (Carlton, 1985). Over half of the non-native marine species in British waters are thought to have been introduced in association with shipping, whilst ballast water accounts for about 18% of all introductions (Eno et al., 1997). Decapod larvae have been found in the ballast water of 48% of ships arriving from Japan at the Port of Coos Bay, Oregon, USA, and plankton samples taken from Japanese ballast water have been found to contain up to 367 taxa (Carlton & Geller, 1993). *Palaemon macrodactylus* has pelagic larvae that could be transported in ballast water. The adults also move into the water column at night and are mainly nocturnal (Siegfried, 1982), which may increase the likelihood of them being incorporated into ballast water.

It has been suggested (Dawson, 1973; Williams et al., 1988) that decreased transit times, due to the increased speed of vessels, lead to the survival of greater numbers of the organisms contained in ballast water, which may increase the likelihood of successful introductions. Dawson (1973) suggested that the above may have been the reason for the successful introduction of *P. macrodactylus* to California. Following voyages of about two weeks from Japan to Australia, Williams et al. (1988) found living caridean larvae in the water column, and at least three species of adults and juveniles in the sediment, in the ballast tanks of woodchip carriers.

The Orwell estuary lies between the ports of Felixstowe and Ipswich. Large vessels used to transport goods between continents (including Asia) call at Felixstowe; but, most traffic to Ipswich is local, and comprises smaller vessels (Richard Allen and Ian Webster, personal communication). It is likely that *P. macrodactylus* was transported to the area via international shipping at Felixstowe; however, a detailed study of other estuaries, such as the Thames, will be required for certainty in this matter. Other possible means of introduction include release from aquaria, possibly in association with the restaurant trade.

The fate of the *P. macrodactylus* in European waters should be closely monitored. The species may spread rapidly or slowly, or the present population may remain stable or become extinct. All these possible outcomes have been demonstrated by other species introduced into British waters (Eno et al., 1997). It must be assumed that the species is likely to spread, as it has in North America, where it is now common along most of the Pacific coast. Its spread in North America has been accelerated by its use as bait (Williams, 1997). Consistent catches and records of ovigerous females suggest that the Orwell population is stable.

Palaemon macrodactylus is noted as being very hardy and able to survive a wide range of temperatures, salinities and conditions of oxygen availability (Newman, 1963); such hardiness is also demonstrated by the Orwell specimens (Table 1). It is a strong osmoregulator over the salinity range of 2–150‰ seawater, and is known to inhabit a wide range of salinities in San Francisco Bay (Born, 1968), where it is not uncommon to capture *P. macrodactylus* in fresh or nearly fresh water (Siegfried, 1980). The upstream limit of its range has been noted as 1 ppt, the downstream limit being set by prey availability (Siegfried, 1980). The species is common in inlets and estuaries, especially in *Zostera* beds (Omori & Chida, 1988a). Further monitoring will be required to confirm any increase in population. *Palaemon macrodactylus* is currently one of the more common carideans in the Orwell estuary, and is often the most common palaemonid in the mid part of the estuary. *Crangon crangon* (L.) and *Pandalus montagui* (Leach) are the most abundant carideans in the estuary as a whole.

A number of studies on the reproductive behaviour of *Palaemon macrodactylus* have been reported that are of relevance here, and these are reviewed below. Omori & Chida (1988a) described reproduction in *P. macrodactylus* in Japan. The breeding season was noted as being mid-April to early October. Second-year females carry eggs earlier than first-year females. Most 0–1 y-old females were found to produce less than 1000 eggs at temperatures of between 15°C and 27°C. Older females were found to produce 500–2800 eggs at similar temperatures. Brood sizes of between 100 and 2000 have been noted for Californian specimens of the species (Siegfried, 1980). These figures are similar to those recorded for other palaemonids, for example the 4300 eggs carried by *Palaemon serratus* (Jensen, 1958). The eggs of *P. macrodactylus* are protected from fungal attack by a symbiotic bacterium (Gil-Turnes et al., 1989). Each age group produces at least two cohorts per year, with five to nine being possible under controlled laboratory conditions entailing a raised temperature and hence an extended breeding season (Omori & Chida, 1988b). It has been suggested that higher salinities may also extend the breeding season of *P. macrodactylus* (Little, 1969). Females may carry a second brood in their ovaries before the first brood is released (Siegfried, 1980). The larvae of *P. macrodactylus* are photopositive (Little, 1969); however, they become photonegative as they develop, prior to recruitment to the benthos (Siegfried et al., 1978). Photoperiod has been noted as an important parameter in controlling spawning (Siegfried, 1980). In California, ovigerous females are found mainly from May to August (Siegfried, 1980); juveniles are recruited to the benthos after May (Siegfried, 1980, 1982). The breeding season

observed in the Orwell specimens compares favourably with that described for Japan (Omori & Chida, 1988a) and California (Siegfried, 1980) although it is notably shorter than it is in either of the latter cases. It is possible that the small catch sizes obtained in May and October may have excluded ovigerous females, therefore giving the impression of a comparatively short breeding season. It is also curious that ovigerous females were present in the Orwell during December and January, well outside the breeding seasons described by Omori & Chida (1988a) and Siegfried (1980).

