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With compliments,
D. I. Williamson.

A new species of Processidae (Crustacea, Decapoda, Caridea) and the larvae of the north European species

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Introduction

The known Processidae of the eastern Atlantic all belong to the genus *Processa* Leach as at present recognized, and although some discussion on generic groupings is included in the present paper no changes are proposed. The four species recorded from the waters of northern Europe are *P. canaliculata* Leach, *P. edulis* (Risso), *P. nouveli* Al-Adhub & Williamson and a species which has been referred to both *P. aequimana* (Paulson) and *P. parva* Holthuis but which is now proposed as a new species. Lebour (1936) provided descriptions of the larvae of the first two of these species; larvae of the third were identified by rearing during the present work; and those of the fourth had not previously been distinguished from larvae of *P. aequimana*.

Part I of the paper is by the first author, Part II by the second, and Part III by both authors.

I. The *aequimana* group of species

In the majority of the known species of *Processa* Leach the right second leg of adults is longer than the left and the carpus is divided into 15–70 segments; the larvae lack median dorsal abdominal spines and exopods are developed on all legs except the fifth. In adults of *P. aequimana* and closely related species the second legs are approximately symmetrical and the carpus consists of only about 11 segments; the known larvae have median dorsal spines on the third and sixth abdominal somites and do not develop exopods on either the fourth or fifth legs.

European representatives of the *aequimana* group were ascribed to *P. aequimana* by Caroli (1947) and by Rees & Catley (1949), the former author suggesting that they had spread to the Mediterranean from the Red Sea. These and later European records were, however, referred to *P. parva* by Holthuis (1954) and Nouvel & Holthuis (1957). This species was originally described from West Africa, but larvae from West Africa examined during the present work were found to be readily distinguishable from European specimens. This led to the present re-assessment of the members of the group.

The species recognized are listed below. The European and Mediterranean forms, which are referred to a new species comprising two subspecies, are described as adults and larvae, and some diagnostic features of all the species are compared in table 1.

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Processa aequimana (Paulson)

(Figs. 3 (*d*), (*e*), 6 (*b*), (*e*), (*h*))

Nika aequimana Paulson, 1875: 103, pl. 14, figs. 6, 6 (*a*) (adult).
Processa aequimana (Paulson): Gurney, 1937: 87, 92–94, figs. 1–10, 33–36 (adults and larvae).

TYPE LOCALITY: Red Sea.

KNOWN DISTRIBUTION: Red Sea and Malaysia.

MATERIAL EXAMINED: One young male, 22 larvae and early post-larvae (including specimens hatched and reared in captivity), R. Gurney, Ghardaqa, Red Sea coast of Egypt, 1936 [British Museum (Natural History)].

Processa parva Holthuis

(Figs. 3 (*a*)–(*c*), 6 (*c*), (*f*), (*i*))

Processa sp. ' Discovery ' station 277: Gurney, 1937: 94, pl. 3, fig. 37 (larva).
Processa parva Holthuis, 1951: 47–50, fig. 8 (adults).

TYPE LOCALITY: Off Bathurst, Gambia.

KNOWN DISTRIBUTION: West Africa between 29° N. and 2° S.

MATERIAL EXAMINED: Paratypes (females) from off Monrovia, Liberia and off Accra, Ghana ['Atlantide ' Expedition, 1946: British Museum (Natural History)]. 2 males, 1 female, 2 juveniles, 29 larvae from off North-west Africa, 29° N.–21° N. [R.R.S. *Discovery*, 1968 and 1972: Institute of Oceanographic Sciences, Wormley].

Processa hemphilli Manning & Chace

Processa hemphilli Manning & Chace, 1971: 23–25, figs. 11, 12 (adults).

TYPE LOCALITY: Marco, Collier County, Florida, U.S.A.

This species is known only from the holotype and two paratypes, all females, collected on the west coast of Florida, and no specimens were examined during the present work. In addition to the characters given in table 1, it differs from the other species in that the rostrum is more tapered, with the dorsal tooth almost as long as the ventral, and the apex of the telson is acutely pointed.

Processa modica sp. nov.

(Figs. 1, 2, 3 (*f*)–(*i*), 4, 6 (*a*), (*d*), (*g*), 9 (*d*))

SYNONYMY AND MATERIAL EXAMINED: See under respective subspecies.

HOLOTYPE: Female, 25 mm, station K11, 52° 19′ N., 4° 22′ E. (about 25 km north of The Hague, The Netherlands). ' Boomkor ' net, 2205–2220 15 April 1952, leg. J. A. G. Delfos, ship *Antonie van Leeuwenhoek* [Rijksmuseum van Natuurlijke Historie, Leiden, Cat. No. 9130].

PARATYPES: See under respective subspecies.

KNOWN DISTRIBUTION: Southern North Sea, Irish Sea, western Ireland, Brittany, Atlantic coast of south-west Spain, Mediterranean (including Adriatic) coasts of Spain, France, Monaco, Italy, Jugoslavia, Turkey, Tunisia and Algeria.

DIAGNOSIS: Females attaining 33 mm (total length), males 28 mm. Posterior margin of sixth pleuron with prominent ventral tooth, at least $\frac{1}{3}$ length of lateral plate at base of uropod. Stylocerite with distal margin slightly convex, projecting to level of outer tooth or slightly beyond. Pleopod 1 of male with outer lobe of endopod longer than inner, inner lobe broader than long. Larvae normally without spines on abdominal somite 4. Larval rostrom projects about as far as frontal lobe.

The specific name of *P. modica* alludes to the fact that it is appreciably bigger than *P. parva* and other members of the group, and hence 'medium sized' in relation to the described species of *Processa*.

Processa modica modica subsp. nov.

(Figs. 1, 2 (*a*)–(*e*), 3 (*f*), (*g*), 4, 5, 9 (*d*))

Processa aequimana (Paulson): Rees & Catley, 1949: 367 (larvae).
Processa parva Holthuis: Holthuis, 1954: 7 (adults).
Nouvel & Holthuis, 1957 (North Sea and Brittany specimens only): 31–33 (adults).

HOLOTYPE: As for species.

PARATYPES: Twelve dredged adults (7 males, 5 females) from Netherlands coast, Texel Lightship and 52° 32′ 40″ N, 3° 46′ 0″ E; 15 larvae (all stages) from 54° 24′ N., 2° 10′ E. [Rijksmuseum van Natuurlijke Historie and British Museum (Natural History)].

OTHER MATERIAL: About 160 adults, mostly from fish stomachs, over 100 planktonic juveniles, over 200 larvae from southern North Sea; 40 larvae (stages I–IV) from Galway Bay, western Ireland; 3 larvae (stages VI and VII) from about 54° N., 4° W., Irish Sea; 6 adults from Brittany, France.

KNOWN DISTRIBUTION: southern North Sea (Dogger Bank to coasts of Netherlands and Belgium), eastern Irish Sea, western Ireland and north-west France.

ADULTS: rostrum extending to front of eye or slightly beyond, at least $\frac{3}{4}$ length of proximal segment of antennular peduncle; ventral tooth at least twice length of dorsal; a few subterminal and ventral setae (fig. 1 (*a*) and (*b*)). Antennal carapace spine acutely pointed (fig. 1 (*a*)). Abdominal pleura 1–5 rounded, sixth with large postero-ventral tooth extending almost as far as plate at base of uropod (fig. 1 (*c*)). Posterior width of telson about half anterior width; anterior pair of spines arising from about same level as transverse row of setae, second pair arising just inside posterior half of telson, length of posterior spines rather variable, no central spine on posterior margin (fig. 1 (*d*)).

Anterior tubercle on narrow part of eye-stalk (fig. 2 (*a*)). Stylocerite of antennule about as broad as length of its inner margin; with outer tooth; distal margin slightly convex, projecting about as far as tooth; inner distal angle with about four very small denticles (figs. 2 (*a*), 3 (*f*)). Inner and outer margins of antennal scale straight, converging slightly towards tip; outer distal spine projecting just beyond terminal lobe, both projecting beyond antennular peduncle (fig. 2 (*a*)). Terminal and penultimate segments of maxilliped 3 of similar length (fig. 2 (*d*)). Right leg 1 chelate, merus longer than carpus + propodus, finger (dactylus) almost as long as palm; left leg 1 rather more slender, ends in simple claw (fig. 2 (*b*) and (*c*)). Right and left leg 2 very similar, chelate; merus usually subdivided into four to six indistinct segments, carpus into 11 or 12; mero-carpal articulation reaching to middle of cornea of eye in

Table 1

Comparison of known members of the *aequimana* group.

