

Pelagic Shrimps of the
Sergestes edwardsii Species Group
(Crustacea: Decapoda: Sergestidae)

DAVID C. JUDKINS

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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 256

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SMITHSONIAN INSTITUTION PRESS
City of Washington
1978

ABSTRACT

Judkins, David C. Pelagic Shrimps of the *Sergestes edwardsii* Species Group (Crustacea: Decapoda: Sergestidae). *Smithsonian Contributions to Zoology*, number 256, 34 pages, 21 figures, 4 tables, 1978.—This global study of the systematics and distribution of the *edwardsii* species group is based upon examination of several hundred micronekton samples collected at stations scattered throughout the world ocean. Eight species, including three new ones, are recognized and described. Although the group is represented in all tropical and in certain subtropical oceanic regions, individual species have geographically restricted ranges. Conventional and numerical phyletic analyses reveal at least two, and perhaps three, closely related yet distinct lineages within the group. Species distributions tend to be allopatric or parapatric, overlap being most extensive between species of different lineages. Evidence of character divergence in reproductive structures of co-occurring species is discussed.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* Linnaeus).

Library of Congress Cataloging in Publication Data

Judkins, David C.

Pelagic shrimps of the *Sergestes edwardsii* species group (Crustacea: Decapoda: Sergestidae)

(Smithsonian contributions to zoology; no. 256)

Bibliography; p.

1. Sergestes. 2. Crustacea—Classification. 3. Crustacea—Geographical distribution. I. Title. II.

Series: Smithsonian Institution. Smithsonian contributions to zoology; no. 256.

QL1.S54 no. 56 [QL444.M33] 591'.08s [595'.3843] 77-608177

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Introduction

Systematic studies of pelagic marine taxa have been hindered by the circumglobal extent of many of these groups and the frequently slight degree of difference distinguishing their species. Consequently, many pelagic groups are in need of revision on a global scale, a task only recently made possible by the combined efforts of many oceanographic organizations. Recent revisions of oceanic taxa based on comparisons of material collected from throughout the world ocean invariably have revealed undescribed species (e.g., Ebeling, 1962; Frost and Fleminger, 1968; Bowman, 1973; Fleminger, 1973; Fleminger and Hulsemann, 1974; Johnson, 1974). In addition to refining our taxonomic resolution of important marine groups, such studies also have contributed greatly to our knowledge of their evolution and distribution. The present work is a global study of the taxonomy, distribution, and relationships of the *Sergestes edwardsii* species group, a monophyletic assemblage of pelagic decapod shrimps.

The *edwardsii* group is one of six species groups comprising the holopelagic penaeidean genus *Sergestes*. Species of the *edwardsii* group occur throughout tropical and certain subtropical regions of the world ocean. They are frequent and often abundant components of micronekton collections made

within their ranges. The present study was prompted by the near absence of distributional data on the group and the need for full taxonomic treatment of species, previously described in only preliminary fashion by Burkenroad (1940). Early in the study, I discovered several undescribed populations, three of which are sufficiently divergent in morphology and geographical habitat from other members of the group to be recognized as separate species. In this report, I describe all species and morphologically divergent populations of the *edwardsii* group and delimit their geographical distributions. I also examine and discuss phylogenetic relationships and biogeographic patterns within the group.

METHODS.—The majority of specimens examined in this study were taken with either the Isaacs-Kidd midwater trawl (IKMT) or the Blackburn micronekton net (BMN). However, a substantial number were collected with other gear, including the Tucker trawl and conical nets of various mouth diameters. Collections varied greatly in speed and duration of haul and in season, time of day, and depth interval sampled. A listing of station data and data sources has been deposited in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D. C.

With few exceptions, collections were examined in their entirety for adults of the closely related genera *Sergestes* and *Sergia* (cf. Omori, 1974). Figure 1 depicts the geographical distribution of collections containing specimens of those genera.

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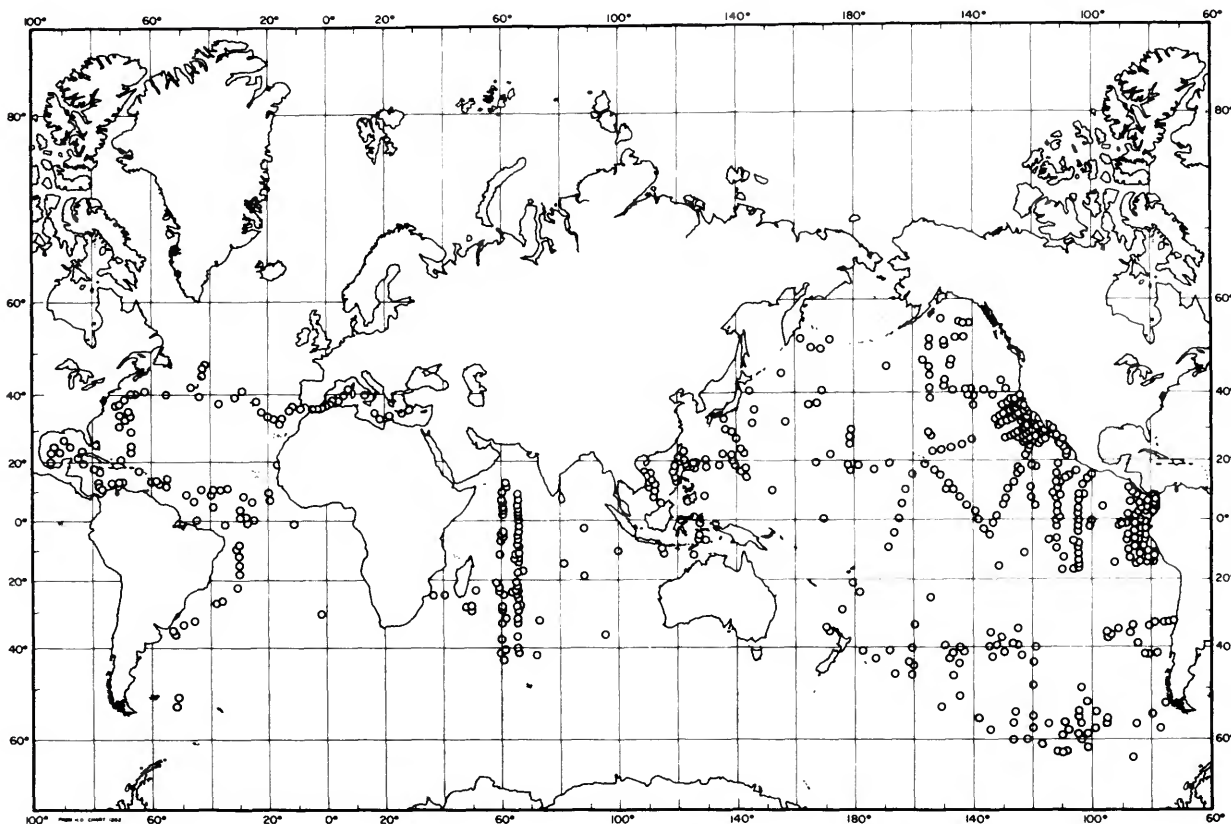


FIGURE 1.—Distribution of collections yielding specimens of the genera *Sergestes* and *Sergia* (more than one collection may be represented by a single open circle at localities where stations overlap).

These collections cover virtually the entire geographic range of the *edwardsii* species group.

Specimens of the *edwardsii* group were removed from the collections and examined initially in water with the aid of a stereomicroscope at magnifications of $\times 6$ to $\times 50$. Approximately 30 to 60 males and 10 to 25 females of each species were selected from widely scattered samples for dissection and measurement. These specimens were prepared for dissection by digesting away all soft tissue in heated aqueous KOH and then staining in aqueous chlorazol-black-E. Stained material was mounted in glycerine on glass slides and examined with a compound or stereo microscope at magnifications of $\times 24$ to $\times 200$. All illustrations were made from stained, glycerine-mounted specimens with the aid of either a Wild M5 or M20 camera lucida.

Length measurements were taken with an ocular micrometer mounted in a stereomicroscope. All intact, identifiable specimens were immersed in water and measured for carapace length (CL) at $\times 6$ or $\times 12$; stained, glycerine-mounted specimens were again measured for CL at $\times 12$ or $\times 24$. The left petasmata of all stained, glycerine-mounted males were dissected off and measured at $\times 100$ along their several distal lobes. The morphological details of these are discussed under "Taxonomically Useful Characters."

Species descriptions are based solely on sexually mature individuals. Values of measurements, counts, and ratios are listed for each species after its description. For counts and length measurements, the mean (\bar{x}) and its 95% confidence limits (cl) are presented along with the range (R) and sample size (N). In the case of ratios, a median

(Md) rather than a mean value is listed. Citation of material includes, in order, the lending institution, the expedition or cruise, the station or collection number, and the number of specimens and their sex. Type specimens of new species have been deposited in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D. C., under the catalog numbers of the former United States National Museum (USNM). Other material deposited in NMNH and listed herein by original collectors' numbers may be located through NMNH's cross reference index. Abbreviations appearing above for lending institutions, programs, and gear are used in all citations of material examined.

