

OCCURRENCE OF THE ASIAN SHRIMP *PALAEEMON MACRODACTYLUS*  
IN THE SOUTHERN BIGHT OF THE NORTH SEA, WITH A KEY TO  
THE PALAEMONIDAE OF NORTH-WESTERN EUROPE (CRUSTACEA:  
DECAPODA: CARIDEA)

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The Asian shrimp *Palaemon macrodactylus* is native to the north-western Pacific Ocean. After introduction in the USA it has spread rapidly. The species has recently been found in two distant regions along the European Atlantic coasts: south-western Spain and the southern North Sea. In the present paper the first records of the species in the southern bight of the North Sea are presented and discussed. The morphology and colour pattern of *P. macrodactylus* is described and illustrated, based on European specimens. A detailed identification key to the Palaemonidae of north-western Europe, southwards down to the Bay of Biscay, is given. In the field, adult and subadult specimens of *P. macrodactylus* can be readily identified by the presence of a whitish longitudinal dorsal stripe running all along their back.

#### INTRODUCTION

As a consequence of human activities, a steadily increasing number of marine species have established breeding populations outside and far away from their natural geographic range. They can become extremely abundant and can modify the structure of the local ecosystem which may result in the decline of indigenous species. The European coasts have not been spared by this process (Eno 1997, Galil et al. 2002) and several introduced species have become dominant components of the coastal and estuarine biocenoses of north-western Europe.

Recently the shrimp *Palaemon macrodactylus* Rathbun, 1902 has been recorded in European waters. The species originates from the temperate north-western Pacific: Japan, Korea and China (Holthuis 1980). In the 1950s it has accidentally been introduced to the Pacific coast of the USA (Newman 1963), where it is now widely distributed and locally very abundant (Jensen 1995). Afterwards it has been found in Australia (Davie 2002) and Argentina (Spivak in press).

In Europe Cuesta et al. (2004) found large populations in estuaries on the Atlantic coasts of south-western Spain and Ashelby et al. (2004) caught the shrimp in the Orwell and Stour estuaries in south-eastern England, near the ports of Felixstowe and Harwich.

In this study different sites along the southern bight of the North Sea were sampled to map out the distribution of *P. macrodactylus*. The results are presented in a table and on a map. The morphology and colour pattern of European *P. macrodactylus* are described, and a new illustrated identification key to the Palaemonidae of north-western Europe is presented.

#### MATERIAL AND METHODS

Several sheltered biotopes such as marinas, estuaries and lagoon-like habitats (tidal and non-tidal) have been sampled from June until early October 2004 in the southern bight of the North Sea. In addition, a single sample collected in November 1999 was also considered, since it included



a



b



c

Figure 1. *Palaemon macrodactylus*, ovigerous females (Belgium, Zeebrugge, marina, 20.VII.2004), a. lateral view (weakly pigmented specimen), b. anterior part in lateral view (strongly pigmented specimen), c. dorsal view, showing characteristic dorsal pale stripe (strongly pigmented specimen).  
 Figuur 1. Rugstreepsteurgarnaal *Palaemon macrodactylus*, eierdragende wijfjes (België, Zeebrugge, marina, 20.VII.2004), a. zij-aanzicht (zwak gekleurd exemplaar), b. zij-aanzicht voorste deel (sterk gekleurd exemplaar), c. rugzijde met karakteristieke bleke rugstreep (sterk gekleurd exemplaar).

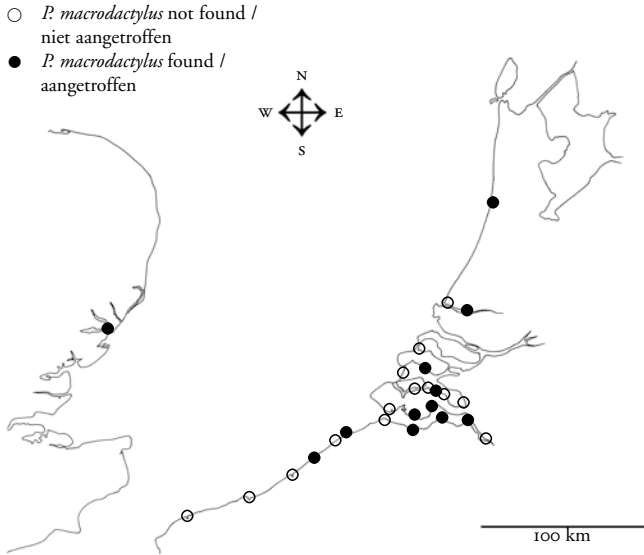


Figure 2. Distribution of *Palaemon macrodactylus* in the southern bight of the North Sea. When a positive and a negative record are too close to each other, only the positive record is indicated. For details see table 1. *Figuur 2.* Verspreiding van de rugstreepsteurgarnaal *Palaemon macrodactylus* in de zuidelijke bocht van de Noordzee. Als een positieve en negatieve waarneming te dicht bij elkaar liggen wordt alleen de positieve waarneming aangeduid. Voor details zie tabel 1.

some *P. macrodactylus*. So far no attention has been paid to open coasts because the occurrence of *P. macrodactylus* is less probable in such habitats. Most specimens have been collected with a hand net operated between rocks covered by algae or amongst the epifauna and epiflora of floating pontoons in marinas and other harbour infrastructures. Two scuba-dives in the Oosterschelde, one in the Grevelingen and one in the Veerse Meer resulted in some additional data.

The shrimps have initially been identified in the field on the basis of their colour pattern (especially by the presence of a whitish longitudinal dorsal stripe running all along the back, which is lacking in European native Palaemonidae) (fig. 1) and morphological characters visible with the naked eye, such as the shape and the tooth pattern of the rostrum (fig. 6). When necessary, they have been checked afterwards under a dissecting microscope. Some living specimens were photographed. The specimens were killed by freezing and were fixed afterwards in ethanol 70%. Line drawings have been made with a camera lucida mounted on an 'aus Jena' Technival II dissecting microscope. Some voucher specimens have been

deposited in the Nationaal Natuurhistorisch Museum Naturalis, Leiden (RMNH D 51414, specimens from Hansweert, 30.VII.2004; and RMNH D 51413, specimens from Rozenburg, 17.VIII.2004), in the Tromsø Museum (TMU 13 637 and TMU 13 638, respectively 1 and 2 specimens from Zeebrugge, 20.VII.2004) and in the Royal Institute for Natural Sciences of Belgium, Brussels (IG 30 347, 12 specimens from the sluice dock of Oostende, 31.VIII.2004). The rest of the material is deposited in the collection of the authors.

## RESULTS

Shrimps were caught in a number of sites in the Netherlands, Belgium and along the French North Sea coast. The results are summarised in table 1 and plotted on a map (fig. 2).