	P. aequimana	*P. parva*	*P. hemphilli*	*P. modica modica*	*P. modica carolii*
Adults:					
Postero-ventral margin of sixth pleuron	Short tooth, about 1/10 length of lateral plate	Angled or very short tooth	Acutely angled but not produced	Tooth almost as long as lateral plate	Tooth about $\frac{1}{2}$ length of lateral plate
Distal teeth on stylocerite	Small outer	Medium outer, small inner	Small outer	Medium outer	Medium outer
Distal margin of stylocerite	Large inner lobe projects well beyond tooth	Straight between teeth	Large inner lobe projects well beyond tooth	Slightly convex, does not project beyond tooth	Small lobe usually projects slightly beyond tooth
Lobes of endopod of pleopod 1 of male	Of similar length, both longer than broad	Inner much bigger, both longer than broad	Male unknown	Outer slightly longer, inner much broader than long	Outer much longer, inner much broader than long
Maximum recorded length ♂	18 mm	18 mm	—	26 mm	28 mm
♀		17 mm	17 mm	33 mm	33 mm
Larvae:					
Spines on fourth abd. somite	0	2	larvae unknown	Usually 0	0
Length rostrum: frontal lobe	1·5 ×	1·5 ×	larvae unknown	Usually equal	Equal
Number of zoeal stages	9	9	larvae unknown	7	9

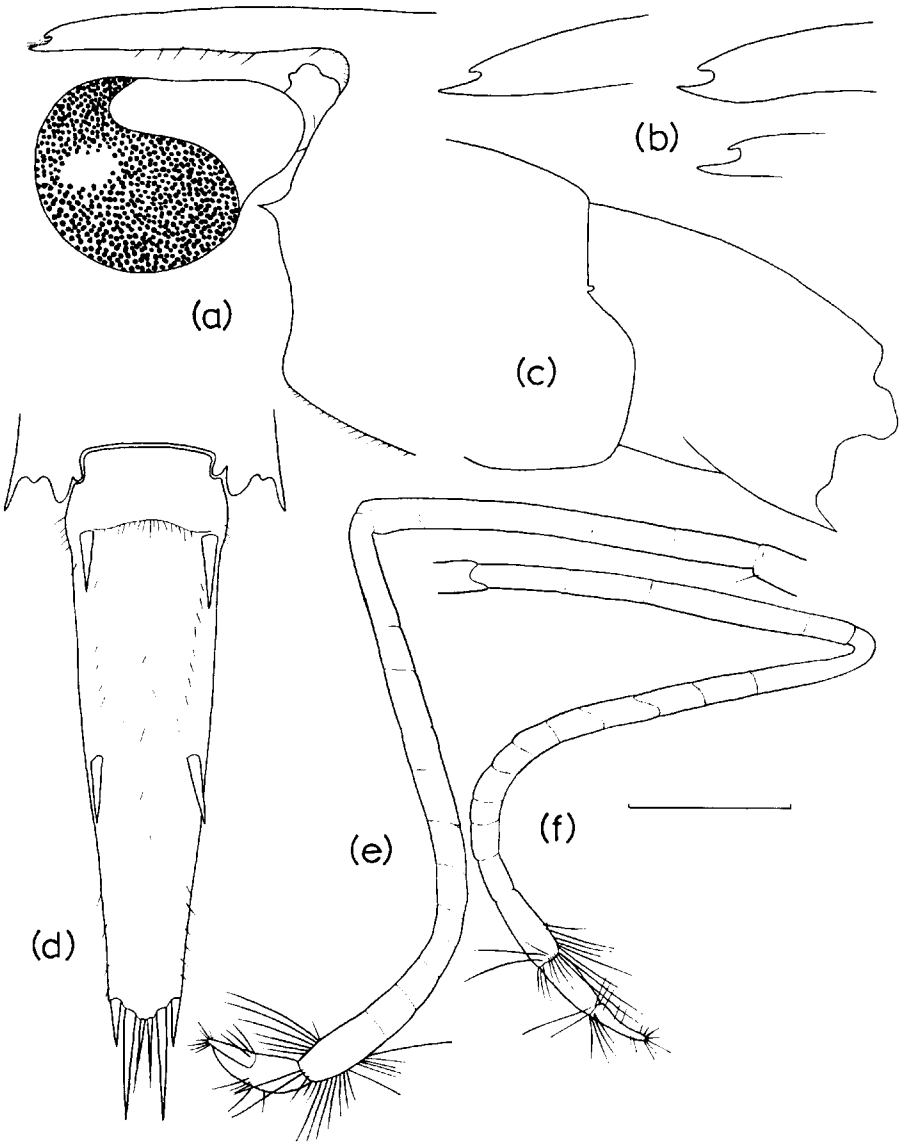

FIG. 1. *Processa modica modica* from the southern North Sea. (*a*, *e*, *f*) Female, 25 mm (holotype); (*c*, *d*) male, 20 mm. (*a*) Anterior carapace and eye, lateral; (*b*) variation in tip of rostrum, lateral; (*c*) fifth and sixth pleura, lateral; (*d*) telson, dorsal; (*e*) left second leg; (*f*) right second leg. Apparent differences in the chelae in (*e*) and (*f*) are due to differences in orientation. Scale-line represents 1 mm (*a*, *c–f*); 0·5 mm *b*.

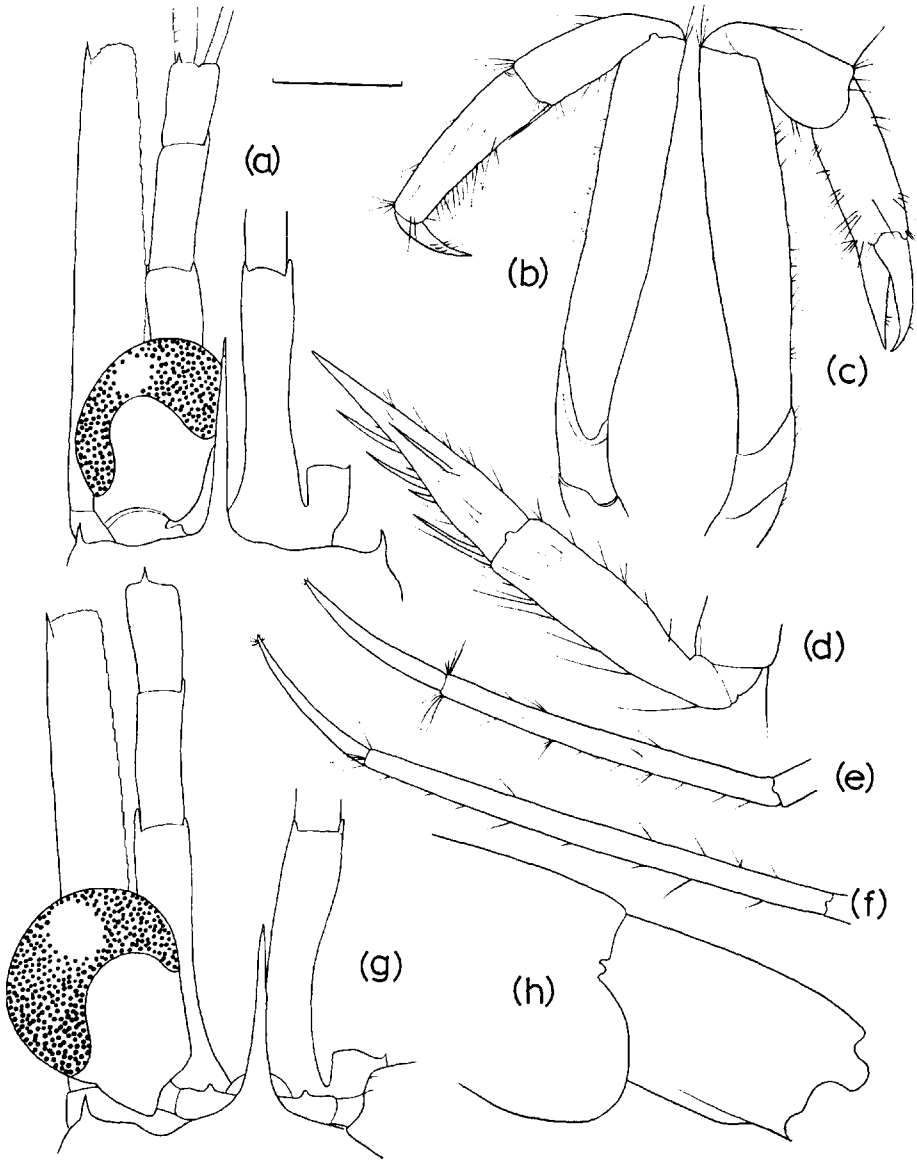

FIG. 2. (*a–e*) *Processa modica modica* from the southern North Sea. (*a*) Male, 20 mm; (*b–e*) female, 25 mm (holotype). (*a*) head, dorsal; (*b*) left first leg; (*c*) right first leg; (*d*) first maxilliped; (*e*) fifth leg; (*f–h*) *Processa modica carolii* from the western Mediterranean. (*f*) female, 26·5 mm; (*g*) male, 21 mm; (*h*) female, 18 mm. (*f*) fifth leg; (*g*) head, dorsal; (*h*) fifth and sixth pleura, lateral. Scale-line represents 1 mm (*a–h*).