Because of the wide variety of gear and sampling methods used in collecting the material examined in this study, no attempt is made to estimate densities. Hence, the maps depicting the geographical distribution of species show only their presence or absence at the sampling localities that yielded *Sergia* or *Sergestes*. However, the relative abundance and frequency of occurrence of several species have been determined from standardized samples collected on EASTROPAC (ETP) Cruises 12 and 14 (Figure 7a,b). Both sets of samples were collected at night with BMNs towed obliquely from about 200 m depth. ETP 12 sampled the sector of the eastern tropical Pacific between 105° and 113°W, whereas ETP 14 sampled the sector between 77° and 92°W. Both cruises took place during late winter and early spring, 1967.

ABBREVIATIONS.—Appearing in "Taxonomically Useful Characters," the key, species descriptions, tables, and illustrations are the following morphological abbreviations:

AP	apical prominence	Max1	maxilla 1
ASR	aperture to sperm receptacles	Mxp3	maxilliped 3
CL	carapace length	Op	operculum
COL	coxal lamella	Ov	oviduct
F	foramen to body cavity	PA	pars astringens
GC	genital cavity	PB	processus basalis
LA	lobus armatus	Per3	pereopod 3
LC	lobus connectans	PM	pars media
LE	lamina externa	PP	proximal projection
LI	lobus inermis	PU	processus unifer
LT	lobus terminalis	PV	processus ventralis
		SP	sternal protuberance

ACKNOWLEDGMENTS.—I am most grateful to the following individuals and their institutions for loan

of material examined in this study: A. Fleminger, H. G. Snyder, Scripps Institution of Oceanography (SIO), La Jolla, California; R. M. Laurs, Southwest Fisheries Center (SWFC), National Marine Fisheries Service, La Jolla, California; R. H. Backus, J. E. Craddock, R. L. Haedrich, D. L. Shores, Woods Hole Oceanographic Institution (WHOI), Woods Hole, Massachusetts; D. Damkaer, J. Bradford, R. Houbriek, Smithsonian Oceanographic Sorting Center (SOSC), Smithsonian Institution, Washington, D. C.; J. Walters, Department of Oceanography, University of Hawaii (UH), Honolulu, Hawaii; E. Bertelsen, T. Wolff, Universitetets Zoologiske Museum (UZM), Copenhagen, Denmark; S. Pinkster, Instituut voor Taxonomische Zoologie (ITZ), Universiteit van Amsterdam, the Netherlands.

This paper is derived from a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at the University of California, San Diego. E. Brinton, A. W. Ebeling, E. W. Fager, A. Fleminger, J. A. McGowan, H. Stern, and B. A. Taft served on my guidance committee and made many useful suggestions towards improvement of the dissertation. R. K. Johnson, M. D. Knight, and J. H. Wormuth discussed various aspects of the problem with me and provided many insights from their own researches. I am especially grateful to E. Brinton and A. Fleminger for their helpful advice and criticisms throughout the course of this work and also to F. A. Chace, Jr., and R. B. Manning for their careful and thoughtful review of the final version of the manuscript.

My thanks also go to H. G. Snyder for curatorial aid and to K. Akutagawa for assistance in preparing the illustrations.

This work was supported by a National Defense Education Act Title VI Fellowship and by various grants from the National Science Foundation, including the Sea Grant Program. Publication is under the auspices of the U.S. Department of Energy under contract No. EY-76-C-02-0016.

Genus *Sergestes* Milne-Edwards, 1830

DIAGNOSIS.—Sergestidae with specialized luminescent modifications of the gastrohepatic gland (organs of Pesta) but without dermal photophores. Body semitransparent; color in life due primarily

to red stellate subcuticular chromatophores concentrated mainly on anterior part of body. Maxilliped 3 and pereopods 1, 2, and 3 elongate, slender, bearing stiff outstanding setae; pereopod 1 lacking chela; pereopod 2 and pereopod 3 nearly always with very small chelae; pereopod 4 and pereopod 5 without dactyli, pereopod 5 much shorter than pereopod 4. Maxilla 1 usually with palp; maxilla 2 with two lobes; maxilliped 1 with segmented palp. Possessing branchial lamellae as well as arthrobranchs; two arthrobranchs on pereopod 4, none on pereopod 5. Petasma with processus ventralis not forked. (Modified from Yaldwyn, 1957, according to Omori, 1974.)

PRESENT STATUS AND SUBDIVISIONS OF *Sergestes*.—In a recent revision, Omori (1974) elevated *Sergestes* sensu stricto and *Sergia*, the two subgenera composing *Sergestes* sensu lato (Burkenroad, 1940, 1945; Yaldwyn, 1957), to full genera. In Omori's opinion, differences between the two taxa in luminous structures and larval development justified their separation at the generic level. Adults of the revised genus *Sergestes* are distinguished by a semi-transparent body and organs of Pesta. *Sergia* species lack organs of Pesta, although many possess dermal photophores instead. Most *Sergia* have fully pigmented cuticles, although some are only "half red."

Although clearly of common lineage, *Sergestes* is readily divisible into six distinct species groups: *arcticus*, *corniculum*, *atlanticus*, *sargassi*, *vigilax*, and *edwardsii* (Yaldwyn, 1957). These groups are easily distinguished from one another and appear to be natural phyletic units.

Sergestes edwardsii Species Group

DIAGNOSIS.—*Sergestes* with outer uropod (Figure 3*m*) setose along entire outer margin. Antennular peduncle (Figure 2*b*) with segment 3 subequal to segment 1; stylocerite immobile. Maxilliped 3 much longer than pereopod 3 (Figure 2*a*); dactylus (Figure 5*g*) with six subsegments and two terminal spines. Pereopod 5 (Figure 3*f*) without setae on leading margins of distal two segments. Petasma (Figures 3*g*, 4*a-c*) with short, broad pars media and very short, unarmed processus unifer and processus ventralis. Organs of Pesta spherical in shape. Pereopod 3 with minute branchial lamella located posterodorsally to single plumose arthrobranch.

GENERAL MORPHOLOGY.—Body (Figure 2*a*) long, slender, fragile. Abdomen, when extended, somewhat less than twice length of cephalothorax; segment 6 strongly compressed, about twice as long as high. Carapace (Figure 2*a,b*) with short, acute hepatic and supraorbital spines, strong branchial, hepatic, and anterior ridges, and weak cervical and postcervical sulci. Rostrum (Figure 2*a,b*) short, ascendent, armed with single terminal tooth reaching barely beyond base of eyestalk.

Eyestalk (Figure 2*b*) lacking ocular tubercle; brown cornea wider than stalk.

Antennular peduncle (Figure 2*a,b*) about three-fourths as long as carapace; outer margin of segment 1 considerably longer than that of segment 2 but only slightly longer than that of segment 3; stylocerite (Figure 2*b*) short, acute, immobile. Antennular outer flagellum about three times as long as peduncle; inner flagellum in female (Figure 2*d*) short, simple; inner flagellum in male (clasp organ) (Figure 2*c*) with deep proximomesial notch and opposed curved spine.

Antennal peduncle armed with distolateral tooth on basal segment (Figure 2*b*). Antennal flagellum more than twice length of body, divided into proximal and distal parts by short section of annuli forming a double bend (cf. Foxton, 1969). Scaphocerite (Figure 2*b*) distally tapered, reaching slightly beyond antennular peduncle, armed with small terminal tooth.

Mandibular cutting blades (Figure 2*e,f*) asymmetrical; right blade anteriorly armed with single acute tooth occluding with deep notch on left blade; both blades possessing posterolateral molar-like processes. Mandibular palp (Figure 2*e*) reaching to distal segment of antennular peduncle, first of three segments very short.

Maxilla 1 (Figure 2*g*) with two paddle-shaped lobes distally bearing numerous stiff setae; outer lobe larger, usually with short fingerlike palp on proximolateral margin. Maxilla 2 (Figure 2*h*) with lamellar outer lobe (scaphognathite), fingerlike inner lobe, and three mesial endites.

Maxilliped 1 (Figure 2*i*) with flat, semirectangular inner and outer lobes, lamellar exopodite, and small epipodite (not shown); outer lobe with three-segmented leglike palp, segment 2 divided into two unequal subsegments. Maxilliped 2 with very short exopodite (not shown) and heavily bristled seven-segmented endopodite (Figure 2*j*) flexed posteriorly

at merocarpal articulation. Maxilliped 3 (Figure 2*k*) much stouter and longer than pereopod 3 and over twice as long as carapace (Figure 2*a*); propodus with two subsegments, first nearly twice as long as second; dactylus (Figure 5*g*) with six subsegments, first slightly shorter than second, proximal two together about as long as distal four; inner margin of dactylus bearing constant number of large spines and variable number of shorter ones, large spines consisting of single long distal spines on subsegments 1 to 5 and single shorter mesial spines on subsegments 1 and 2; outer margin of dactylus bearing single distal spines of variable length on subsegments 1, 2, and 4 and one or two short mesial spines on subsegments 1 and 2; subsegment 6 bearing two terminal spines.