### Key to the Palaemonidae of northwestern Europe

Identification of European Palaemonidae is not an easy matter and the arrival of *P. macrodactylus* further complicates the situation. Many previous identification keys were unpractical because they

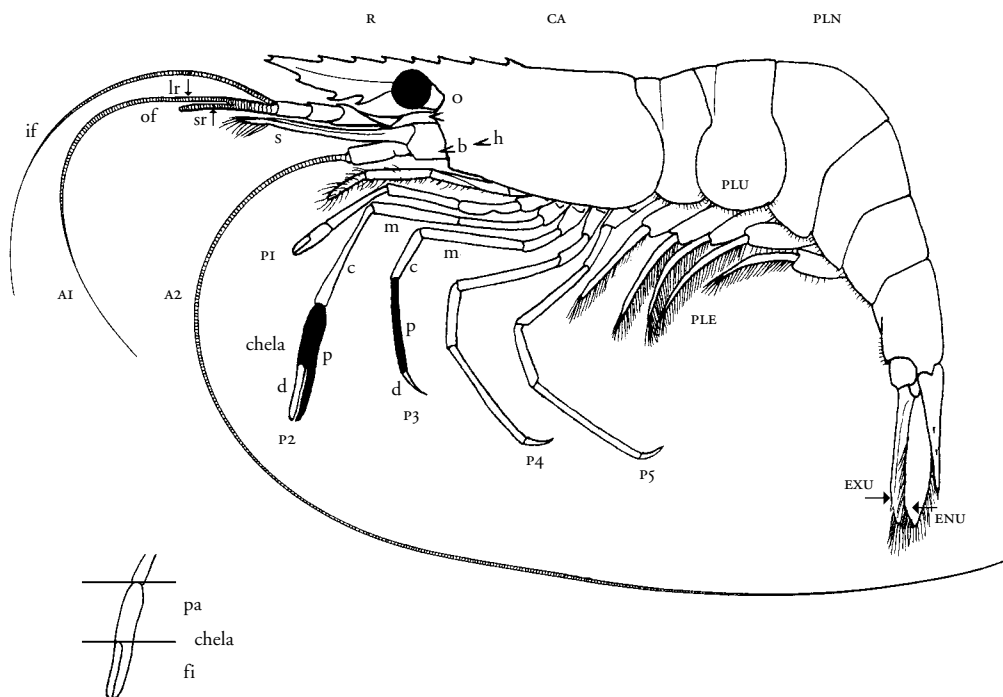


Figure 3. Technical terms used in the identification key and description (drawing after Holthuis et al. 1986).

CA - carapace, R - rostrum, O - orbit, b - branchiostegal spine, h - hepatic spine, A1 - antennula (first antenna), if - inner flagellum of antennula, of - outer flagellum of antennula, lr - longer ramus of outer flagellum of antennula, sr - shorter ramus of outer flagellum of antennula, A2 - second antenna, s - scaphocerite or antennal scale (blade-shaped appendage here seen on the edge), P1-P5 - first to fifth pereopods (clawed legs and walking legs), m - merus, c - carpus, p - propodus (in black), d - dactylus (in P1 and P2 the propodus and the dactylus are modified to form a claw or chela), pa - palm of chela, fi - fingers of chela, PLN - pleon or abdomen (the pleon consists of six segments or pleonites), PLU - pleuron (ventro-lateral expansion of each abdominal segment), PLE - pleopods or swimming legs, EXU - exopod of uropod (outer branch of lateral appendage of tail fan), ENU - endopod of uropod (inner branch of lateral appendage of tail fan).

Figuur 3. Technische termen gebruikt in de determinatiesleutel en in de beschrijving (tekening naar Holthuis et al. 1986). CA - rugschild, R - rostrum, O - oogkas, b - branchiostegale steekel, h - hepaticale steekel, A1 - antennula (eerste voelspriet), if - binnenste flagel van de eerste voelspriet, of - buitenste flagel van de eerste voelspriet, lr - langste tak van de buitenste flagel van de eerste voelspriet, sr - kortste tak van de buitenste flagel van de eerste voelspriet, A2 - antenna (tweede voelspriet), s - scaphoceriet of antennale spaan (lamelvormig aanhangsel, hier te zien tegen de zijrand), P1-P5 - eerste tot vijfde pereopoden (schaar- en looppoten), m - merus, c - carpus, p - propodus (zwart), d - dactylus (in P1 en P2 zijn de propodus en de dactylus tot een schaar of chela vergroeid), pa - schaarpalm, fi - schaarvingers, PLN - pleon of achterlijf (het achterlijf bestaat uit zes segmenten of pleonieten), PLU - pleuron (ventro-laterale plaatvormige uitgroeiing van elk achterlijfssegment), PLE - pleopoden of ventrale zwempoten, EXU - exopodiet of buitenste tak van de uropoed (staartpoot), ENU - endopodiet of binnenste tak van de uropoed.

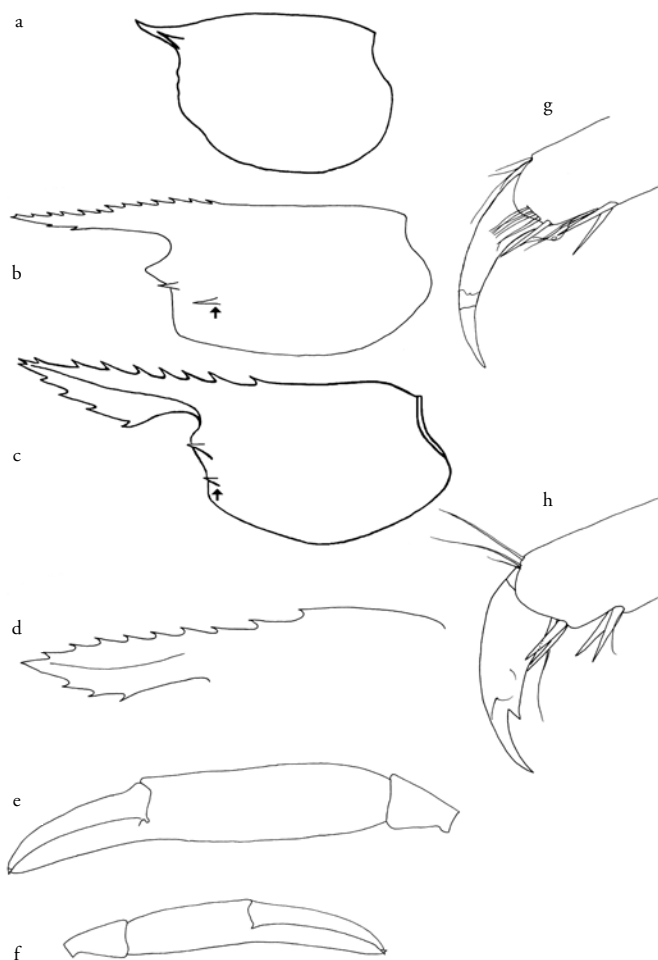


Figure 4. a-c. carapace in lateral view, d. upper part of carapace in lateral view, e. chela of right P2, f. chela of left P2, g-h. dactylus of left P3.