mature specimens, shorter in juveniles (fig. 1 (*e*) and (*f*)). Leg 3 shorter than leg 4 but relative lengths of segments similar: carpus less than twice propodus, propodus more than twice dactylus; ischium of each with two spines, merus with four or five. Leg 5 intermediate in length between legs 4 and 3; carpus only slightly longer than propodus, propodus about twice (1·8–2·3 times) length of dactylus; no spines on ischium or merus (fig. 2 (*e*)). Endopod of pleopod 1 of male ending in two lobes: inner lobe (appendix interna) broader than long, bearing about five small hooks; outer lobe longer than inner but narrower, bearing long setae on all margins (fig. 3 (*g*)). Appendix masculina on pleopod 2 usually with five terminal spines.

Largest male examined during present work 26 mm, largest female 33 mm.

Colour (from Heerebout, 1974, as *P. parva*): carapace and abdomen light pink, abdomen banded; rostrum, eye-stalks and antennal peduncles pinkish red; cornea greyish; dactylus and propodus of third maxilliped red; telson and inner uropods pinkish red; overall colour semi-hyaline.

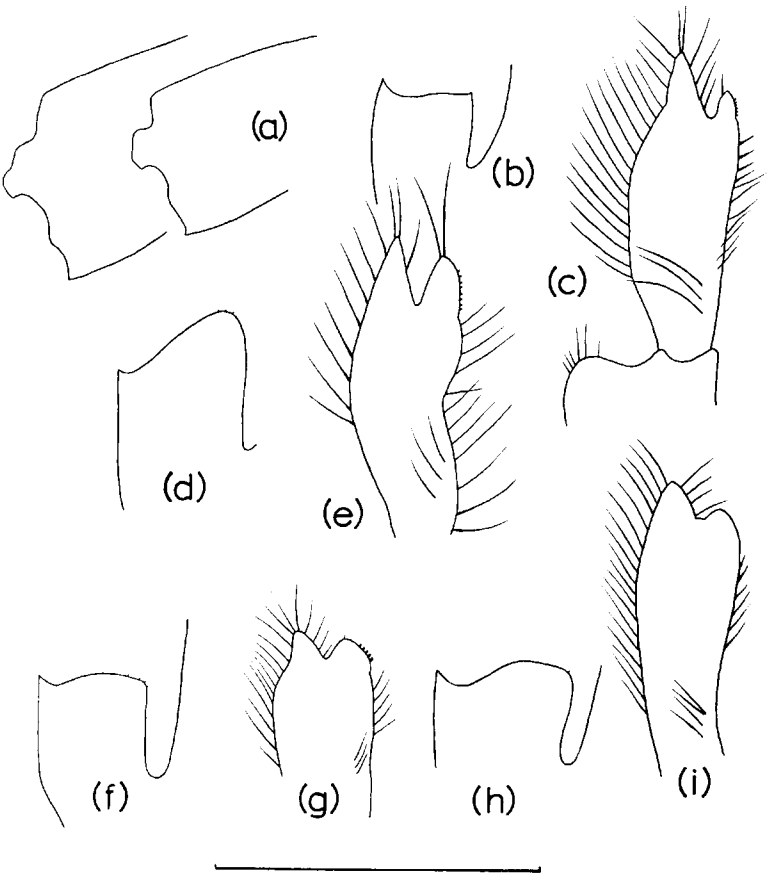

FIG. 3. (*a–c*) *Processa parva* from off north-west Africa: (*a*) sixth pleuron of two specimens; (*b*) stylocerite; (*c*) endopod of first pleopod of male. (*d, e*) *Processa asquimana* from the northern Red Sea, redrawn from Gurney (1937): (*d*) stylocerite; (*e*) endopod of first pleopod of male; (*f, g*) *Processa modica modica* from the southern North Sea: (*f*) stylocerite; (*g*) endopod of first pleopod of male; (*h, i*) *Processa modica carolii* from the western Mediterranean: (*h*) stylocerite; (*i*) endopod of first pleopod of male. Scale-line represents 2 mm (*a*); 1 mm (*b–i*).

LARVAE: Usually seven zoeal stages of approximate average length 1·4, 1·8, 2·4, 2·9, 3·5, 4·3 and 5·1 mm.

Rostrum and supra-orbital spines absent in stage I (fig. 4 (*a*)); rostrum projecting about as far as frontal lobe in stages II–VII, supra-orbitals about $\frac{1}{3}$ length of rostrum (fig. 5). Pterogostomian spine longer than rostrum, arising from carapace margin in stage I (fig. 4 (*a*)), just within margin in later stages (fig. 9 (*d*)); four small marginal denticles behind spine. Anterior dorsal tubercle fairly prominent. Small median dorsal spine on abdominal somite 3 at about $\frac{3}{4}$ length of somite, usually not extending as far as posterior margin of somite; rather larger pair of dorso-lateral spines on posterior margin of somite 5; somite 6 with median dorsal posterior spine of similar length to those on somite 5 and longer anal spine, both present from stage III (fig. 9 (*d*)). Telson broader than long in stages I–III, rather broader posteriorly than anteriorly in stage IV, approximately parallel-sided in stages V and VI, waisted in stage VII; with 7 + 7 marginal spines in stage I, 8 + 8 in stage II, 7 + 7 in stage III (outermost pair of previous stage lost), 5 + 5 in stage IV (two further outer pairs lost), 7 + 7 in stages V and VI (including lateral pair at $\frac{3}{4}$ length of telson and further pair at angle, overlapping large pair), 8 + 8 in stage VII (anterior lateral pair added at $\frac{1}{4}$–$\frac{1}{3}$ length of telson (figs. 4 (*a*), 5).

Maximum diameter of eye slightly less than $\frac{1}{4}$ length of carapace in stage I (fig. 4 (*a*)), slightly greater in all subsequent stages (fig. 5); length of eye + stalk 1·5–1·7 times maximum diameter in stages II–VII. Peduncle of antennule curved, two-segmented from stage III, proximal segment partly subdivided in last zoeal stage; ventral spine present from stage III (figs. 4 (*b*) and (*g*), 5). Antennal endopod in stage I produced into long spine with spicules, length (including spine) at least $\frac{3}{4}$ scale (fig. 4 (*c*)); spine reduced in stage II, total length about $\frac{1}{2}$ scale; length about $\frac{1}{3}$ scale in stages III and IV; $\frac{1}{2}$–$\frac{7}{8}$ scale in stage V; $\frac{3}{4}$–$1\frac{1}{4}$ times scale in stage VI, with basal segment formed; $1\frac{1}{2}$–2 times scale in stage VII, with additional segments forming distally (figs. 4 (*h*), 5). Antennal scale (exopod) with small terminal segment in stage I (fig. 4 (*c*)), usually still visible in stage II, occasionally in stage III; outer margin with two setae in stages I and II, with terminal spine in stage III, spine projects slightly beyond terminal lobe in later stages; length of scale three to four times maximum width in stage I, increasing to seven to eight times by stage VII (figs. 4 (*h*), 5). Mandible without palp in any stage (fig. 4 (*i*)). Maxillule with two-segmented palp bearing two and three long spines, respectively; exopodal seta in stages I and II (fig. 4 (*d*)). Coxal lobes of maxilla overlapping; palp of five partly-fused segments, articulation between second and third clear in late stages, setal formula 2–4, 2, 1, 1, 1 + rudiment; exopod broad in all stages, with proximal lobe and straight distal margin in late stages (fig. 4 (*e*) and (*j*)). Exopods on maxillipeds 1–3 each with three terminal and 1 or 2 lateral setae in stage I (fig. 4 (*f*)). Leg 1 a biramous bud in stage I, exopod functional from stage II; small rudiments of legs 2–5 present in stage II, bigger in stage III, exopod of leg 2 functional from stage IV, that of leg 3 functional from stage V; legs 4 and 5 segmented from stage V but no exopods in any stage. Pleopods may appear as small uniramous buds in stage IV but still absent in many specimens; biramous in most specimens in stage V. Uropods present from stage III, with spine on exopod from stage IV (fig. 5).