Pereopod 1 (Figure 2*l*) about two-thirds as long as pereopod 2 (Figure 3*a*); pereopod 3 (Figure 3*c*) slightly longer than pereopod 2; pereopod 4 (Figure 3*e*) about equal in length to pereopod 1; pereopod 5 (Figure 3*f*) about half as long as pereopod 4. Pereopod 1 armed with numerous barbed spines at carpopropodal articulation (Figure 2*m*). Pereopod 1 and pereopod 2 armed with curved tooth on lateral margin of ischium. Chelae (Figure 3*b,d*) with dactylus slightly longer than palm, both dactylus and palm bearing terminal tufts of long setae. Pereopod 4 and pereopod 5 laterally flattened, bearing natatory setae on all but leading margin of distal two segments.

Maxilliped 2 with branchial lamella and podobranch. Maxilliped 3 and pereopods 1 to 3 each with large, plumose anterior arthrobranch and minute posterodorsal branchial lamella. Pereopod 4 with anterior arthrobranch about twice as long as posterior arthrobranch.

Organs of penta consisting of single anterior midventral organ and three pairs positioned anterolaterally, midlaterally, and posterolaterally (cf. Foxton, 1972).

Thelycum of female (Figure 4*d*) consisting of modified portions of pereopod 3 coxa and thoracic sternite 6. Pereopod 3 coxa with broad, flat proximal projection at proximomesial corner, low apical prominence at distomesial corner, and elongate, greatly hollowed genital cavity containing ovipore occupying most or all of intervening mesial margin; narrow, membranous coxal lamella protruding mesially from coxosternal articulation. Thoracic sternite 6 anteriorly forming operculum projecting post-

eriorly over common slitlike aperture of sperm receptacles (Figure 4*e*); posterior half of sternite with low transverse ridge terminating beneath proximal projections on coxa in two low anteriorly directed sternal protuberances and with shallow groove extending along midline between transverse ridge and sperm receptacle aperture.

Petasma of male emerging from proximomesial margin of pleopod 1 (Figure 3*g*) and interlocking with member of opposite side by means of cincinulli on inner margin of pars astringens. Pars externa with flat, rectangular lamina externa and short, distally rounded processus unifer. Processus basilis large, triangular, bluntly rounded mesially (Figure 4*a*). Pars media very short, wide, bearing two or three conspicuous lateral projections. Processus ventralis very short (Figure 4*b,c*). Lobus armatus elongate, usually bilobed, directed distally and/or laterally. Lobus connectans with one to three short, rounded lobes. Lobus terminalis with elongate anterior and posterior lobes. Lobus inermis directed distally, usually extending beyond outer lobes.

Pleopod 1 of female (Figure 3*h*) armed with curved tooth at about same location on propodus as origin of petasma of male. Pleopod 2 in both sexes armed with small tooth near midpoint of inner margin of propodus; propodus in male (Figure 3*j*) armed with second, slightly curved tooth at distomesial corner. Appendix masculina (Figure 3*k*) single, paddle-shaped lobe bearing spines of varying length on distal margin.

Telson (Figure 3*l*) distally rounded, lacking terminal spines. Outer uropod (Figure 3*m*) about one-third longer than inner uropod and setose along entire outer margin.

TAXONOMICALLY USEFUL CHARACTERS.—Species of the *edwardsii* group are morphologically very uniform, differing significantly only in the features discussed below.

Carapace Length (CL): Although overlapping to varying degrees in CL, species differ significantly in mean value of the measurement. In all species, females tend to be somewhat larger than males, and, hence, the two sexes are considered separately in this feature. CL was measured from the tip of the rostrum to the dorsal midpoint of the posterior margin of the carapace.

Maxilla 1 (Max1) Palp: Although relatively large in the majority of species, in *Sergestes edwardsii*

TABLE 1.—Spination of the Mxp3 dactylus in the *edwardsii* group (additional data for columns four and five in species descriptions)

Species	Outer Margin			Inner Margin Total No. Spines	Terminal Spines	
	Subsegment 1	Subsegment 2	Subsegment 4		Length Inner/Length Outer	
<i>S. edwardsii</i>	Distal spine ~ 3/4 length subsegment 2; 1 mesial spine	Distal spine > length subsegments 3 + 4; 1 mesial spine	Distal spine ~ 3/4 length subsegment 5	♂: 34-43 ♀: 35-46	♂: 0.85-1.20 ♀: 0.59-1.17	
<i>S. brevispinatus</i>	Distal spine ~ 1/2 length subsegment 2; 1 mesial spine	Distal spine < total length subsegments 3 + 4; 1 mesial spine	Distal spine very short	♂: 27-37 ♀: 36-42	♂: 0.52-0.83 ♀: 0.50-0.95	
<i>S. consobrinus</i> , California Current Form	Distal spine < 1/2 length subsegment 2; 1 mesial spine	Distal spine < total length subsegments 3 + 4; 1 mesial spine	Distal spine very short	♂: 33-41 ♀: 38-47	♂: 0.49-0.92 ♀: 0.48-0.72	
<i>S. consobrinus</i> , Central Form	Distal spine ≥ 3/4 length subsegment 2; 1 mesial spine	Distal spine ~ total length subsegments 3 + 4 + 5; 1 mesial spine	Distal spine ~ 3/4 length subsegment 5	♂: 27-41 ♀: 29-41	♂: 0.75-1.10 ♀: 0.77-1.30	
<i>S. tantillus</i>	Distal spine ≥ 3/4 length subsegment 2; 1 mesial spine	Distal spine ~ total length subsegments 3 + 4; 1 mesial spine	Distal spine ~ length subsegment 5	♂: 50-68 ♀: 53-59	♂: 0.86-1.15 ♀: 0.77-1.00	
<i>S. semissis</i>	Distal spine ≤ length subsegment 2; 1 mesial spine	Distal spine ~ length subsegment 3; 1 mesial spine	Distal spine minute	♂: 36-49 ♀: 46-57	♂: 0.76-1.19 ♀: 0.44-1.95	
<i>S. orientalis</i>	Distal spine < 1/4 length subsegment 2; 2 mesial spines	Distal spine < 1/2 length subsegment 3; 2 mesial spines	Distal spine minute	♂: 33-40 ♀: 36-42	♂: 0.37-1.00 ♀: 0.40-0.89	
<i>S. geminus</i>	As in <i>orientalis</i>	As in <i>orientalis</i>	As in <i>orientalis</i>	♂: 33-45 ♀: 35-42	♂: 0.38-0.72 ♀: 0.40-0.59	
<i>S. gibbilobatus</i>	As in <i>orientalis</i>	As in <i>orientalis</i>	As in <i>orientalis</i>	♂: 39-48 ♀: 40-48	♂: 0.43-0.80 ♀: 0.40-0.71	

and the Central form of *S. consobrinus* this structure is usually vestigial, and occasionally entirely absent.

Maxilliped 3 (Mxp3) Dactylus: Aspects of the spination of this structure can be of use in separating species of the group (Table 1). Unfortunately, the Mxp3 is often damaged or missing in preserved specimens. Features exhibiting interspecific differences are the number of spines on the inner margin, the length of the outer distal spines on subsegments 1, 2, and 4, the number of outer mesial spines on subsegments 1 and 2, and the relative length of the terminal spines on subsegment 6. Certain of these features also show ontogenetic and sexual differences; i.e., within species, inner margin spines tend to be more numerous and outer margin spines rela-

tively shorter in adult females than in adult males or subadults of either sex. When the sexes are considered separately, significant interspecific differences are discernible in the mean or median values of these features, yet considerable overlap still occurs in the data. Characters of the Mxp3 dactylus should be used with caution in separating species of the *edwardsii* group.

Pereopod 3 (Per3) Coxa in Female: Species differ slightly but consistently in size and shape of the proximal projection (PP), apical prominence (AP), and genital cavity (GC). Unfortunately, these structures can be easily observed only in cleared and stained specimens from which the thelyca have been carefully dissected (see "Methods"), and this inaccessibility minimizes their diagnostic value.