a. *Typton spongicola* (after Smaldon 1979), b, g. *Periclimenes kornii* (after d'Udekem d'Acoz 1999), c. *Palaemon longirostris* (after De Man 1915), d-f, h. *Periclimenes sagittifer* (after d'Udekem d'Acoz & Wirtz 2003).  
 Figuur 4. a-c. rugschild in zijaan-zicht, d. bovendeele van rugschild in zijaan-zicht, e. schaarppoot van rechter tweede pereiopood (P2), f. schaarppoot van linker tweede pereiopood, g-h. dactylus van linker derde pereiopood (P3).  
 a. *Typton spongicola* (naar Smaldon 1979), b, g. *Periclimenes kornii* (naar d'Udekem d'Acoz 1999), c. *Palaemon longirostris* (naar De Man 1915), d-f, h. *Periclimenes sagittifer* (naar d'Udekem d'Acoz & Wirtz 2003).

include a couplet based on the mandibular palp only, i.e. on a character which cannot be observed without dissection. Therefore a new key to the Palaemonidae of north-western Europe down to the Bay of Biscay is presented. As far as possible, characters taken from literature have been checked against actual specimens. Since *P. elegans*, *P. longirostris* and *P. macrodactylus* are very similar, they are compared in a triple alternative. The key is intended to be used for mature and large immature specimens only (total body length > 40 mm). Attempts to identify juveniles with this key are likely to result in misidentifica-

tions, since several specific characters appear only at an advanced stage of development. It should be taken into account that the disposition of rostral teeth can exhibit occasional anomalies and that the number of teeth given here is the most frequently occurring number, not the extreme values. Additional characters are given between square brackets.

The technical terms used in the key and the description are explained in figure 3. The most important characters indicated in the key are illustrated in figure 4 and 5. More detailed

accounts of the species are given in literature. All native Palaemonidae except *Periclimenes kornii* (Lo Bianco, 1903) are described and illustrated in Smaldon et al. (1993). Several other publications, such as Kemp (1910), De Man (1915, 1923), Gurney (1923), Holthuis (1950, 1987), Holthuis et al. (1986), Neves (1970) and Lagardère (1971) include good drawings on European *Palaemon* (sometimes under the generic name *Leander*) and *Palaemonetes*. *Periclimenes kornii* has been described by de Saint Laurent & García Raso (1993) and d'Udekem d'Acoz (1999). Further illustrations have been given for *Periclimenes sagittifer* (Norman, 1861) by Grippa & d'Udekem d'Acoz (1996), d'Udekem d'Acoz & Wirtz (2003), Wirtz & Debelius (2003: colour photograph) and for *Typton spongicola* Costa, 1844 by Neves (1970). Unlike Ashelby et al. (2004) we have not included *Leander tenuicornis* (Say, 1818), a species usually found far offshore among the pleustonic alga *Sargassum natans* (Linnaeus) Gaillon. There are no reliable records of this species around the British Isles and in north-western Europe. Ashelby et al. (2004) included it because it was present in the older key of Allen (1967) treating the decapods found or likely to be found in Great Britain, and in the species list of Howson & Picton (1997). Inclusion in the latter list is probably also based on Allen's book (pers. comm. C.W. Ashelby 2004).

- 1 Rostrum toothed on upper and lower borders, well-developed, blade-shaped, reaching or overreaching tip of peduncle of antennula (fig. 4b-d); scaphocerite well developed; p2 slender or fairly slender; exopod of uropod with one fixed tooth followed by one mobile spine . . . . . 2
- Rostrum toothless, reduced, styliform, far from reaching tip of peduncle of antennula (fig. 4a); scaphocerite vestigial; p2 very stout and strong; exopod of uropod with about 5 teeth . . . . . *Typton spongicola* Costa, 1844  
In sponges, 8-100 m depth, rare; southern species, northernmost limit: Bretagne and extreme southwest of Great Britain.

- 2 Carapace with hepatic spine, far behind the anterior margin; without branchiostegal spine (fig. 4b: arrow); dactylus of p3-p5 entire or cleft . . . . . 3
- Carapace without hepatic spine, with branchiostegal spine (fig. 4c: arrow); dactylus of p3-p5 entire . . . . . 4
- 3 Dactylus of p3-p5 entire (fig. 4g); rostrum narrow (fig. 4b); colourless; below 300 m depth . . . . . *Periclimenes kornii* (Lo Bianco, 1903)  
Southern species, very rare in northwestern Europe: a single old record in the north of the Bay of Biscay.
- Dactylus of p3-p5 cleft (fig. 4h); rostrum high (fig. 4d); [p2 with very short carpus (fig. 4e-f)]; body with large purple or pink spots; carapace and legs mottled with blue dots; intertidal and coastal waters . . . . . *Periclimenes sagittifer* (Norman, 1861)  
Usually associated with *Anemonia viridis* (Forskål, 1775); southern species reaching Bretagne and the Channel Isles (a single old record from the Strait of Dover: Boulogne-sur-Mer).
- 4 Usually 3 teeth or more on lower border of rostrum (fig. 5a-e); shorter ramus of the outer flagellum of antennula fused to the longer for at most 55% of its length (fig. 5g-k); mandibular palp present (fig. 5m-n); propodus of p2 longer than or equal to carpus (sometimes very slightly shorter than carpus) (fig. 5p, 5t). . . . . 5
- Usually 2 teeth on the lower border of rostrum (fig. 5f); shorter ramus of the outer flagellum of antennula fused to the longer for at least 80% of its length (fig. 5l); mandibular palp absent (fig. 5o); propodus of p2 distinctly shorter than carpus (fig. 5u); [rostrum with 4-6 dorsal teeth, one of which is behind the orbit (fig. 5f)]; body weakly pigmented, often almost transparent, without stripes . . . . . *Palaemonetes varians* (Leach, 1814)  
Brackish water of salt marshes, ponds, canals, etc.