Larval records are restricted to the months July–October.

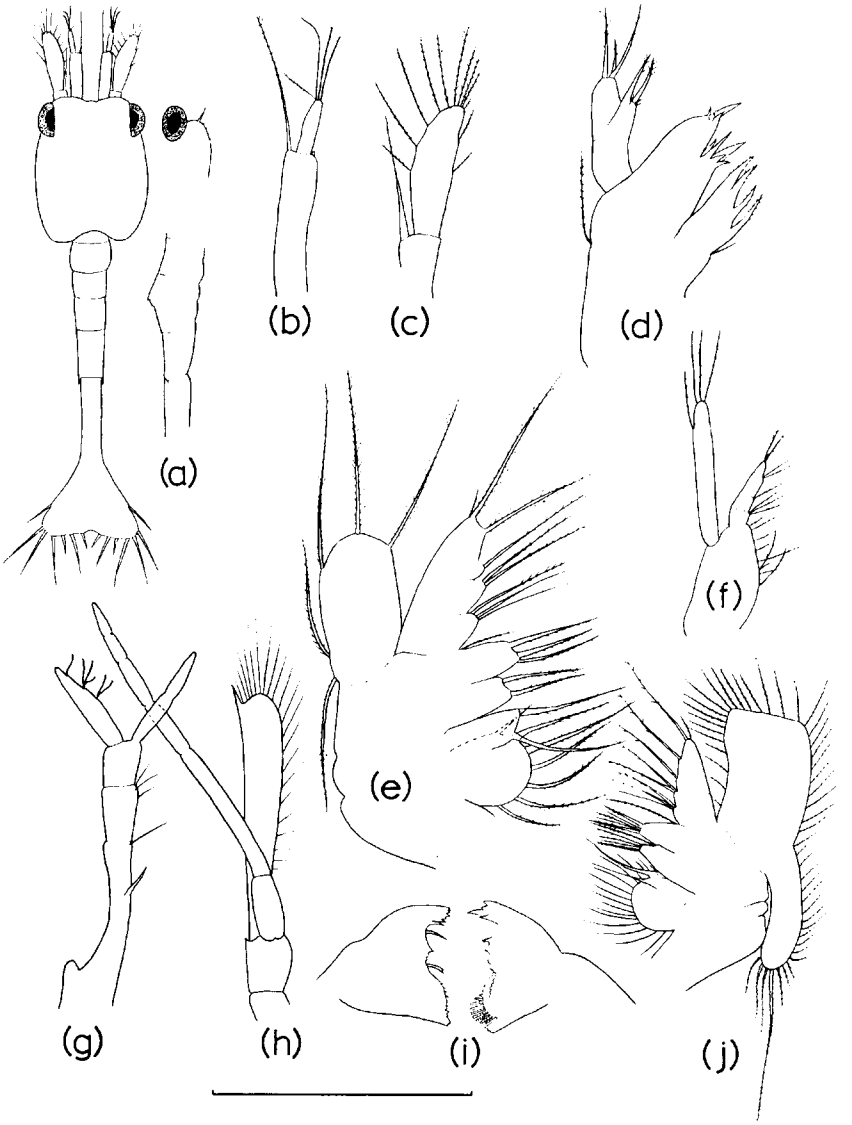

FIG. 4. *Processa modica modica:* larvae. (*a–f*) Zoeal stage I from Galway Bay, Ireland: (*a*) dorsal view, with lateral views of pterygostomian region and abdomen; (*b*) antennule; (*c*) antenna; (*d*) maxillule; (*e*) maxilla; (*f*) first maxilliped; (*g–j*) last zoeal stage from Netherlands coast: (*g*) antennule; (*h*) antenna; (*i*) mandibles; (*j*) maxilla. Scale-line represents 1 mm (*a, g, h*); 0·5 mm (*i, j*); 0·4 mm (*b, c, f*); 0·13 mm (*d, e*).

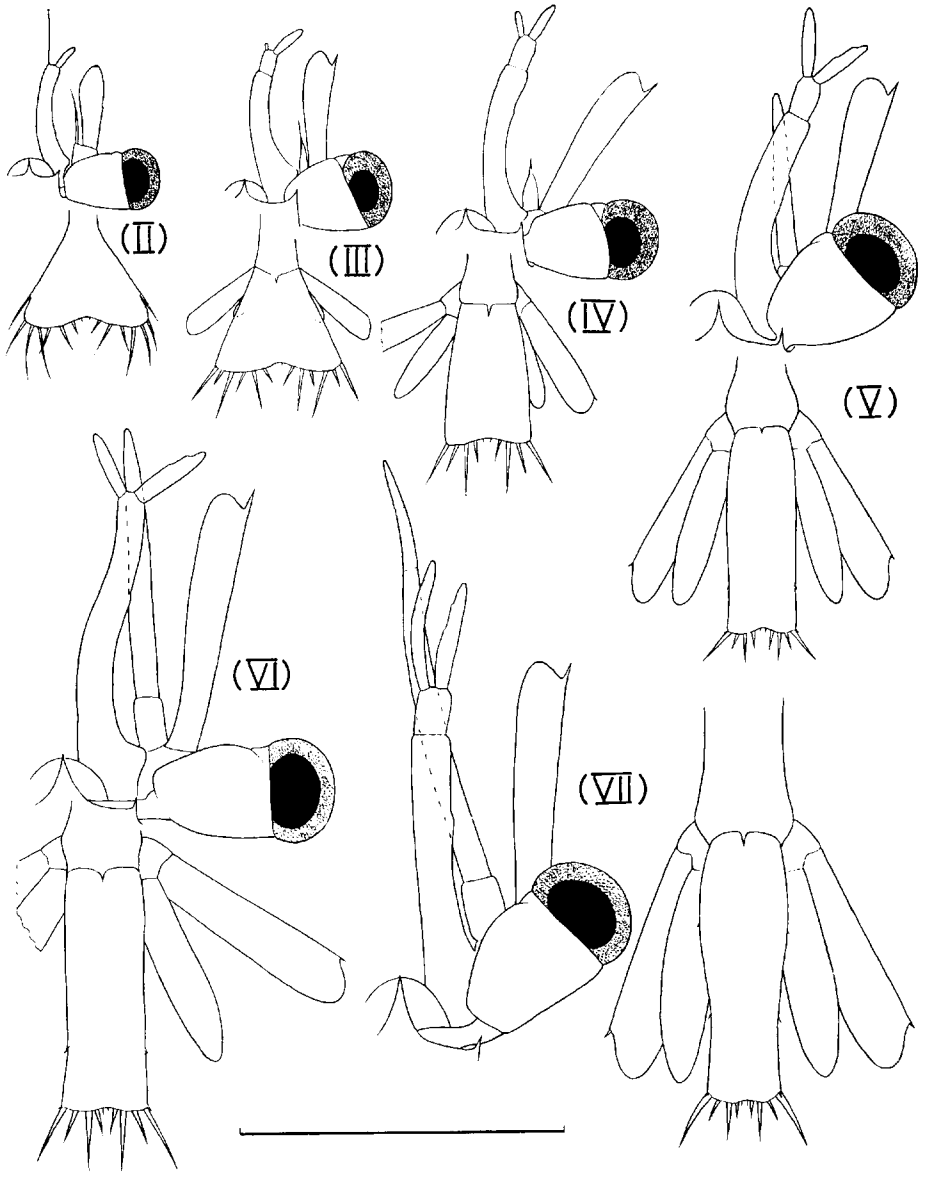

FIG. 5. *Processa modica modica:* larvae from Dogger Bank, southern North Sea. Head (dorsal) and telson and uropods (dorsal) in zoeal stages II–VII. Scale-line represents 1 mm.

LARVAL VARIATIONS: out of over 200 larvae examined from the North Sea, two (both in stage III) have the rostrum extending well beyond the frontal lobe and the supra-orbital spines are of similar length to the rostrum. In this they approach the usual condition in *P. aequimana* and *P. parva*, but the pterygostomian spine and all the abdominal spines are no longer than is usual in *P. modica* and much shorter than in the other two species.

In two specimens in the last zoeal stage, also from the North Sea, there is a pair of dorso-lateral spines on abdominal somite 4 of similar size to those on somite 5. The distribution of spines is therefore the same as in *P. parva* (fig. 6 (*f*)), although all (including the carapace spines) are considerably shorter.

The three larvae from the Irish Sea, all in the last two zoeal stages, have all the spines rather better developed than in typical North Sea specimens, although not as long as in *P. aequimana* and *P. parva*. They are very similar to larvae of the Mediterranean subspecies of *P. modica*.