Petasma: Interspecific differences occur in the shape, configuration, and, in some cases, length and armature of the lobus inermis (LI), lobus terminalis (LT), lobus connections (LC), lobus armatus (LA), processus ventralis (PV), and pars media (PM). Diagnostically, these are the most useful characters within the group. Features measured include the LI, the anterior and posterior lobes of the LT, the outer lobe of the LC, and LA (cf. Figure 4*b,c*). The LI, LT, and LC were measured distally from a baseline connecting the inflection points on the inner and outer margins of the PM. The LA, a laterally directed lobe, was measured along its axis

from the inflection separating it from the LC. To standardize these measurements against size effects, they are presented in the text as ratios (LI/CL, LT anterior/LI, LT posterior/LI, LC outer/LI, LA/LI). Scattergrams of LI length and LT anterior lobe length versus CL are useful in demonstrating differences in the petasmata of closely related populations (Figures 8, 11, 18).

Males usually were identified readily by examination of their petasmata. However, not all females from regions of overlap could be separated to species because of the frequent absence of easily accessible diagnostic features.

Key to Species of the *edwardsii* Group

ADULT MALES

1. No inflection at base of LI; LT posterior lobe thumblike, unarmed, directed posteriorly (Figure 14*b-d*); inhabiting northern Indian Ocean, Bay of Bengal, Arabian Sea (Figure 15) 5. *S. semissis*
Strong inflection at base of LI; LT posterior lobe cylindrical or fingerlike, armed distally with single tooth, directed distally 2
2. LI bearing distal protuberances; LI anterior lobe lamellar, twisted, armed distally with single exposed hook 3
LI without distal protuberances; LT anterior lobe fingerlike, armed with several hooks 5
3. LI posterior lobe with distal end strongly bent laterally; PV not reaching inflection between LA inner and outer lobes (Figure 19*b,c*); inhabiting central and eastern tropical Pacific (Figure 20) 8. *S. gibbilobatus*
LI posterior lobe with distal end not bent laterally, PV reaching to or beyond inflection between LA inner and outer lobes 4
4. LC usually trilobed, outermost lobe about equal in size to innermost lobe (Figure 16*b,c*); inhabiting tropical Indian Ocean, Indo-Australian archipelago, western tropical Pacific, Hawaiian archipelago (Figure 17) 6. *S. orientalis*
LC usually bilobed; outermost lobe, when present, tending to be smaller than innermost lobe (Figure 16*g,h*); inhabiting eastern tropical Pacific (Figure 17) 7. *S. geminus*
5. LA and LC both single lobes (Figure 12*b,c*); inhabiting central and eastern tropical Pacific (Figure 13) 4. *S. tantillus*
LA and LC bilobed 6
6. LA outer lobe directed laterally, distal half bent forward onto proximal half 7
LA outer lobe directed distolaterally, distal half not bent forward onto proximal half 8
7. Outer distal spine on subsegment 4 of Mxp3 dactylus very short; outer terminal spine on subsequent 6 about two-thirds length on inner (Figure 9*g*); inhabiting outer California Current region (Figure 10) 3a. *S. consobrinus*, California Current form
Outer distal spine on subsegment 4 very long; terminal spines on subsegment 6 subequal (Figure 9*h*); inhabiting central north Pacific (Figure 10) 3b. *S. consobrinus*, Central form
8. LT anterior lobe usually longer than posterior lobe (Figure 5*b*); outer distal spine on subsegment 4 of Mxp3 dactylus long, terminal spines on subsegment 6 subequal (Figure 5*g*); inhabiting tropical Atlantic (Figure 6) 1. *S. edwardsii*
LI anterior lobe usually shorter than posterior lobe (Figure 5*e*); outer distal spine on subsegment 4 of Mxp3 dactylus very short, outer terminal spines on subsegment 6 noticeably unequal (Figure 5*h*); inhabiting eastern tropical Pacific (Figure 6) 2. *S. brevispinatus*

ADULT FEMALES

1. Two mesial spines on outer margin of either or both subsegments 1 and 2 of Mxp3 dactylus 2

Key to Species of the *edwardsii* Group (cont'd)

- One mesial spine on outer margin of subsegments 1 and 24
2. Per3 coxa with distinct bulge on distal margin of PP (Figure 16l)3
Per3 coxa without distinct bulge on distal margin of PP (Figure 19h); inhabiting central and eastern tropical Pacific (Figure 20)8. *S. gibbilobatus*
3. Inhabiting tropical Indian Ocean, Indo-Australian archipelago, western tropical Pacific, Hawaiian archipelago (Figure 17)6. *S. orientalis*
Inhabiting eastern tropical Pacific (Figure 17)7. *S. geminus*
4. Outer distal spine on subsequent 4 of Mxp3 dactylus very short5
Outer distal spine on subsegment 4 long, reaching to or beyond midpoint of subsegment7
5. GC of Per3 coxa extending distally to AP (cf. Figure 4d)6
GC not extending distally to AP (Figure 14g); inhabiting northern Indian Ocean, Bay of Bengal, Arabian Sea (Figure 15)5. *S. semissis*
6. GC of Per3 coxa broad, viewed ventrally; PP long, acute (Figure 9i). Inhabiting outer California Current region (Figure 10)3a. *S. consobrinus*, California Current form
GC relatively narrow, viewed ventrally; AP relatively short, blunt (as in *S. edwardsii*, cf. Figure 5i); inhabiting eastern tropical Pacific (Figure 6)2. *S. brevispinatus*
7. Mxp3 dactylus with 50 or more spines on inner margin (Figure 12d); GC of Per3 coxa with indentation on dorsal margin (Figure 12e); inhabiting central and eastern tropical Pacific (Figure 13)4. *S. tantillus*
Mxp3 dactylus with less than 50 spines on inner margin; GC without indentation on dorsal margin8
8. GC of Per3 coxa very broad, viewed ventrally (Figure 9j); inhabiting central north Pacific (Figure 10)3b. *S. consobrinus*, Central form
GC relatively narrow, viewed ventrally (Figure 5i); inhabiting tropical Atlantic (Figure 6)1. *S. edwardsii*

1. *Sergestes edwardsii* Kröyer, 1855

FIGURES 2e,f,h-m, 3, 4a,b,d,e, 5a-c,g,i,j, 6, 8, 21b

- Sergestes edwardsii* Kröyer, 1855:28; 1859:246, 277, 284, 285, pl. 4: fig. 9a-k.—Hansen, 1896:961 [in part]; 1919:26, pl. 2: fig. 3.—Illig, 1914:363, fig. 25 [in part]; 1927:320, figs. 86, 89, 90, 91 [in part].
- Sergestes occulataus* Kröyer, 1855:28; 1859:243, 277, 284, 285, pl. 3: fig. 5a-f.—Bate, 1888:406, pl. 74: fig. 1 [in part].—Hansen, 1896:963
- Sergestes brachyorrhos* Kröyer, 1859:272, 281, 284, 285, pl. 5: fig. 13a,b.
- Sergestes edwardsi* Bate, 1888:403, pl. 73: fig. 2 [in part].—Borradaile, 1916:81.—Sund, 1920:27.—Hansen, 1922:182, pl. 11: figs. 1a-i, 2a-f.—Gurney and Lebour, 1940:62, fig. 56.—Dennell, 1940:314, 320.
- Sergestes (Sergestes) edwardsi*.—Yaldwyn, 1957:8.—Milne, 1968: 29–31.—Crosnier and Forest, 1973:307, 320–322, figs. 108b, 109b, c, 110c, d.

TYPES.—Although Kröyer did not publish type specimens or material examined in his description of *S. edwardsii*, three of the specimens on which the description is based have been labeled "Types." The available data on these specimens, which were loaned to me by the UZM, are summarized: (1) 1 ♀, 3.5 mm CL, collected in the Atlantic at 20°N, unspecified longitude; (2) 1 ♀, 3.5 mm CL,

collected in the Atlantic at 10°22'N, 21°16'W; (3) 1 ♂, 4.8 mm CL, collected in the Atlantic at 7°N, 30°W. I have designated the last specimen listed, the only male in the series, as the lectotype.

ADDITIONAL MATERIAL.—WHOI, *Chain* 35: RHB 953(1 ♂), 958(1 ♂, 1 ♀), 959(1 ♂), 962(7 ♂ ♂, 8 ♀ ♀), 966(6 ♀ ♀), 970 (2 ♂ ♂, 3 ♀ ♀), 975(1 ♀), 980(8 ♂ ♂, 12 ♀ ♀). WHOI, *Atlantis II* 13: RHB 1026(2 ♂ ♂). WHOI, *Atlantis II* 20: RHB 1201(1 ♂, 5 ♀ ♀), 1203(5 ♂ ♂, 3 ♀ ♀), 1204(4 ♂ ♂, 17 ♀ ♀), 1206(2 ♂ ♂, 1 ♀), 1207(12 ♀ ♀), 1208(3 ♂ ♂, 21 ♀ ♀), 1209(7 ♂ ♂, 14 ♀ ♀), 1210(1 ♂, 1 ♀), 1213(2 ♀ ♀), 1214(37 ♂ ♂, 32 ♀ ♀), 1215(4 ♂ ♂, 17 ♀ ♀), 1216(1 ♂, 2 ♀ ♀), 1217(4 ♂ ♂), 1219(1 ♂, 7 ♀ ♀), 1222(1 ♂). WHOI, *Chain* 60: RHB 1253(1 ♂, 1 ♀), 1257(4 ♂ ♂), 1258(1 ♂, 6 ♀ ♀), 1267(1 ♀), 1271(7 ♀ ♀), 1272 (2 ♂ ♂, 3 ♀ ♀), 1273(3 ♀ ♀), 1276(1 ♂, 1 ♀), 1277(6 ♀ ♀), 1282(6 ♂ ♂, 11 ♀ ♀), 1290(8 ♂ ♂, 16 ♀ ♀), 1291(2 ♀ ♀), 1312 (2 ♂ ♂, 1 ♀), 1314(2 ♂ ♂, 2 ♀ ♀). WHOI, *Chain* 72: RHB 1505(1 ♂), 1516(1 ♂, 5 ♀ ♀). WHOI, *Atlantis II* 49: RHB 1935(1 ♂), 1942(2 ♀ ♀).