In this species, growth rate is very high in the first year and there is a spurt of growth just before spawning: little growth occurs after spawning until the following year. Sexual characteristics are noted on individuals 20 mm in length (Siegfried, 1980) and females grow faster than, and are larger than, males (Omori & Chida, 1988a). Siegfried (1980) recorded a maximum length of 55 mm for females and 44 mm for males. More large specimens (those over 60 mm) are reported from the Orwell than are reported by the Californian studies considered above, though the California Resources Agency (2002) has recorded a maximum length of 73 mm. Life spans of two to three years have been recorded for individuals of *P. macrodactylus* in Japan (Omori & Chida, 1988a).

The impact *P. macrodactylus* has on the ecology and fisheries of European estuaries should be a subject of further study, as it is not currently possible to predict the implications its introduction may have. A summary of the potential effects of introductions is provided by Eno et al. (1997). Should there be an increase in range, then, as an edible species, *P. macrodactylus* would become part of the prawn fishery. However, it has been described as being of low commercial value in Japan, where it is caught in brash traps (Omori & Chida, 1988a). Were its range to increase, it would also become a food source for fish, along with the native species, as has been noted in California (Ganssle, 1966). Many introduced species have, in the past, proved to be damaging to indigenous biota, although in British waters the effects of non-native species have not generally been as detrimental as those reported in other parts of the world (Eno et al., 1997). There exists the possibility that *P. macrodactylus* may compete with indigenous species for food and habitat, and that it may have an advantage over more vulnerable species.

Like other carideans, *Palaemon macrodactylus* is largely carnivorous, its diet being mainly made up of animal fragments (at least 75%); plant material forms a smaller proportion of its diet (Sitts & Knight, 1979). Newman (1963) noted that in San Francisco Bay *P. macrodactylus* occupied a different ecological niche to the native shrimp species, and so did not seem to have a damaging effect. However, Sitts & Knight (1979) and Siegfried (1982) found that there was dietary overlap, with size-related resource partitioning, between this species and an indigenous species—*Crangon franciscorum* (Stimpson)—in California, with mysids, *Corophium* spp. and polychaetes being the main prey. Copepods have also been reported to be an important prey item (Sitts & Knight, 1979) and are probably the main food of larvae and juveniles. Dietary overlap with the European *Crangon crangon* should also be expected. *Crangon franciscorum* is generally larger than *P. macrodactylus* (Siegfried, 1982), allowing for slight

dietary differences. However, *C. crangon* is of a similar size to *P. macrodactylus*. Therefore, dietary overlap with European *C. crangon* may be expected. In contrast to American waters there are a greater variety of palaemonid taxa in European waters, where habitat and food preferences are more likely to overlap. *Palaemon macrodactylus* currently occurs alongside other palaemonids: several related prawns are found in close proximity in the Orwell (Ashelby et al., 2002; Table 1). There is thus the potential for resource competition to occur; however, it is not known whether the introduced species is either a stronger competitor, or more robust, than any of the native species. The number of eggs produced appears to be similar to the number produced by *P. serratus* (see above).

It is also possible that *P. macrodactylus* may prey on other caridean species. There is evidence of cannibalism when individuals are kept in crowded laboratory conditions (Newman, 1963) and this aspect of the feeding behaviour of the species could be extended to include other carideans in the diet. While little data exists on its competitive interactions, Ricketts et al. (1968) observed that it eclipsed native (American) *Crangon* spp. in terms of numerical abundance, while Siegfried (1980) felt that careful management of water projects may be necessary to protect the native shrimp (*C. franciscorum*) in the Sacramento/San Joaquin Delta. In California, *P. macrodactylus* also serves as an important food resource for fish, including striped bass (Ganssle, 1966; Ricketts et al., 1968) and the larvae are prey for *C. franciscorum* (Siegfried, 1980). It is probable that *P. macrodactylus* may serve as a similar food resource for native *Crangon* and fish species in the Orwell estuary. However, the fact that fungi are associated with the species (Gil-Turnes et al., 1989) raises the possibility that new diseases may be introduced to native prawns.

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