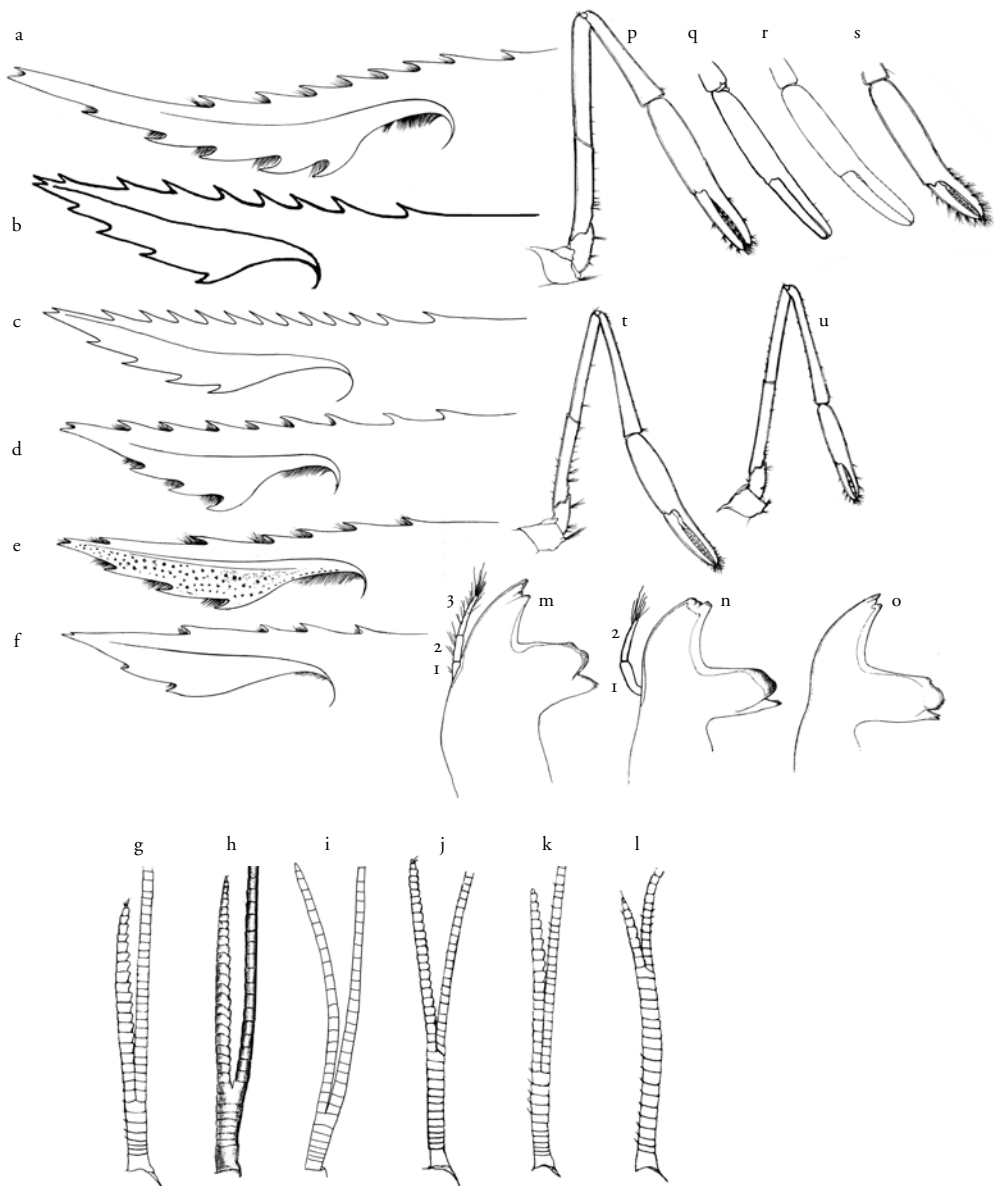


Figure 5. a-f. rostrum, g-l. outer flagellum of antennula (A1), m-o. mandible, p-u. second pereiopod (P2).

a, g, m, p. *Palaemon serratus* (after Kemp 1910), b, h, q. *P. longirostris* (after De Man 1915), c, i, r. *P. macrodactylus* (original), d, j, n, s. *P. elegans* (after Kemp 1910), e, k, t. *P. adspersus* (after Kemp 1910), f, l, o, u. *Palaemonetes varians* (after Kemp 1910).

Figuur 5. a-f. rostrum; g-l. buitenste flagel van de eerste voelspriet (A1), m-o. mandibel, p-u. tweede pereiopod (P2). a, g, m, p. *Palaemon serratus* (naar Kemp 1910), b, h, q. *P. longirostris* (naar De Man 1915), c, i, r. *P. macrodactylus* (origineel), d, j, n, s. *P. elegans* (naar Kemp 1910), e, k, t. *P. adspersus* (naar Kemp 1910), f, l, o, u. *Palaemonetes varians* (naar Kemp 1910).

- 5 Rostrum not or scarcely upcurved, distally not especially slender, with dorsal teeth on 85% of its length or on all its length (fig. 5b-e); merus of p2 shorter than or equal to carpus (fig. 5t) . . . . . 6
- Rostrum distinctly upcurved and distally slender, with dorsal teeth on 50 to 65% of its length (i.e. distal third without dorsal teeth) in adults and large immatures with body length 50 mm or more (fig. 5a); merus of p2 1.25 x as long as carpus (fig. 5p); [rostrum usually with 6 to 8 dorsal teeth (tooth of apical cleft not considered), 2 of which behind the posterior edge of orbit (or one well behind the orbit and one directly above edge of orbit); space between the 1st and the 2nd tooth 1.5 x as long as space between 2nd and 3rd (fig. 5a); mandibular palp 3-jointed (fig. 5m); fingers of p2 = 0.7 x length of palm or more (fig. 5p)]; body usually with regular transverse stripes (in turbid waters it may be completely transparent) . . . . .  
. . . . . *Palaemon serratus* (Pennant, 1777)  
Lower half of the shore and shallow subtidal waters; usually on open coasts (especially on rocky bottoms) but also present in harbours and lagoons.
- 6 Dorsal teeth of rostrum numerous (normally at least 7, tooth of apical cleft not considered), 2 or 3 of these teeth behind the orbit; posterior edge of dorsal teeth pointing obliquely upwards; lower half of rostrum without red pigment dots (fig. 5b-d) . . . . . 7
- Dorsal teeth of rostrum few in number (normally 5 or 6, tooth of apical cleft not considered), 1 of these teeth behind the orbit, second tooth often directly above edge of orbit; posterior edge of dorsal teeth parallel to rostrum (not or barely pointing upwards); lower half of rostrum with red pigment dots (fig. 5e); [mandibular palp 3-jointed. Fingers of p2 0.8 x as long as palm (fig. 5t)]; colour uniformly greenish to brownish, with a very finely dotted pattern (without transverse stripes or reticulations), often with a short whitish longitudinal dorsal mark or spot on the third pleonite, sometimes additional whitish mid-dorsal spots present, but never a long stripe all along the back . . . . .  
. . . . . *Palaemon adspersus* Rathke, 1837  
Lower half of the shore and shallow subtidal waters; a seawater and slightly brackish water species, always found in very sheltered habitats such as lagoons and harbours.
- 7 Rostrum usually with 7 to 9 dorsal teeth (tooth of apical cleft not considered), 2 of which are behind the orbit; space between 1st and 2nd tooth 1.5 x as long as space between 2nd and 3rd; proximal third of rostrum often significantly expanded ventrally (but not always) (fig. 5b); shorter ramus of the outer flagellum of antennula fused to the longer for about 30% of its length (fig. 5h); shorter ramus of outer flagellum of antennula 0.7 x as long as antennular peduncle; mandibular palp 3-jointed (fig. 5m); fingers of p2 = 0.7 x as long as palm (fig. 5q); dactylus of p3 variable in length and slenderness (morphology population dependent, possibly longer and more slender on soft than on hard bottoms); almost translucent or well pigmented; pigmented specimens with transverse reticulations on carapace and abdomen; no whitish longitudinal dorsal stripe . . . . .  
. . . . . *Palaemon longirostris*  
H. Milne Edwards, 1837  
Estuaries of large and small rivers; variable species.
- Rostrum usually with 10 to 12 dorsal teeth (tooth of apical cleft not considered), 3 of which are usually behind the orbit; space between 1st and 2nd tooth 1.5 to 2 x as long as space between 2nd and 3rd. Proximal third of rostrum only weakly expanded ventrally (fig. 5c); shorter ramus of outer flagellum of antennula fused to the longer for about 20% of its length (fig. 5i); shorter ramus of outer flagellum of antennula equal to antennular peduncle; mandibular palp 3-jointed (fig. 5m, 6b); fingers of p2 = 0.7 x as long as palm (fig. 5r); dactylus of p3 very slender and about 0.9 x as long as carpus; a few oblique