In the only specimen in stage IV from Galway Bay, western Ireland, the eyes are longer and more slender than in specimens from the North Sea and Irish Sea. No later larvae from western Ireland have been seen.

Processa modica carolii subsp. nov.

(Figs. 2 (*f*)–(*h*), 3 (*h*) and (*i*), 6 (*a*), (*d*) and (*g*))

Processa canaliculata Leach var., exemplaire 1: Nouvel, 1944: 3 (adult).
Processa aequimana (Paulson): Caroli, 1947: 34–36 (adults and larvae).
Latreutes sp?: Kurian, 1956: 54–56, figs. 107–109 (larvae).
Processa parva Holthuis: Nouvel & Holthuis, 1957 (Mediterranean specimens only): 31–33, figs. 134–148 (adults). Bourdillon-Casanova, 1960: 49–50 (larvae).

HOLOTYPE: Ovigerous female, 29 mm, Tunisia: Carthage–Salammbô, from off Baths of Antoninus to INSTOP, 4–5 m, 0800–0830, 20 February 1974. Coll. Manning & Ingle (RBM/TUN 292) [British Museum (Natural History), Cat. No. 1974: 178].

PARATYPES: Fifteen dredged adults (five males, ten females) from near Otranto (Italy), Cadaqués (Spain) and Monaco; 15 larvae (assorted stages) from Naples (Italy) [Rijksmuseum van Natuurlijke Historie and British Museum (Natural History)].

OTHER MATERIAL: Three adults from Mersin (Mediterranean coast of Turkey), one from Bay of Cadiz (Atlantic coast of south-west Spain); 55 larvae from Bay of Naples, six from Algiers.

KNOWN DISTRIBUTION: Northern coasts of Mediterranean from Mersin, Turkey, to Cadaqués, Spain; southern coasts of Mediterranean from Tunis to Algiers; Atlantic coast of south-west Spain.

ADULTS: Very similar to *P. modica modica* but differing on the following points: Rostrum extending not quite as far as front of eye (fig. 2 (*g*)). Postero-ventral tooth on sixth pleuron projects $\frac{1}{3}$–$\frac{2}{3}$ as far as plate at base of uropod (fig. 2 (*h*)). Breadth of stylocerite greater than length of inner margin; inner lobe usually extending just beyond tip of outer tooth (fig. 3 (*h*)). Antennular peduncle slightly longer than antennal scale (fig. 2 (*g*)). Propodus of fifth leg about three times as long as dactylus (fig. 3 (*f*)).

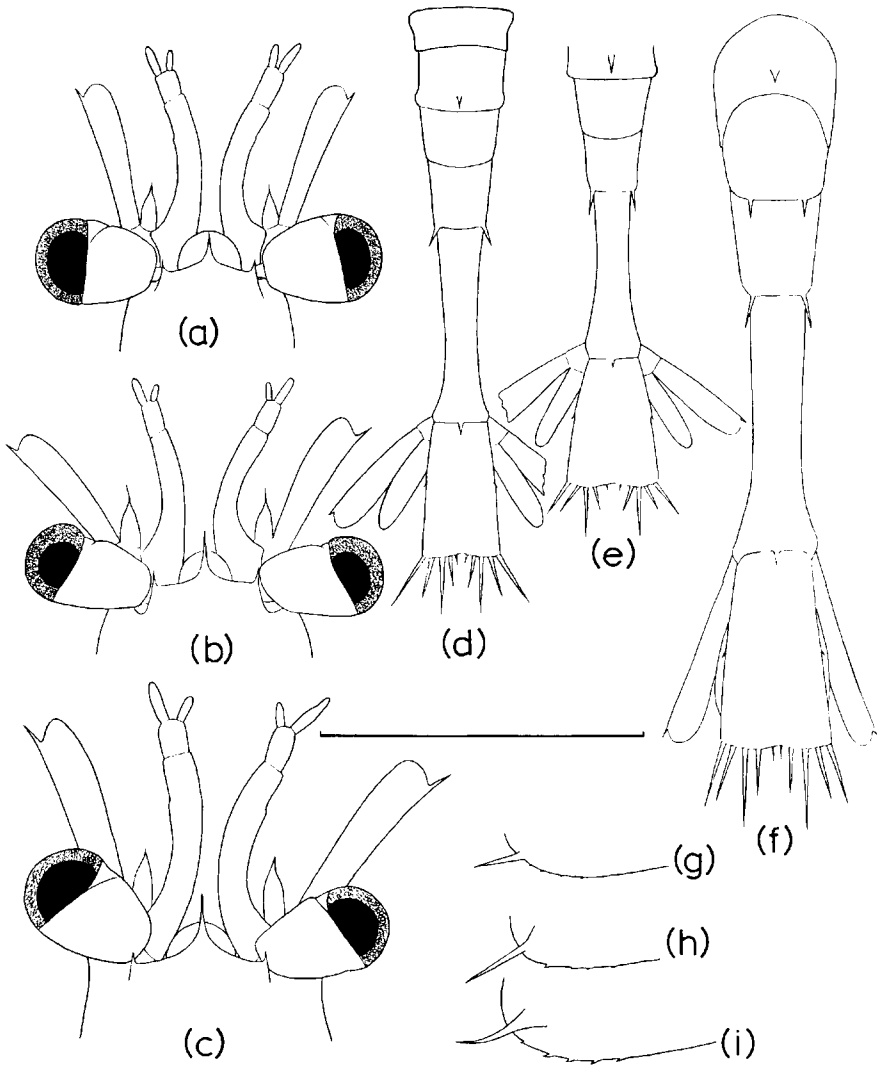

FIG. 6. Larvae in zoeal stage IV: (*a*, *d*, *g*) *Processa modica carolii* from Naples; (*b*, *e*, *h*) *Processa aequimana* from the northern Red Sea; (*c*, *f*, *i*) *Processa parva* from off north-west Africa. (*a–c*) Head (dorsal); (*d–f*) posterior abdomen and telson (dorsal); (*g–i*) pterygostomian region (lateral). Scale-line represents 1 mm (*a–i*).

Size very similar to *P. modica modica:* largest male examined during present work 27 mm, largest female 29 mm (28 and 33 mm recorded by Nouvel & Holthuis, 1957).

LARVAE: usually nine zoeal stages of approximate average length 1·8, 2·0, 2·2, 2·5, 3·0, 3·5, 4·0, 4·5 and 5·0 mm.

Very similar to larvae of *P. modica modica* but abdominal spines usually longer: tip of median dorsal spine on third somite usually about level with posterior margin of somite (fig. 6 (*d*)). Pleopod buds do not appear until stage V (uniramous if present) or stage VI.

LARVAL VARIATIONS: the six larvae from Algiers have relatively short abdominal spines and resemble larvae of *P. modica modica*. The Adriatic specimen of 3·6 mm drawn by Kurian (1956) was probably in stage VI and thus of very similar size to larvae in the same stage from Naples examined during the present work. Kurian, however, also recorded a larva in the last zoeal stage of 8·7 mm, which is very much bigger than specimens from Naples.

Discussion

Manning & Chace (1971) remarked that " the differences between *P. parva*, *P. aequimana* . . . and *P. hemphilli* are so slight that additional material might very well show that they are the same " and suggested that they may represent subspecies or populations of the same species. The apparently consistent morphological differences between the regional representatives of the *aequimana* group seem to justify their taxonomic recognition at least at the level of subspecies, but the question of which, if any, merit separation at the species level is a matter of subjective opinion. It seems possible that *carolii* may come into contact with *modica* to the north or *parva* to the south, but no zones of overlap between these or any of the taxa are known, and any consideration of interbreeding or intergrading can be only hypothetical. The appreciable differences in the proportions of the sexually modified endopod of the male first pleopod in *aequimana*, *parva* and *modica* s.l. does, however, suggest that interbreeding would not take place freely between these groups if they did come into contact, while the greater similarity of this appendage in *modica* s.s. and *carolii* makes the possibility of interbreeding more likely in this case. The recognition of *aequimana*, *parva* and *modica* s.l. as separate species reflects this view and also seems in accord with the consistent larval differences between them. The larvae of *modica* s.s. and *carolii*, however, are not always morphologically distinct, a minority of each resembling the majority of the other, but there remains a distinction in the number of zoeal stages. The number of larval stages of carideans of the same genetic stock can be affected by temperature, with those developing below the optimum temperature tending to pass through more stages (Rochanaburanon & Williamson, 1976). The northern form, *modica* s.s., extends to the low temperature limit of the *aequimana* group as a whole, and its breeding period appears to be limited by temperature. It might, therefore, be expected to pass through more zoeal stages than representatives of the group in warmer waters. The fact that it passes through fewer stages (seven, as opposed to nine) points to a genetic adaptation to a restricted breeding season. This difference alone would not justify subspecific separation, but taken with the morphological differences in adults and most larvae such a taxonomic distinction seems merited.