The material listed is deposited in NMNH.

DESCRIPTION.—Max1 palp (Figure 5j) usually vestigial and without setae, occasionally entirely absent.

Mxp3 dactylus (Figure 5g, Table 1) with single mesial spines on outer margins of subsegments 1 and 2. Outer distal spine on subsegment 1 usually reaching to origin of outer distal spine on subsegment 2; outer distal spine on subsegment 2 usually

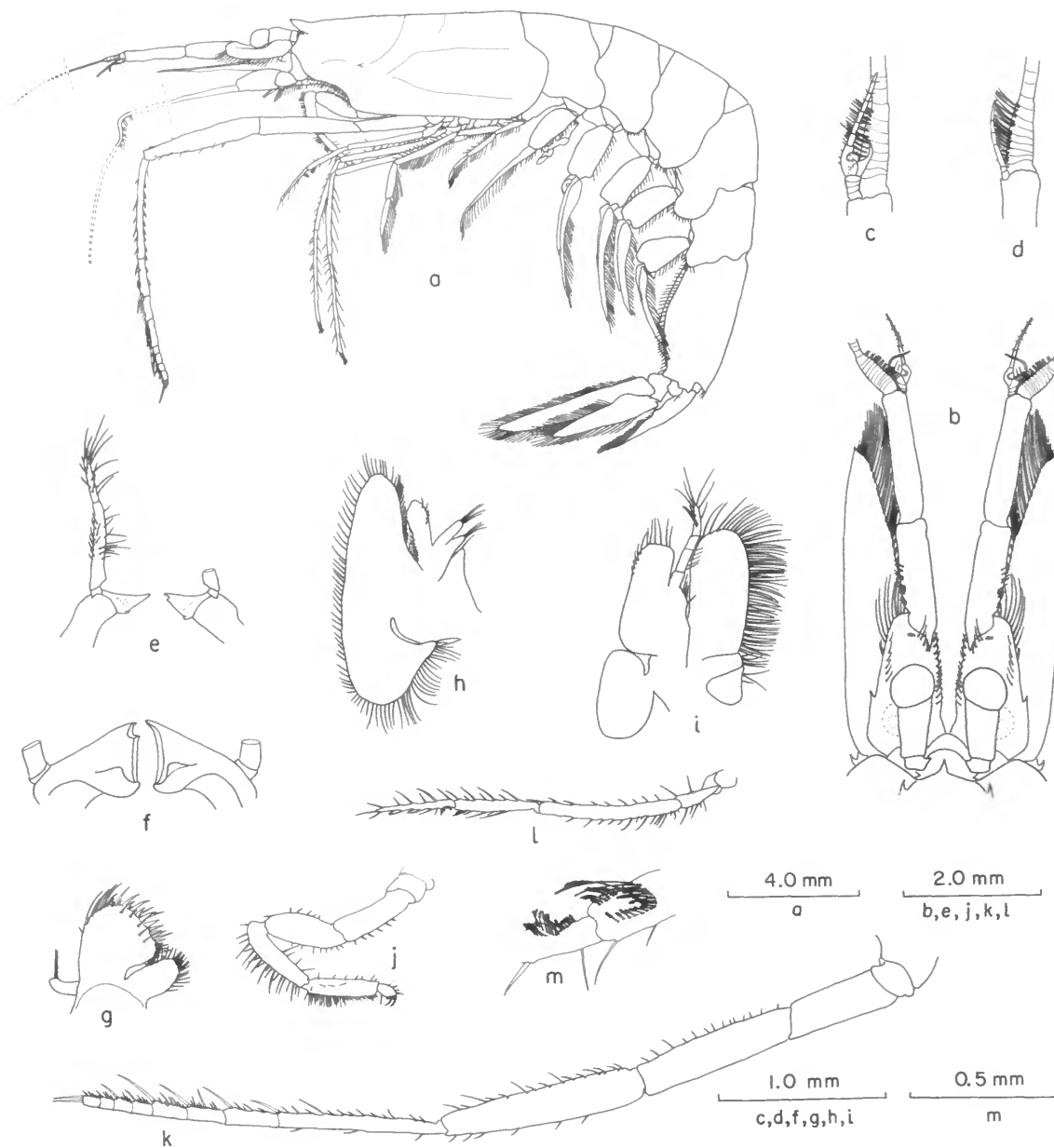


FIGURE 2.—*Sergestes geminus*, ♂, 6.4 mm CL: *a*, habitus lateral; *b*, anterior cephalothorax, dorsal; *c*, distal end of ♂ antennular flagellum showing clasper, ventral. *S. brevispinatus*, ♀, 6.3 mm CL: *d*, distal end of ♀ antennular peduncle showing lower flagellum, ventral. *S. edwardsii*, ♂, 5.1 mm CL: *e*, mandibles (left palp incomplete), ventral; *f*, mandibles (palps incomplete), dorsal. *S. gibbilobatus*, ♂, 6.9 mm CL: *g*, left maxilla 1, anterior. *S. edwardsii*, ♂, 5.1 mm CL: *h*, left maxilla 2, anterior; *i*, left maxilliped 1, anterior; *j*, left maxilliped 2, lateral; *k*, left maxilliped 3, lateral; *l*, left pereopod 1, lateral; *m*, articulation between carpus and propodus of left pereopod 1, mesial.