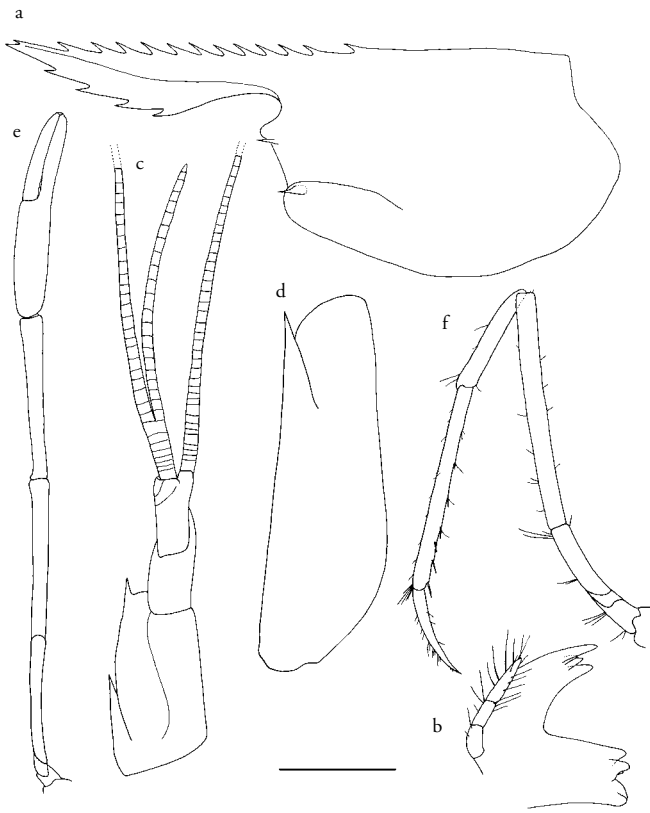


Figure 6. *Palaemon macrodactylus*, ovigerous female (Belgium, Zeebrugge, marina, 20.vii.2004, Tromsø Museum, reg. nr. 13 637). a. carapace in lateral view, b. left mandible, c. left antennula (A1), d. left scaphocerite, e. left P2, f. left P3 (setae not shown except for mandibular palp and for P3). Scale bar: a, e. 4.1 mm, f. 2.9 mm, c, d. 2.5 mm, b. 1.2 mm.

Figuur 6. *Palaemon macrodactylus*, eierdragend wijfje (België, Zeebrugge, marina, 20.vii.2004, Tromsø Museum, reg. nr. 13 637). a. rugschild in zijaanzicht, b. linker mandibel, c. linker eerste voelspriet (A1), d. linker scaphoceriet, e. linker tweede pereiopod (P2), f. linker derde pereiopod (P3) (haren niet afgebeeld behalve bij de mandibelpalpen en bij P3). Maatstreepje: a, e. 4,1 mm, f. 2,9 mm, c, d. 2,5 mm, b. 1,2 mm.

transverse stripes on carapace on a pigmented background; abdomen with at most 1 or 2 very short dark transverse marks (often none at all) on a pigmented background; a whitish longitudinal dorsal stripe running over the entire body . . . . .

. . . . . *P. macrodactylus* Rathbun, 1902

In Europe so far only found in marinas, estuaries, brackish canals and sluice docks.

- Rostrum with 7 to 9 dorsal teeth (tooth of apical cleft not considered), 3 of which are usually behind the orbit (sometimes 2 behind the orbit and 1 directly above edge of orbit). Space between 1st and 2nd tooth equal to space between 2nd and 3rd; proximal third of rostrum strongly expanded ventrally (the rostrum being extremely high at this level) (fig. 5d); shorter ramus of the outer flagellum

of antennula fused to the longer for about 50% of its length (can be a little less or a little more than 50%) (fig. 5j); shorter ramus of outer flagellum of antennula equal to antennular peduncle; mandibular palp 2-jointed (fig. 5n); fingers of P2 = 0.4 x as long as palm (fig. 5s); dactylus of P3 robust and about 0.5 x as long as carpus; usually with irregular transverse/reticulate stripes on carapace and abdomen (in turbid habitats sometimes yellowish with scarcely distinct transverse/reticulate stripes); no whitish longitudinal dorsal stripe . . . . .

. . . . . *Palaemon elegans* Rathke, 1837

Intertidal (especially on the upper half of the shore): in rock pools and amongst seagrasses; both on open coasts and in sheltered habitats (such as harbours and lagoons), in seawater and in slightly brackish water.

*Palaemon macrodactylus* Rathbun, 1902

Figs. 1, 2, 5c, 5i, 5t, 6

*Palaemon macrodactylus* Rathbun, 1902: 52, fig. 21; Kubo 1942: 36, tables 9-12, fig. 7, 8, 9, 19D, 19O, 20D, 21D, 22D, 23D, 23K, 24D, 24O, 25D, 25D', 26D, 26Q, 27D, 27N, 30 (middle); Newman 1963: 119-132, fig. 1; Jensen 1995: 52, unnumbered colour photograph; Ashelby et al. 2004: 1046, fig. 3-4; Poore, 2004: 90, fig. 23g.