Unfortunately neither male nor larval characters are available for the western Atlantic form *hemphilli*. The stylocerite resembles that of *aequimana*, but the differences in the shape of the rostrum and the posterior margin of the telson probably justify specific separation from the other members of the group.

At a higher taxonomic level it may be asked whether the *aequimana* group of species is sufficiently distinct from the remainder of the genus *Processa* to merit recognition as a separate genus. The status of the symmetrical genus *Ambidexter* Manning & Chace (1971) is not under consideration, but the question of how, or whether, to subdivide the remainder of the known Processidae may be raised again. It was discussed by Gurney (1937), who employed adult and larval characters in assessing the relationship of *P. aequimana* and *Nikoides danae* Paulson to such species as *P. canaliculata* and *P. edulis*. He noted that the adult of *Nikoides* Paulson " differs from *Processa* in having an exopod on leg 1, but in all other respects the two genera are completely identical. The larval characters are precisely the same, and there is more difference between the larvae of *P. aequimana* and other species of *Processa* than between *N. danae* and *P. edulis* for example ". Gurney's remarks on *P. aequimana* may now be extended to cover closely related species, and his opinion that the genus *Nikoides* is separated on rather unsatisfactory grounds and can be maintained only as a matter of convenience remains valid. The case of *Nikoides* is, however, not unique, and the separation of the pandalid genera *Dichelopandalus* Caullery and *Pandalus* Leach is closely comparable (Pike & Williamson, 1964).

In contrast to *Nikoides*, species of the *aequimana* group differ from *P. canaliculata* and *P. edulis* in a number of well defined adult and larval characters, and the case for regarding these as generic differences seems, at first sight, strong. There are, however, a number of known species which tend to bridge the gap between the two groups. Regarding adult characters, the form of the second legs shows every gradation from complete symmetry in the *aequimana* group and *P. vicina* Manning & Chace, through slight asymmetry in such species as *P. robusta* Nouvel & Holthuis, to very marked asymmetry in *P. canaliculata* and other species. *P. vicina* differs from *P. aequimana* and its close relatives in having no antennal carapace spine and no outer tooth on the stylocerite of the antennule. It shares these characters with *P. bermudensis* (Rankin), to which it is probably closely related (Manning & Chace, 1971), although the second legs of *P. bermudensis* are very asymmetrical. Larvae are unknown for *P. vicina* but were described for *P. bermudensis* by Gurney (1936). They lack median dorsal spines but resemble larvae of the *aequimana* group in having no exopods on the last two pairs of legs. Gurney (1937) also mentioned late larvae of an unidentified Red Sea species " which agree in almost all respects with *P. aequimana*, but differ in having no spine on abdominal somite 3 and in lacking the anterior pair of spines on the telson ".

There is thus at least one group of species which appears to occupy a position intermediate between the *aequimana* group and the *canaliculata* group, and the genus also contains other species or groups with distinctive larvae, such as *P. wheeleri* Lebour (1941) and the larval genus *Hectarthropus* Bate (see Gurney, 1937). The *aequimana* group is therefore one of several which make up the genus *Processa*, and there seems little point in giving it a

new generic or subgeneric name unless other groups are similarly treated. Defining these other groups is beyond the scope of the present work, and would be greatly complicated by the fact that in so many cases adults and larvae cannot be linked.

II. Larvae of *Processa nouveli*

Adults of the present species were first distinguished from those of *P. canaliculata* Leach [= *P. mediterranea* (Parisi)] by Nouvel & Holthuis (1957), who unfortunately attached Leach's name to the wrong species. The specific name *nouveli* was proposed by Al-Adhub & Williamson (1975), who recognized separate subspecies from the Mediterranean and from northern Europe under the names *P. nouveli nouveli* and *P. nouveli holthuisi* respectively.

Material and methods

Ovigerous females of *P. nouveli holthuisi* were trawled 15–20 km north-west of Port Erin, Isle of Man, in depths of 75–125 m on a muddy bottom during the period February–September 1973, and laboratory hatchings were obtained in March and later months. Larvae were reared in seawater in 300 cm^3 plastic beakers, with ten larvae per beaker, or larger numbers in 2500 cm^3 plastic buckets. The water was changed every 2 or 3 days, and at each change fresh supplies of recently-hatched *Artemia* nauplii (San Francisco strain) were added as food. The larvae survived best without aeration or stirring at 20°C, at which temperature 6–7% survived to metamorphosis. At 15°C the survival rate was reduced to 2–3%, and at 10°C no larvae survived beyond stage II. These survival rates were shown graphically and discussed by Rochanaburanon & Williamson (1976). Most of the mortality was in zoeal stages I and II, and it is suggested that *Artemia* nauplii are well above the optimum size as food for such small larvae. Survival was slightly increased by feeding a mixture of *Artemia* nauplii and the flagellate *Isochrysis* to the early larvae, but survival on *Isochrysis* alone was little better than for starved larvae.

Larvae for comparison with reared specimens were obtained from plankton taken off Port Erin throughout the summer and autumn of 1973.

Larvae

At both 15 and 20°C about half the larvae passed through eight zoeal stages before metamorphosis, the others through nine. The time to metamorphosis averaged about 49 days at 15°C, about 25 days at 20°C. The lengths of the respective stages were 1·8–2·2, 2·2–2·5, 2·3–2·8, 3·0–3·2, 3·3–3·5, 3·7–4·2, 4·4–4·9, 4·9–5·0 and 5·9–6·2 mm.

Rostrum absent in stage I (fig. 7 (*a*)), tip extending to front of frontal lobe in stages II and III, projecting beyond lobe by $\frac{1}{3}$–$\frac{1}{2}$ its own length in subsequent stages (fig. 8). Supra-orbital spines present from stage II, less than half length of rostrum (fig. 8). Pterygostomian spine rather small, arising very close to carapace margin, followed by three or four marginal denticles (figs. 7 (*b*), 9 (*c*)). No median dorsal abdominal spines; dorso-lateral spines on somite 5 only, $\frac{1}{7}$–$\frac{1}{8}$ length of somite; anal spine present in later stages (figs. 7 (*a*), 9 (*c*)). Telson with well-marked median indentation in stages I and II, flat median protrusion in stages VIII and IX; telson broader than long in stages I–III;