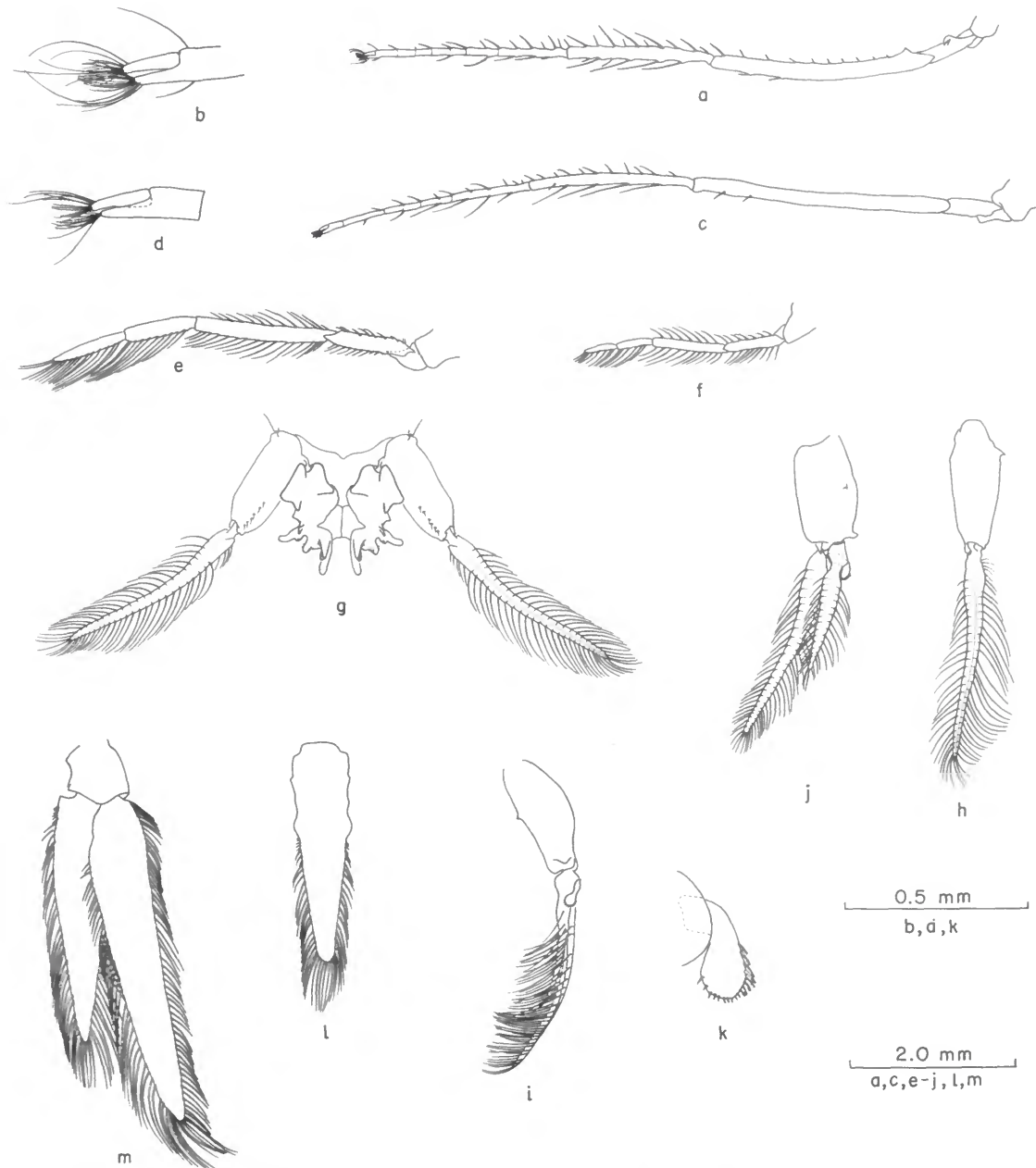
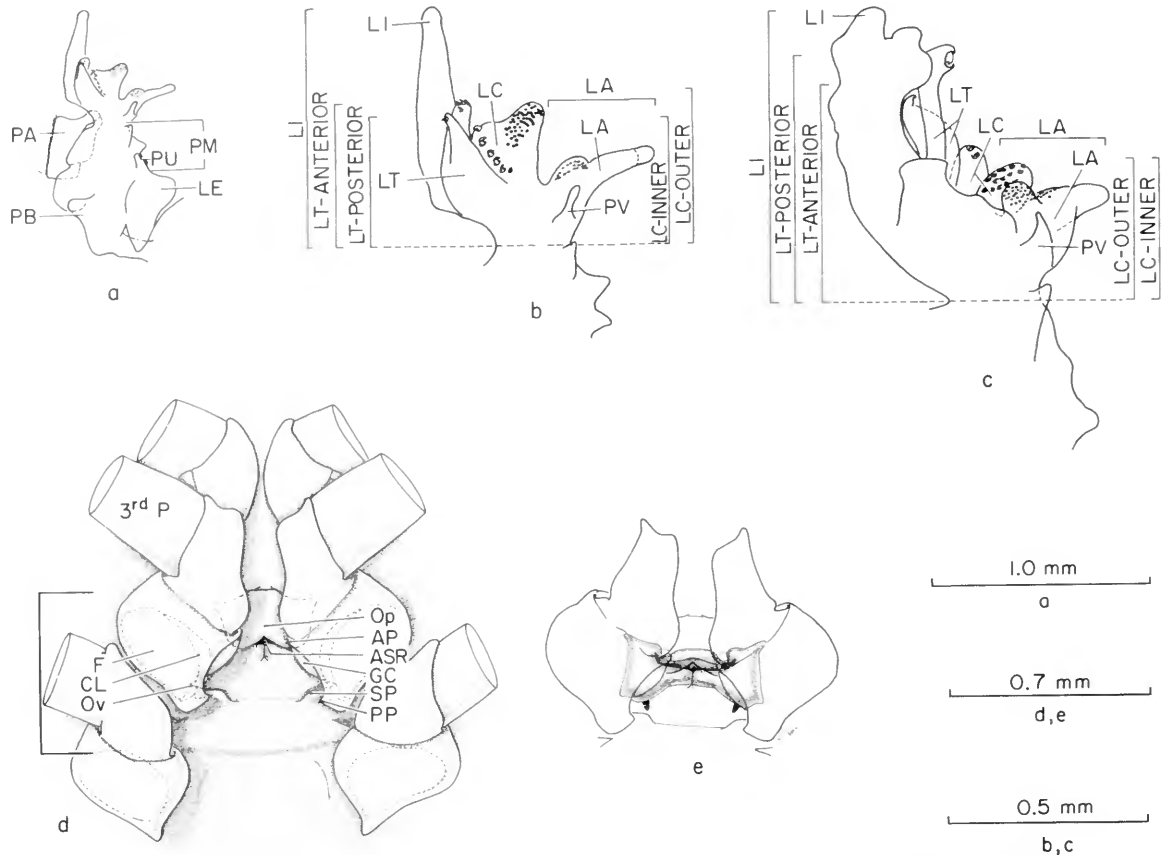


FIGURE 3.—*Sergestes edwardsii*, ♂, 5.1 mm CL: *a*, left pereopod 2, lateral; *b*, chela of left pereopod 2, lateral; *c*, left pereopod 3, lateral; *d*, chela of left pereopod 3, lateral; *e*, left pereopod 4, lateral; *f*, left pereopod 5, lateral; *g*, ♂ pleopod pair 1 with petasmata attached, posterior. ♀, 6.1 mm CL: *h*, ♀ left pleopod 1, posterior. ♂, 5.1 mm CL: *i*, ♂ left pleopod 2, mesial; *j*, ♂ left pleopod 2, posterior; *k*, ♂ left appendix masculina, mesial; *l*, telson, ventral; *m*, left uropod, ventral.



♀, 6.3 mm CL: *d*, ♀ thelycum and adjacent features (bracket on left side delimits sixth thoracic segment), posteroventral view; *e*, sperm receptacles (stippled, lying beneath line drawing of external features of thelycum), posteroventral.

reaching beyond end of subsegment 4; outer distal spine on subsegment 4 usually reaching beyond midpoint of subsegment 5; outer terminal spine on subsegment 6 usually more than three-fourths length of inner spine. Distal spines on outer margin of subsegments 1, 2, and 4, and outer terminal spine on subsegment 6 tending to be relatively shorter in female.

Per3 coxa in female (Figure 5i) with short, blunt PP and low, blunt AP; GC narrow in ventral view, extending distally to DP.

Petasma (Figure 5a-c) with LI fingerlike, strongly inflected at proximomesial margin, sometimes slightly expanded distally. LT lobes both fingerlike;

anterior lobe distally rounded, armed both anteriorly and posteriorly with large hooks; posterior lobe slender, usually slightly shorter than anterior lobe, armed with single large terminal hook. LC bilobed; inner lobe low, rounded, armed with row of large hooks extending longitudinally along posterior face, over distal margin, and then laterally along anterior face to point below base of outer lobe; outer lobe bulbous, directed distolaterally, distally armed with several small hooks. LA bilobed; inner lobe low, rounded, distally covered with numerous minute hooks; outer lobe slender, elongate, directed distolaterally, armed with large terminal hook and lateral row of four to six smaller