**Diagnosis** (based on Belgian specimens).

Rostrum straight, overreaching antennular peduncle, rather narrow on proximal third, usually with 10-12 dorsal teeth (dorsal tooth of apical cleft not considered). In one specimen with an abnormal rostrum we found 9 teeth. Three teeth on carapace just behind orbit (sometimes 2 teeth distinctly on carapace and one just above edge of orbit). First tooth separated from second tooth by a space 1.5-2 x (or sometimes more) as long as the space between second and third tooth. More distally the space between the teeth gradually and slightly increases in length, the space between the two last teeth being as long as the space between the two most proximal, or shorter (the tooth of the apical cleft being not considered as a dorsal tooth). On the most distal part of the dorsal border of the rostrum sometimes a short toothless space occurs (about as long as the ultimate and penultimate tooth together, or shorter). Dorsal teeth pointing obliquely upwards. 3 to 5 ventral teeth (mostly 4). Carapace with branchiostegal spine. Shorter ramus of outer flagellum of antenna fused to the longer for about 20% of its length. Shorter ramus of outer flagellum of antenna equal to antennular peduncle. Mandibular palp 3-jointed. Chela of P2 with fingers 0.7 x as long as palm (i.e. fingers = 0.4 x length of whole chela). Propodus of P2 equal to carpus. P3-P5 slender with dactylus long and slender. In P3-P4, dactylus almost as long as carpus.

**Colour pattern.** Reddish to brownish or greenish to bluish-green. Lower half of rostrum without red pigment dots. A whitish longitudinal dorsal

stripe runs all over the body. Under magnification light pink dots are visible in this stripe. Carapace with a weakly developed pattern of oblique stripes on a finely dotted background. Pleon with a finely dotted background; no distinct transverse stripes at all or just one or two very short, broad transverse marks or spots. Pleura in ovigerous females with brown and white chromatophores, the brown ones forming distinct marks. Peduncle of A1 with many large dot-like dark chromatophores. Pereiopods brownish to reddish (sometimes translucent light bluish) with a tinge of orange at articulations and a small indistinct brownish band above them. Under the dissecting microscope the pereiopods (especially P2) look mottled with dark brown chromatophores. Peduncle of pleopods with an anterior longitudinal brown stripe and a posterior longitudinal white stripe. Eggs brown.

**Total length.** Up to 61 mm (in an ovigerous female).

**Ecology.** 'Estuarine brackish water' (Holthuis 1980). 'Usually found in estuaries and the brackish water of tidal creeks' (Jensen 1995). The present specimens were found in sheltered, polluted marine habitats (marina of Zeebrugge, sluice dock at Oostende), in the mesohaline part of the Westerschelde estuary (several marinas and harbours) and in brackish canals (IJmuiden, Rotterdam). All specimens were collected between fouling of pontoon floats, along harbour walls or between litter and reeds (*Phragmites australis*) in canals.

**Distribution.** In her original description, Rathbun (1902) gives the following localities for the species: 'Aomori, Rikuoku (type locality, Cat. No. 26162); Matsushima, Rikuzen; Nagasaki, Hizen. Also collected by P.L. Jony in Korea, at Fusan, Gensan, and Chemulpo.' Holthuis (1980) and Liu et al. (1990) mention that it also occurs in China, but the Chinese records need confirmation since the Chinese specimen illustrated by Liu et al. (1990) has an unusually long distal dorsal

part of the rostrum without teeth. *Palaemon macrodactylus* has been introduced to the north-eastern Pacific (San Francisco Bay area) where it was recorded for the first time in 1954 (Newman 1963). The species has progressively spread north and south, recently appearing in Willapa, Washington and also in Malibu Lagoon and Long Beach Harbour, California (Jensen 1995). The identity of the eastern Pacific specimens does not seem questionable as Newman (1963) states that he has compared his material with type specimens. Furthermore his drawings are good and very similar to those of Rathbun (1902). *Palaemon macrodactylus* has also been introduced in Australia (Davie 2002, Poore 2004) and in Argentina (Spivak in press).

**Remarks.** Rathbun (1902) and Newman (1963) state that their largest specimens were 55 mm long, whilst Ashelby et al. (2004) record specimens of 70 mm. One ovigerous female from Zeebrugge had a total length of 61 mm. Rathbun (1902) and Newman (1963) indicate that the species may have 9-15 dorsal rostral teeth. Our specimens have 9 (rarely) to 12 dorsal teeth (tooth of the apical cleft excluded). Specimens from Taiwan identified as *P. macrodactylus* by Chan & Yu (1985) are smaller, with a smaller average number of dorsal rostral teeth than those from colder areas (average number = 9, with 2 behind the orbit edge). Furthermore in the Taiwanese form the pereopods are blue and there is a distinct transverse stripe on the posterior border of the third pleonite. On the other hand, Japanese *P. macrodactylus* would have a colour pattern similar to the European form (pers. comm. J. Okuno 2004). Chan and Okuno (pers. comm. 2004) think that the Taiwanese form deserves further studies to ascertain whether or not they are really *P. macrodactylus*.

## DISCUSSION

Like *P. macrodactylus* many introduced species in northwestern Europe originate from the temperate northwestern Pacific, e.g. the algae *Sargassum muticum* (Yendo) Fensholt, *Undaria*

*pinnatifida* (Harvey) Suringar and *Lomentaria hakodatensis* Yendo, the bristle worm *Hydroides ezoensis* Okuda, 1934, the tunicates *Styela clava* Herdman, 1882, *Botrylloides violaceus* Oka, 1927 and *Perophora japonica* Oka, 1927, the oyster *Crassostrea gigas* Thunberg, 1793 and the clam *Ruditapes philippinarum* (Adams & Reeve, 1850), the amphipod *Caprella mutica* Schurin, 1935, the crabs *Eriocheir sinensis* H. Milne Edwards, 1854, *Hemigrapsus takanoi* Asakura & Watanabe, 2005 and *Hemigrapsus sanguineus* (De Haan, 1835).