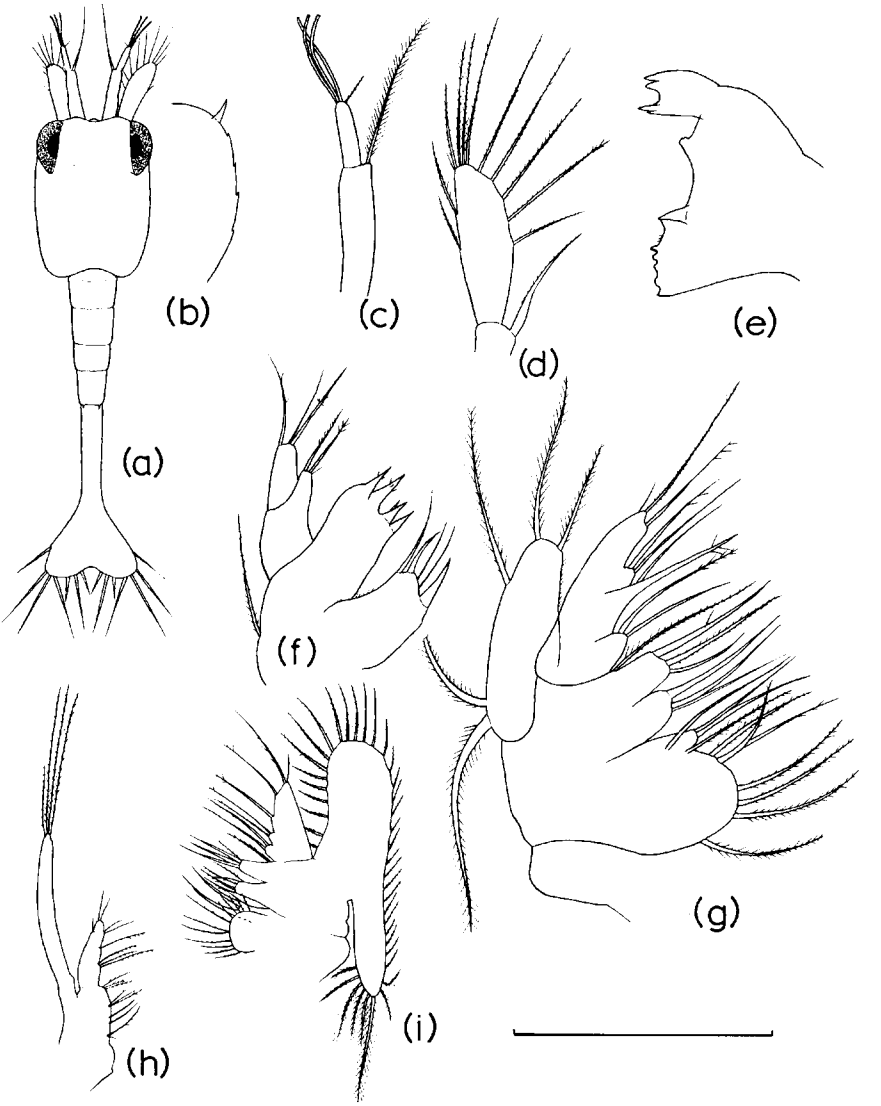

FIG. 7. *Processa nouveli holthuisi:* larvae hatched and reared at Port Erin, Isle of Man. (*a–h*) Zoeal stage I: (*a*) dorsal view; (*b*) pterygostomian region; (*c*) antennule; (*d*) antenna; (*e*) mandible; (*f*) maxillule; (*g*) maxilla; (*h*) first maxilliped; (*i*) last zoeal stage, maxilla. Scale-line represents 1 mm (*a*); 0·4 mm (*b–d, h*); 0·13 mm (*e–g*); 0·5 mm (*i*).

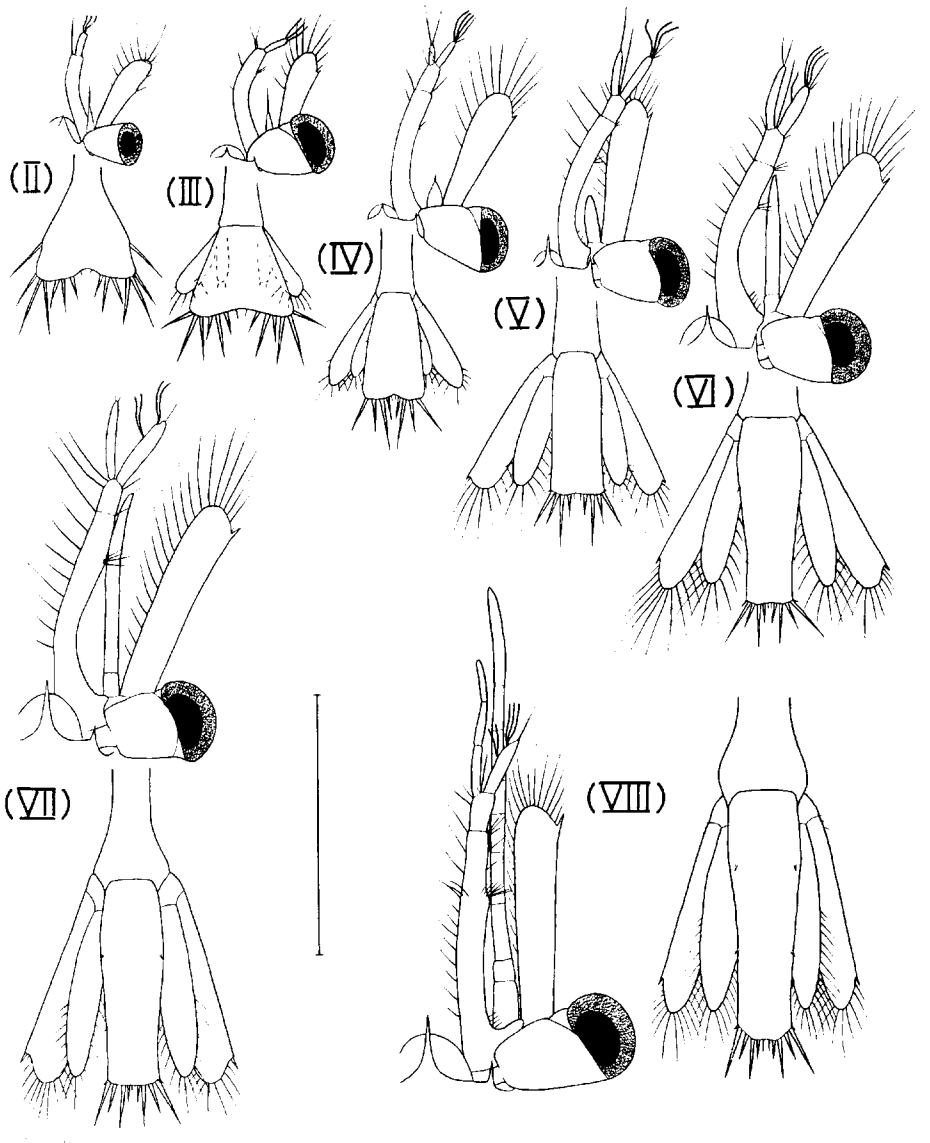

FIG. 8. *Processa nouveli holthuisi:* larvae hatched and reared at Port Erin, Isle of Man. Head (dorsal) and telson and urooods (dorsal) in zoeal stages II–VIII. Scale-line represents 1 mm.

lateral margins slightly divergent towards posterior end in stage IV, parallel in stage V, convergent in stage VI and subsequent stages; 7 + 7 marginal spines in stage I, 8 + 8 in stages II and III with outermost pair very small in stage III, 6 + 6 in stage IV with spines 2 and 3 not represented, 8 + 8 in stages V–IX with anterior pair submarginal in stages VII–IX (figs. 7 (*a*), 8).

Maximum diameter of eye about $\frac{1}{3}$ length of carapace in stage I (fig. 7 (*a*)), $\frac{1}{4}$–$\frac{1}{5}$ in subsequent stages; length of eye + stalk 1·3–1·5 times maximum diameter in stages II–IX (fig. 8). Peduncle of antennule almost straight in stage I (fig. 7 (*c*)), curved in all other stages, two-segmented in stages IV–VIII, three-segmented in stage IX, ventral spine present from stage IV; inner ramus represented by a seta in stages I and II, by a segment with two terminal setae in stages III–VI, by two segments in stage VII, three in stage VIII, four in stage IX; outer ramus with three terminal aesthetascs from stage I, two terminal setae added in stage IV, two lateral aesthetascs in stage VI (fig. 8). Antennal endopod short and pointed with terminal seta extending to about middle of scale in stages I–III; seta extending to about $\frac{1}{4}$ length of scale in stage IV, absent in subsequent stages; endopod pointed in stage V, length about $\frac{1}{3}$ that of scale; with basal segment in stage VI, length at least half that of scale; one or two terminal segments in some specimens in stage VII, as long as scale or slightly longer; segmented for most of length in stage VIII, $1\frac{1}{2}$–2 times length of scale; fully segmented in stage IX, more than twice length of scale (figs. 7 (*d*), 8). Antennal scale with small terminal segment in stages I and II; outer margin with two setae in stages I and II, proximal absent and distal replaced by a short spine in stage III, spine slightly longer in later stages but never extends beyond terminal lobe (figs. 7 (*d*), 8). Mandible with distinct incisor and molar processes from stage I (fig. 7 (*e*)); no palp in any stage. Maxillule with two-segmented palp, proximal with two setae and rudiment, distal with three setae; exopod represented by a plumed seta in early stages (fig. 7 (*f*)). Coxal endites of maxilla overlap; endopod partly divided into five segments with setal formula 2, 2, 1, 1, 1 + rudiment; exopod only about as broad as endopod in stage I, becoming rather broader and with long proximal lobe in late stages (fig. 7 (*g*) and (*i*)). Right first leg with developing chela in stage VI; second legs also chelate in stage VIII. Setose exopods on maxillipeds 1–3 in stage I (4, 5, 5 setae), also on leg 1 in stage II (5, 5, 6, 6 setae), on leg 2 in stage III (5, 6, 6, 6, 6 setae), on legs 3 and 4 in stage IV (5, 6, 6, 6, 6, 6, 5 setae), no exopod on leg 5. Uniramous pleopod buds in stage VI (fig. 9 (*c*)), biramous in stage VII. Uropods without spine on outer margin of exopod in stages III and IV, spine present in stages V–IX (fig. 8).

One dorsal pink-orange chromatophore on each eye-stalk, others on mouth region, dorsal carapace, postero-lateral carapace, either side of abdominal somite 1, junction of somites 4 and 5, postero-lateral parts of somite 6, anterior telson and exopod of each uropod.