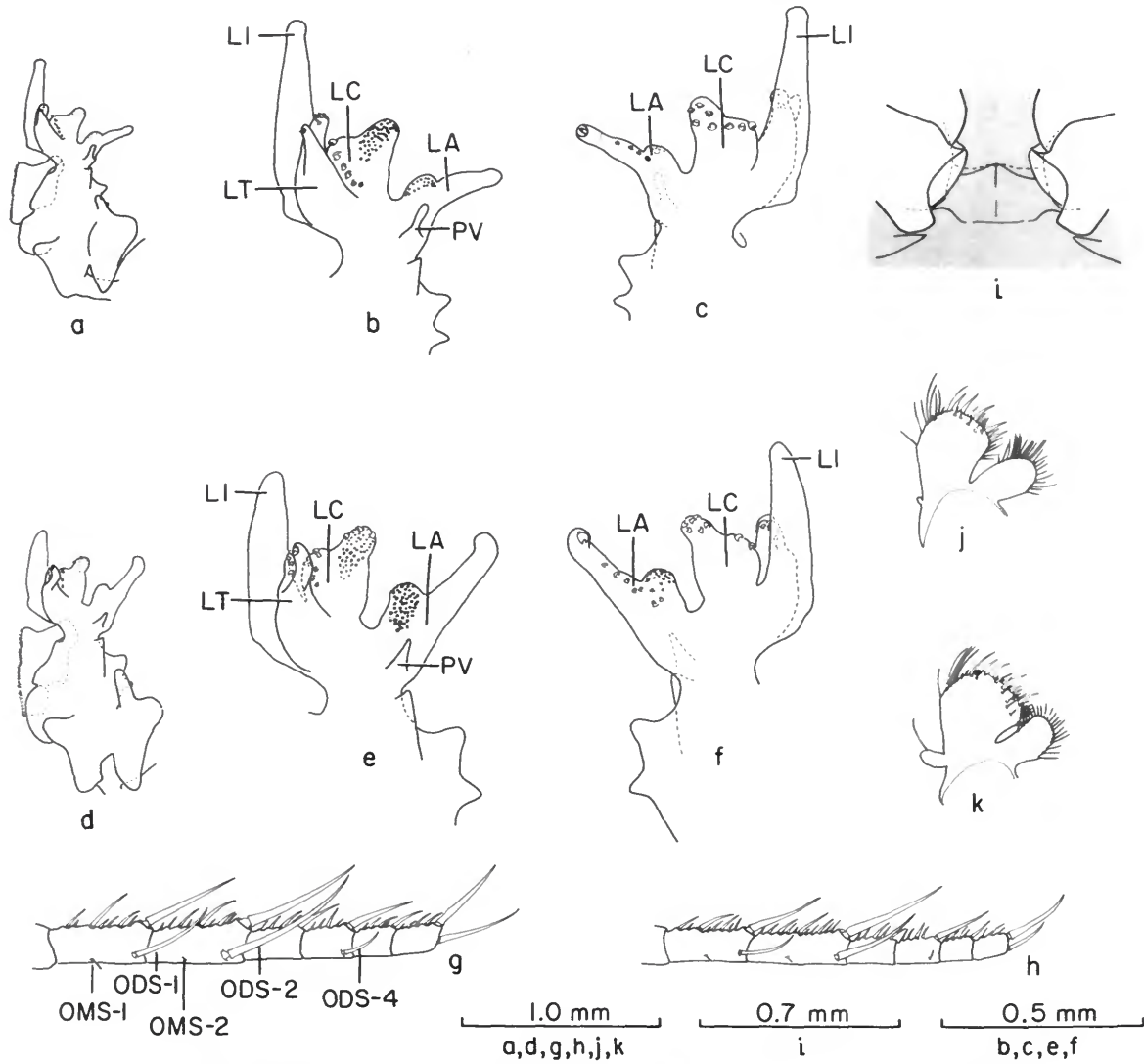


FIGURE 5.—*Sergestes edwardsii*, ♂, 4.5 mm CL: a, left petasma, posterior; b, c, capitulum of left petasma, posterior and anterior. *S. brevispinatus*, ♂, 5.7 mm CL: d, left petasma, posterior; e, f, capitulum of left petasma, posterior and anterior. *S. edwardsii*, ♂, 5.1 mm CL: g, dactylus of left Mxp3, mesial (OMS-1, -2 = outer mesial spines of subsegments 1, 2; ODS-1, -2, -4 = outer distal spines of subsegment 1, 2, 4). *S. brevispinatus*, ♂, 5.4 mm CL: h, left Mxp3 dactylus, mesial. *S. edwardsii*, ♀, 6.3 mm CL: i, thelycum, posteroventral. *S. edwardsii*, ♂, 5.1 mm CL: j, left Max1, anterior. *S. brevispinatus*, ♂, 5.4 mm CL: k, left Max1, anterior.

hooks on proximoanterior margin. PV extending to about level of inflection between LC and LA. PM with three conspicuous projections on lateral margin.

MEASUREMENTS, COUNTS, AND RATIOS

CL				
	\bar{x} (mm)	95% cl (mm)	R (mm)	N
♂	4.6	±0.1	3.6–5.9	112
♀	5.5	±0.1	4.0–7.0	259
Total number of spines on Mxp3 dactylus inner margin				
	\bar{x}	95% cl	R	N
♂	37.2	±1.8	34–43	10
♀	38.4	±2.4	35–46	10
Length of inner/length of outer terminal spines on Mxp3 dactylus				
	Md	R	N	
♂	1.00	0.85–1.20	15	
♀	0.89	0.59–1.17	10	
Petasma ratios				
	Md	R	N	
LI/CL	0.136	0.106–0.153	32	
LT anterior/LI	0.62	0.54–0.71	32	
LT posterior/LI	0.58	0.48–0.67	32	
LC outer/LI	0.51	0.40–0.58	32	
LA/LI	0.48	0.35–0.36	31	

DISTRIBUTION.—*Sergestes edwardsii* is broadly distributed throughout the tropical Atlantic, Caribbean, and Gulf of Mexico (Figure 6). Records at relatively high northern latitudes in the western Atlantic are probably the result of transport by the Gulf Stream.

2. *Sergestes brevispinatus*, new species

FIGURES 2d, 5d–f, h, k; 6–8, 21b

HOLOTYPE.—USNM 155056, adult ♂, 6.0 mm CL.

TYPE-LOCALITY.—Sorted from micronekton collection taken at ETP 14 sta 081 (11°02'S, 81°41'W); 14 Feb 1967; nighttime oblique tow with BMN from ca. 200 m.

ALLOTYPE.—USNM 155058, adult ♀, 9.0 mm CL; sorted from micronekton collection taken at ETP 14 sta 091 (14°48'S, 79°58'W); 16 Feb 1967; nighttime oblique tow with BMN from ca. 200 m.

PARATYPES.—USNM 155057, 5 adult and subadult ♂♂, 5.5, 5.7, 5.8, 5.9, 6.0 mm CL; from same collection as holotype. USNM 155059, 5 adult and

subadult ♀♀, 7.4, 7.5, 7.6, 8.4, 9.0 mm CL, and 1 adult ♂, 5.9 mm CL; from same collection as allotype.

ADDITIONAL MATERIAL.—SIO, Shellback: 13(1♂). SIO, Eastropic: 16(1♂, 9♀♀). SIO, Anton Brunn 12: 65-603(1♂), 65-606(7♂♂), 65-608(1♂). SWFC, ETP 12: 059(32♂♂, 1♀), 084(1♂), 094(1♂), 106(2♂♂), 118(1♂). SWFC, ETP 14: 014(1♂), 018(11♂♂), 022(7♂♂, 4♀♀), 027(1♂), 043(5♂♂), 051(21♂♂, 2♀♀), 081(1♀), 086(10♂♂), 091(20♂♂, 1♀), 099(2♂♂, 1♀), 106(2♂♂), 110(1♂), 120(3♂♂), 124(3♂♂, 1♀), 132(2♂♂), 138(9♂♂, 3♀♀), 154(2♂♂), 232(1♂), 240(1♂), 247(11♂♂, 1♀), 255(19♂♂, 4♀♀), 263(4♂♂), 271(1♂), 287(1♂, 4♀♀), 303(4♂♂, 10♀♀), 326(1♂).

The material listed is deposited in the SIO Zooplankton Collections.

DESCRIPTION.—Max1 palp (Figure 5k) relatively large, with one or two distal setae.

Mxp3 dactylus (Figure 5h, Table 1) with single mesial spines on outer margins of subsegments 1 and 2. Outer distal spine on subsegment 1 seldom reaching beyond subsegment 2; outer distal spine on subsegment 2 seldom reaching beyond subsegment 4; outer distal spine on subsegment 4 very short; outer terminal spine on subsegment 6 usually less than three-fourths length of inner terminal spine. Distal spines on outer margin of subsegments 1, 2, and 4 and outer terminal spine on subsegment 6 tending to be relatively shorter, and inner margin spines more numerous in female.

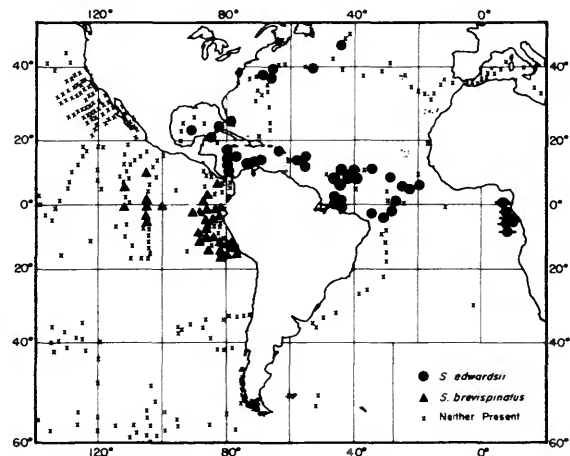


FIGURE 6.—Geographical distribution of records of *Sergestes edwardsii* and *S. brevispinatus* (line through solid circle = literature records; see Crosnier and Forest, 1973).