It is likely that *Palaemon macrodactylus* will colonize, or has already colonized, a large part of the European coasts, but it is not clear if it will become as abundant and widespread as in the temperate eastern Pacific. There are few indigenous Palaemoninae on the west coast of the USA, where this subfamily is almost restricted to tropical waters (Schmitt 1921, Holthuis 1952): *Palaemon ritteri* Holmes, 1895 which is not found north of San Diego, southern California, and *Palaemonetes hiltoni* Schmitt, 1921 which is not found north of San Pedro and San Diego, southern California. Maybe this lack of competition enabled *P. macrodactylus* to occupy different water bodies in high numbers on the Pacific coast of the USA. In Europe on the contrary there is a number of widely distributed native Palaemoninae, occupying a wide range of habitats. On the one hand *P. macrodactylus* may to a certain extent have to share space and food resources with these species. On the other hand it may have an improved fitness in the newly colonized area because it may have escaped, at least for some time, the specific parasites occurring in its natural geographical range. Furthermore a newcomer may transmit alien parasites to indigenous species, which lack the adequate immunity against them (Torchin et al. 2003, Prenter et al. 2004). Generally the interactions between native and alien species are not simple, but involve a large number of interdependent factors (Prenter et al. 2004). Newman (1963) concludes that 'Any introduced species is,

Table 1. Shrimps collected during this survey along the coast in the Netherlands, Belgium and northern France. Collectors: Cédric d'Udekem d'Acoz (CUA), Emmanuel Dumoulin (ED), Hans De Blauwe (HDB), Marco Faasse (MF).  
 Tabel 1. Steurgarnalen tijdens de inventarisatie verzameld langs de kust in Nederland, België en Noord-Frankrijk. Onderzoekers: Cédric d'Udekem d'Acoz (CUA), Emmanuel Dumoulin (ED), Hans De Blauwe (HDB), Marco Faasse (MF).

Species	Abundance	Date	Locality	Long/lat	Collector
<b>THE NETHERLANDS</b>					
<i>Palaemon elegans</i>	common	11.VIII.2004	IJmuiden, Seaport Marina, pontoons	52°28'N 004°34'E	MF
<i>P. macrodactylus</i>	2	11.VIII.2004	IJmuiden, Noordzeekanaal, just inside of locks (Binnenspuikanaal)	52°28'N 004°37'E	MF
<i>P. elegans</i>	about 5	9.VIII.2004	Rotterdam, Calandkanaal, pontoon	51°57'N 004°08'E	MF
<i>P. elegans</i>	about 20	17.VIII.2004	Rotterdam, Nieuwe Waterweg, ferry Rozenburg-Maassluis, wall	51°55'N 004°14'E	MF
<i>P. macrodactylus</i>	6				
<i>Palaemonetes varians</i>	about 5				
<i>P. adspersus</i>	extr. abundant	25.VIII.2004	Scharendijke (Grevelingen), depth 0-3m (SCUBA-diving)	51°44'N 003°50'E	MF
<i>P. elegans</i>	common				
<i>P. serratus</i>	common				
<i>P. elegans</i>	about 5	15.VII.2004	Neeltje Jans (Oosterschelde), Buitenhaven, pontoon	51°37'N 003°40'E	MF
<i>P. elegans</i>	1	09.X.2004	Zierikzee (Oosterschelde), between Pacific oysters, depth 5 m (SCUBA diving)	51°38'N 003°55'E	MF
<i>P. macrodactylus</i>	1				
<i>Hippolyte varians</i>	common				
<i>P. elegans</i>	about 20	21.VII.2004	Zierikzee (Oosterschelde), pontoon in harbour De Val	51°38'N 003°55'E	MF
<i>Hippolyte varians</i>	about 20				
<i>P. elegans</i>	common	20.VII.2004	Yerseke (Oosterschelde), sheltered rocky shore	51°30'N 004°02'E	CUA, ED, HDB
<i>Hippolyte varians</i>	common				
<i>Athanas nitescens</i>	6				
<i>P. adspersus</i>	common	20.VII.2004	Yerseke (Oosterschelde), pontoons of marina	51°30'N 004°03'E	CUA, ED, HDB
<i>P. elegans</i>	common				
<i>Hippolyte varians</i>	common				
<i>P. adspersus</i>	common	20.VII.2004	Sas van Goes (Oosterschelde), pontoons marina	51°32'N 003°56'E	CUA, ED, HDB
<i>P. elegans</i>	common				
<i>P. elegans</i>	about 5	29.VII.2004	Bergsediepsluis (Oosterschelde), pontoon near locks to freshwater	51°30'N 004°12'E	MF
<i>P. elegans</i>	3	02.X.2004	Wemeldinge (Oosterschelde), groyne east of former harbour entrance, between Pacific oysters, depth 5 m (SCUBA diving)	51°31'N 004°00'E	MF
<i>P. macrodactylus</i>	1				
<i>P. serratus</i>	1				
<i>Hippolyte varians</i>	common				
<i>P. adspersus</i>	about 5	20.V.2004	Geersdijk (Veerse Meer), depth 0-7 m (SCUBA diving)	51°33'N 003°46'E	MF

Species	Abundance	Date	Locality	Long/lat	Collector
<i>Palaemonetes varians</i>	1 juv	31.VII.2004	Vlissingen (near mouth of Westerschelde estuary), harbour (first inner basin)	51°27'N 003°36'E	MF
<i>Palaemonetes varians</i>	common	31.VII.2004	Vlissingen (near mouth of Westerschelde estuary), Kanaal door Walcheren (brackish canal)	51°27'N 003°35'E	MF
<i>P. elegans</i>	common	24.VII.2004	Breskens (mouth of Westerschelde estuary), pontoons of marina	51°24'N 003°34'E	MF
<i>P. serratus</i>	about 5 juv				
<i>P. macrodactylus</i>	common	24.VII.2004	Terneuzen (Westerschelde estuary), pontoons of marina	51°20'N 003°49'E	MF
<i>P. macrodactylus</i>	9	30.VII.2004	Hansweert (Westerschelde estuary), pontoon outside of locks	51°27'N 004°00'E	MF
<i>P. elegans</i>	1	31.VII.2004	Hoedekenskerke (Westerschelde estuary), ferry pontoon	51°25'N 003°55'E	MF
<i>P. macrodactylus</i>	7				
<i>P. elegans</i>	7	4.VIII.2004	Ellewoutsdijk (Westerschelde estuary), pontoons of marina	51°23'N 003°49'E	MF
<i>P. macrodactylus</i>	4				
<i>P. serratus</i>	1				
<i>Palaemonetes varians</i>	about 20	19.VIII.2004	Paal (Westerschelde estuary), marina, between phanerogams near high water mark	51°21'N 004°07'E	ED, HDB, MF
<i>P. elegans</i>	2	27.XI.1999	Walsoorden (Westerschelde estuary), pontoon in harbour	51°23'N 004°02'E	MF
<i>P. macrodactylus</i>	about 20				
<i>P. adspersus</i>	5	19.VIII.2004	Walsoorden (Westerschelde estuary), pontoon in harbour	51°23'N 004°02'E	ED, HDB, MF
<i>P. serratus</i>	16				
<i>P. macrodactylus</i>	60				
<i>Palaemonetes varians</i>	2				
<b>BELGIUM</b>					
<i>Palaemonetes varians</i>	common	19.VIII.2004	Fort Liefkenshoek (Westerschelde estuary), outside of small sluice	51°18'N 004°17'E	ED, HDB, MF
<i>P. macrodactylus</i>	5	19.VIII.2004	Doel (Westerschelde estuary), harbour entrance, wall	51°19'N 004°16'E	ED, HDB, MF
<i>P. elegans</i>	2	12.VI.2004	Zeebrugge, pontoons of marina (Oomokaai)	51°20'N 003°12'E	HDB
<i>P. macrodactylus</i>	2				
<i>Palaemonetes varians</i>	1				
<i>P. elegans</i>	about 20	20.VII.2004	Zeebrugge, pontoons of marina (Oomokaai)	51°20'N 003°12'E	CUA, HDB
<i>P. macrodactylus</i>	about 20				
<i>P. serratus</i>	1				
<i>Hippolyte varians</i>	about 3				
<i>P. adspersus</i>	1	22.VIII.2004	Blankenberge, pontoons marinas	51°19'N 003°07'E	ED
<i>P. serratus</i>	abundant				
<i>Palaemonetes varians</i>	common				