Remarks

Gurney (1923) described a series of larval stages under the name *P. canaliculata* at a time when only one species of *Processa* was generally recognized in European waters. The species *P. canaliculata* and *P. edulis* were separated by Lebour (1936), who referred Gurney's larvae to *P. edulis* because

of their lack of spines on the fourth abdominal somite. It now appears that Gurney was dealing with larvae of two species, the early stages *P. edulis*, the later stages *P. nouveli*. His figures of stages VII and VIII show the rostrum projecting well beyond the frontal lobe and eyes less than half as long as the antennal scale, characters in agreement with larvae of *P. nouveli* but not of *P. edulis*.

The separation of *P. nouveli* from *P. canaliculata*, proposed on adult characters by Nouvel & Holthuis (1957), was opposed by Allen (1961) but upheld by Al-Adhub & Williamson (1975). The larvae provide further features whereby the two species can be distinguished, particularly the presence of dorso-lateral spines on the fourth abdominal somite of *P. canaliculata* and their absence in *P. nouveli*.

III. Larvae of the north European species

The Processidae of northern Europe are referrable to *P. canaliculata*, *P. edulis crassipes* Nouvel & Holthuis, *P. nouveli holthuisi* and *P. modica modica*. The known distributions of the four species and subspecies were given by Al-Adhub & Williamson (1975), but the name *P. modica modica* should be substituted for *P. parva* in this context, and the recent record of larvae of this subspecies from the eastern Irish Sea should be added. The present comparison is based on larvae of all four forms from Irish Sea plankton, reared larvae of *P. nouveli holthuisi* and planktonic larvae of *P. edulis crassipes* and *P. modica modica* from the southern North Sea and western Ireland. The identity of larvae of *P. canaliculata* and *P. edulis crassipes* was confirmed by rearing a number of late larvae through metamorphosis to adults or late juveniles.

The main distinguishing features of the four species of larvae are summarized in table 2 and these points are illustrated in fig. 9. The median abdominal spines referred to in table 2 are situated dorsally; all species have an anal (ventral) spine in the later zoeal stages. The median dorsal spine on the 6th somite of *P. modica* is not present in stages I and II, in which this somite is fused with the telson; thereafter it is usually more conspicuous than the spine on the third somite. The very occasional occurrence in larvae of *P. modica modica* of paired spines on the fourth somite in addition to those on the fifth is mentioned in the first section of this paper. The rostrum is absent in stage I of all the species concerned and the eyes are fused to the head; the characters relating to rostral length and eye length are therefore not applicable in this stage. The pterygostomian spine is marginal or almost so in all species in stage I but it arises within the margin in all subsequent stages of *P. edulis* and *P. modica*.

In fig. 9 comparative drawings are given of larvae in a comparable state of development. The larvae of *P. canaliculata*, *P. edulis* and *P. nouveli* are shown in stage VI, while that of *P. modica modica*, which passes through fewer zoeal stages, is shown in stage V. Larvae of *P. canaliculata* and *P. edulis crassipes* can attain about 7–9 mm in the last zoeal stage, which may be stage VIII or IX; *P. nouveli holthuisi* passes through the same number of zoeal stages to metamorphose at 6–7 mm; *P. modica modica* passes through seven zoeal stages, attaining a maximum larval length of about 5·5 mm.

Table 2

Distinguishing features of the larvae of the four north European species of *Processa*. Several characters used do not apply in stage I.

	P. canaliculata	*P. edulis*	*P. nouveli*	*P. modica*
Median abdominal spines	None	None	None	Somites 3 and 6
Paired abdominal spines	Somites 4 and 5	Somite 5	Somite 5	Somite 5
Rostrum: frontal lobe	About twice	Shorter	About equal II, III, longer IV–IX	About equal
Eye length/maximum width	About 1·5	About 2	About 1·5	About 1·5
Pterygostomian spine	Marginal	Sub-marginal	Short, almost marginal	Long, sub-marginal
Carapace denticles	5–8	0–2	3	4

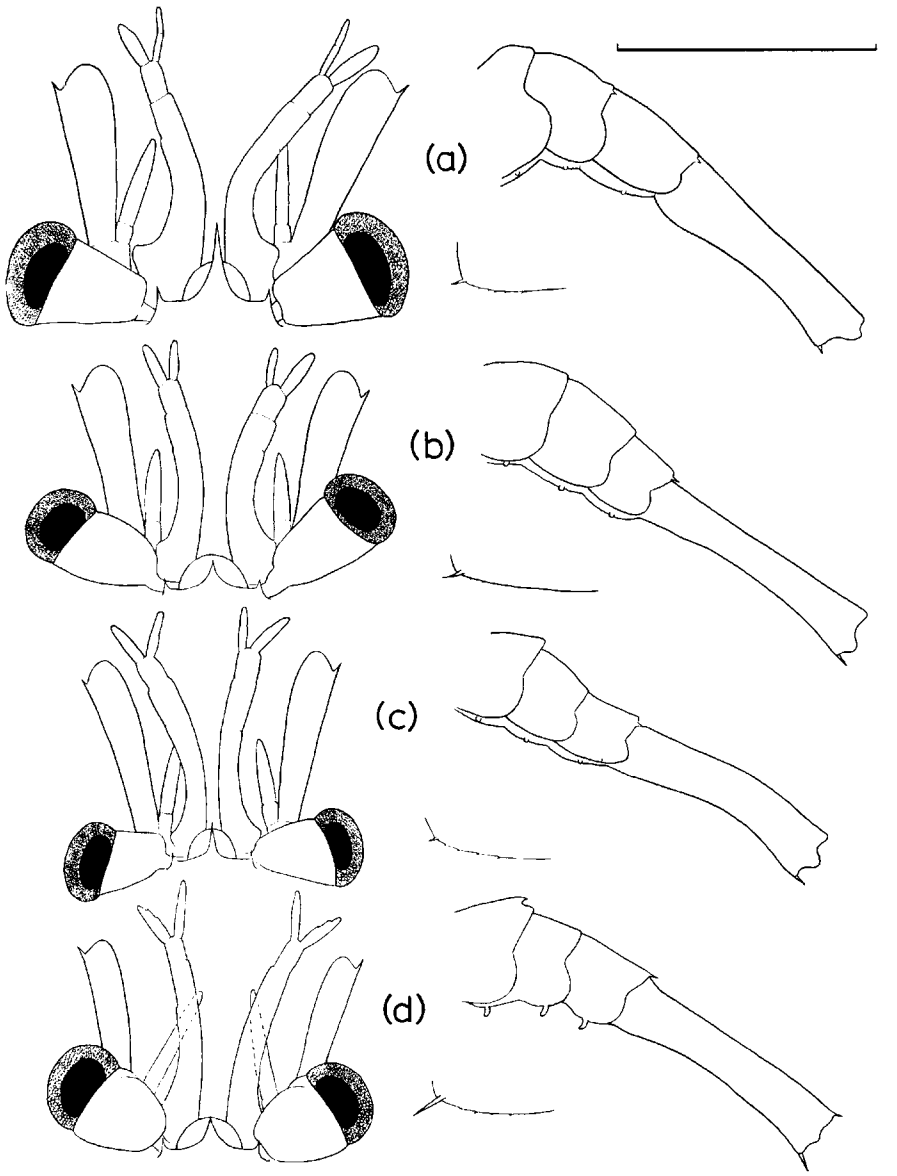

FIG. 9. Larvae of north European species in stage with small pleopod buds: head, pterygostomian region and abdomen. (*a*) *Processa canaliculata*, stage VI; (*b*) *Processa edulis crassipes*, stage VI; (*c*) *Processa nouveli holthuisi*, stage VI; (*d*) *Processa modica modica*, stage V. Scale-line represents 1 mm (*a–d*).

Summary

The European species previously ascribed to *Processa aequimana* (Paulson) or *P. parva* Holthuis is now assigned to a new species, *P. modica*, with the type locality in the southern North Sea. A distinct subspecies from the Mediterranean is recognized as *P. modica carolii*. Adults and larvae of both subspecies are described and compared with corresponding stages of *P. aequimana*, *P. parva* and *P. hemphilli* Manning & Chace.

Larvae of *P. nouveli* Al-Adhub & Williamson are described from material reared in the laboratory. They had not previously been separated from larvae of *P. edulis* (Risso), and they are clearly distinct from larvae of *P. canaliculata* Leach, with which species adults of *P. nouveli* have been confused.

A table and figures comparing the larvae of *P. canaliculata*, *P. edulis*, *P. nouveli* and *P. modica* are provided.

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