Species	Abundance	Date	Locality	Long/lat	Collector
<i>P. adspersus</i>	2	31.VIII.2004	Oostende, sluice dock (non-tidal)	51°14'N	ED
<i>P. elegans</i>	16			002°57'E	
<i>P. macrodactylus</i>	12				
<i>P. serratus</i>	13				
<i>Palaemonetes varians</i>	22				
<i>P. elegans</i>	common	17.VIII.2004	Nieuwpoort (IJzer estuary), pontoons of marinas	51°09'N	ED
<i>P. serratus</i>	some			002°44'E	
<i>Palaemonetes varians</i>	some				
<b>FRANCE</b>					
<i>P. elegans</i>	7	10.VIII.2004	Calais, Bassin Ouest, pontoons of marina	50°58'N	ED, HDB,
<i>P. serratus</i>	80			001°51'E	MF
no shrimps		10.VIII.2004	Dunkerque, Bassin du Commerce (non-tidal), pontoons of marina	51°02'N	ED, HDB,
				02°21'E	MF
<i>P. elegans</i>	3	10.VIII.2004	Dunkerque, Port d'échouage, left bank, pontoons of marina	51°03'N	ED, HDB,
<i>Hippolyte varians</i>	2		'Les Dauphins'	02°23'E	MF
<i>P. elegans</i>	>10	10.VIII.2004	Dunkerque, Port d'échouage, right bank, pontoons of 'Port de Plaisance du Grand Large	51°03'N	ED, HDB,
				02°22'E	MF

in effect, a mutation in a community, for it not only comes into interplay with an already established ecosystem, but is a new part of it, and one can expect a shift to occur to accommodate the newcomer'.

The invasion of *P. macrodactylus* is probably of recent date. Taking into account our collection sample from November 1999 *P. macrodactylus* must have been introduced in the Westerschelde estuary most likely shortly prior to that year. In Spain it was first found in May 1999 (Cuesta et al. 2004) and in Great Britain in December 2001 (Ashelby et al. 2004). Worth mentioning is also that, although the Asian shrimp is now present in the sluice dock of Oostende, it was not found there in 1996, 1998 and 1999 (Kerckhof & d'Udekem d'Acoz 1999).

The species may not yet have colonized all suitable habitats in the southern bight of the North Sea. Some enclosed brackish to marine

water bodies in the Netherlands (Veerse Meer and Grevelingen) seem suitable, but so far no records from these lakes are known to us. The present, although limited, data seem to suggest that *P. macrodactylus* will become most abundant in mesohaline parts of estuaries. Further research will be needed to refute or confirm this hypothesis.

The occurrence of *P. macrodactylus* seems to be associated with (foreign) ship traffic. In the Oosterschelde (the centre of shellfish culture in the Netherlands), lacking foreign shipping trade, only a few specimens of *P. macrodactylus* were found until now. All other water bodies where this species was caught in larger numbers are characterised by intensive intercontinental and regional ship traffic. The Noordzeekanaal connects the port of Amsterdam with the North Sea at IJmuiden. The Nieuwe Waterweg leads to the port of Rotterdam. The Westerschelde estuary is

a waterway with intensive navigation to and from the port of Antwerp. Zeebrugge is a harbour with intercontinental and coastal shipping and yachting. Oostende is mainly a ro-ro harbour with ferry lines to the eastern coast of the U.K. Therefore we presume that *P. macrodactylus* has been introduced to Belgium and the Netherlands via ballast water of ships and not by shellfish importations. It is impossible to trace the original site of introduction in Europe since the species is already present for several years in at least two distant areas (southern Spain and the southern bight of the North Sea). However, it is already clear that *P. macrodactylus* is a very successful invader and it is likely that it will colonize an extensive range of localities along the temperate coasts of the north-eastern Atlantic and probably the Mediterranean and Black Sea.

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## SAMENVATTING

Het voorkomen van de rugstreepsteurgarnaal *Palaemon macrodactylus* in de zuidelijke bocht van de Noordzee, met een determinatiesleutel tot de Palaemonidae van Noordwest-Europa (Crustacea: Decapoda: Caridea)

In 1999 werd de rugstreepsteurgarnaal *Palaemon macrodactylus* Rathbun, 1902, een soort afkomstig uit het noordwesten van de Grote Oceaan (Japan, China en Korea), als nieuwkomer voor de Europese wateren vastgesteld. Aanvankelijk langs de Atlantische kust van Zuidwest-Spanje en in 2001 in de zuidelijke Noordzee bij Engeland. Tijdens een inventarisatie van de auteurs in 2004 werd de rugstreepsteurgarnaal op verschillende plaatsen langs de kust van Nederland (van IJmuiden tot Zeeland) en langs de kust van België alsook ver stroomopwaarts in de Westerschelde, verzameld. Langs de Noord-Franse kust (te Calais en Dunkerque) werd de soort niet gevonden. Het blijkt dat *P. macrodactylus* in de zuidelijke bocht van de Noordzee al op vele plaatsen in diverse wateren voorkomt en het is zeer waarschijnlijk dat dit gebied al verscheidene jaren geleden 'veroverd' werd. Een monster van 1999 uit de Westerschelde (Walsoorden) ondersteunt deze hypothese. De oorspronkelijke locatie van introductie is uit de beschikbare gegevens niet af te leiden. De auteurs maken aannemelijk dat scheepvaart een belangrijke rol heeft gespeeld bij de verspreiding in Europa. Wellicht is een verdere areaaluitbreiding van de soort niet meer te stuiten. De morfologie en het kleurpatroon van de rugstreepsteurgarnaal worden uitgebreid beschreven en geïllustreerd. Een nieuwe determinatiesleutel voor de Palaemonidae van West-Europa wordt gepresenteerd, waarin de nieuwkomer *P. macrodactylus* is opgenomen.

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