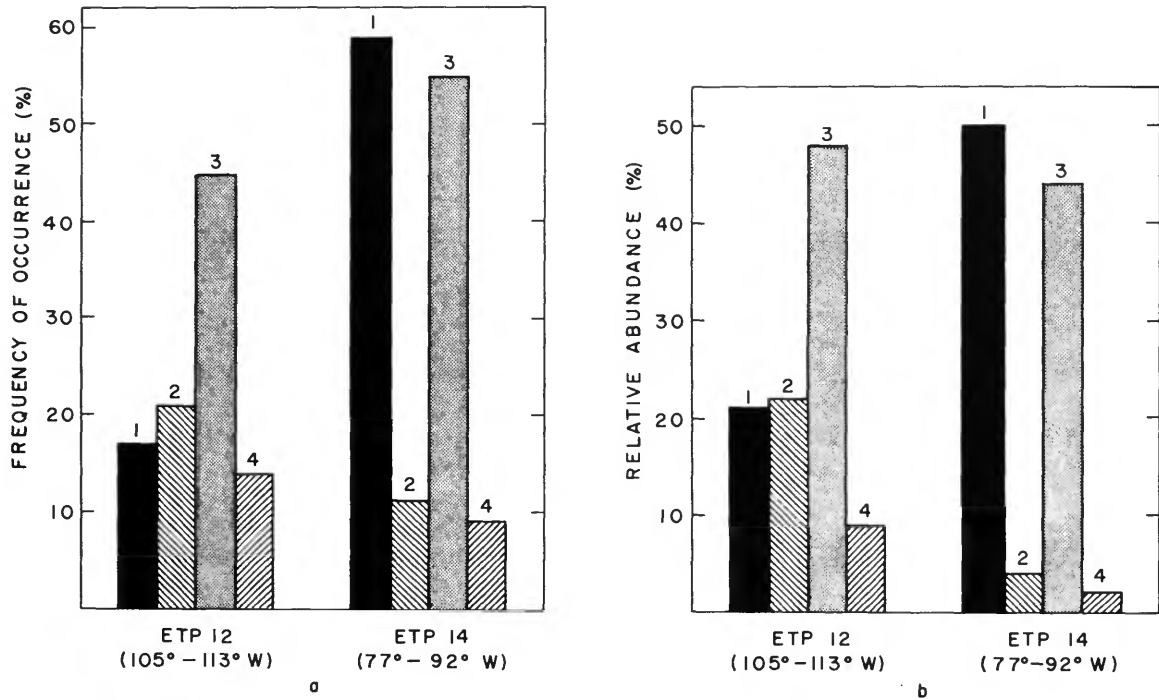


FIGURE 7.—Based on collections from ETP cruises 12 and 14, representing the western and eastern sectors of the eastern tropical Pacific, respectively, four species of *edwardsii* group compared: a, frequency of occurrence; b, relative abundance (frequency of occurrence = the percentage of the total number of collections made on each cruise in which an individual species occurred; relative abundance = the percentage of the total number of specimens taken on each cruise represented by an individual species; 1 = *S. brevispinatus*; 2 = *S. tantillus*; 3 = *S. geminus*; 4 = *S. gibbilobatus*).

Per3 coxa of female as in *S. edwardsii* (cf. Figure 5i).

Petasma (Figure 5d-f) very similar to that in *S. edwardsii* but differing in following features: LI usually more rounded proximally and seldom expanded distally; LT posterior lobe usually slightly longer than anterior lobe (Figure 8c); LC inner lobe armed with hooks posteriorly and distally, but not anteriorly; LA outer lobe armed with six to eleven hooks along proximoanterior margin; LI and LT anterior lobe tending to be longer relative to CL (Figure 8a,b).

MEASUREMENTS, COUNTS, AND RATIOS				
CL	\bar{x} (mm)	95% <i>cl</i> (mm)	<i>R</i> (mm)	<i>N</i>
♂	5.0	±0.1	3.6-6.7	193
♀	6.6	±0.3	4.7-8.7	44

Total number of spines on Mxp3 dactylus inner margin

	\bar{x}	95% <i>cl</i>	<i>R</i>	<i>N</i>
♂	33.8	±2.3	27-37	10
♀	39.3	±1.7	36-42	10

Length of inner/length of outer terminal spines on Mxp3 dactylus

	<i>Md</i>	<i>R</i>	<i>N</i>
♂	0.70	0.52-0.83	10
♀	0.65	0.50-0.95	12

Petasma ratios

	<i>Md</i>	<i>R</i>	<i>N</i>
LI/CL	0.113	0.091-0.023	25
LT anterior/LI	0.66	0.57-0.79	25
LT posterior/LI	0.71	0.58-0.80	25
LC outer/LI	0.69	0.53-0.80	25
LA/LI	0.67	0.51-0.81	25

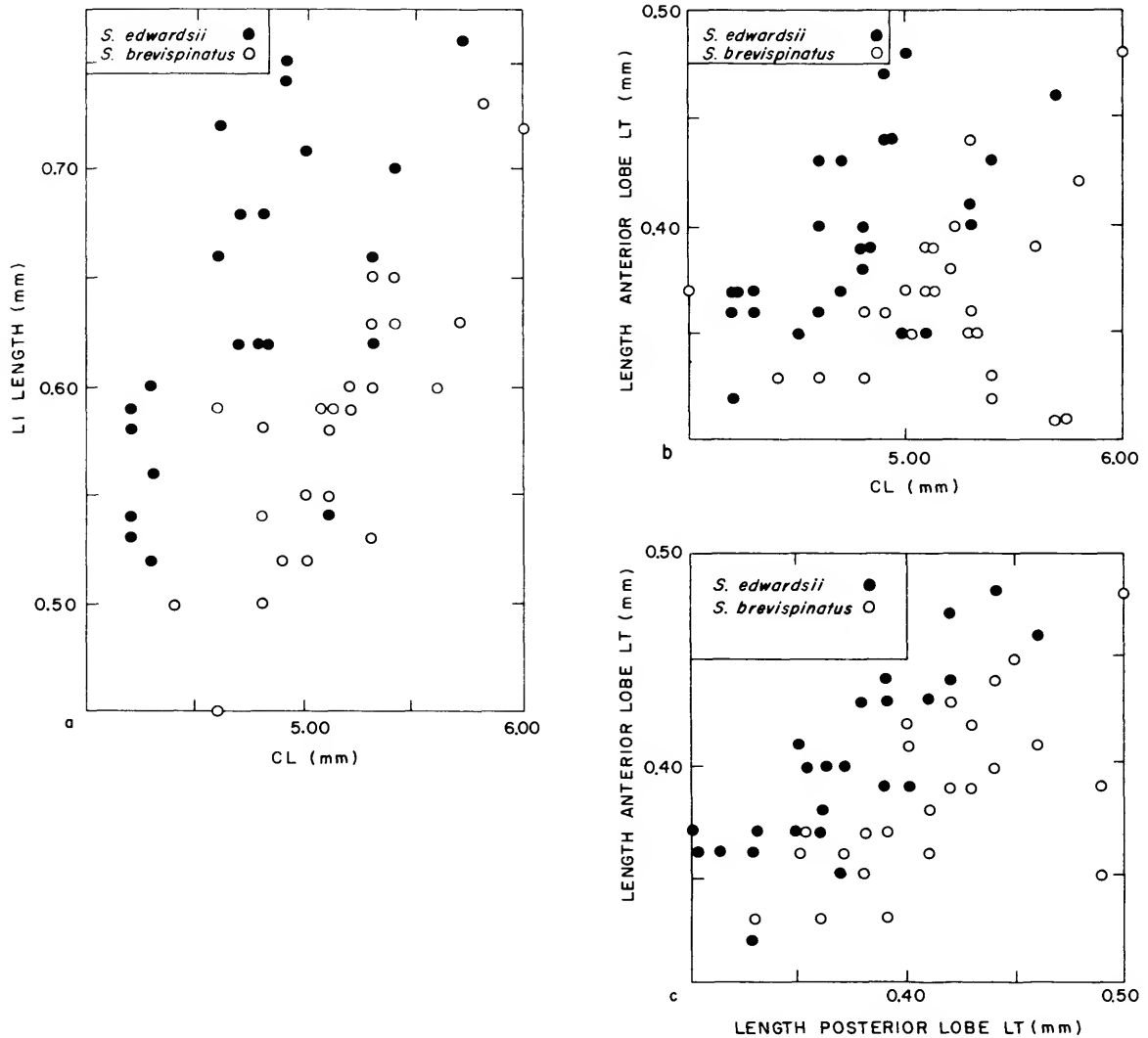


FIGURE 8.—*Sergestes edwardsii* and *S. brevispinatus* compared for certain relationships: a, LI length and CL; b, LT anterior lobe length and CL; c, LT anterior and posterior lobe lengths.

DISTRIBUTION.—*Sergestes brevispinatus* is clearly indigenous to the eastern tropical Pacific (Figure 6). Judging from its frequency of occurrence in collections from ETP 12 and 14 (Figure 7a), this species appears to prefer oceanic waters close to the continental margin of Central and South America. It is by far the most abundant of the four *edwardsii* species present in ETP collections from that sector of the eastern tropical Pacific (Figure 7b).

REMARKS.—Size of the Max1 palp and spination of the Max3 are the most obvious characters separating *S. brevispinatus* from *S. edwardsii*. However, differences in these features may be simply a consequence of differing developmental rates resulting from different levels of food in their respective geographical habitats (cf. Reeve, 1969). This interpretation is supported by the generally smaller size of *S. edwardsii* and the similarity of immature *S. brevispinatus*.

spinatus to mature *S. edwardsii* in features of the Max1 palp and Mxp3 dactylus. It should be noted, however, that the relative importance of environmental versus genetic factors in bringing about these interspecific differences remains a matter of speculation. Moreover, differences in the petasmata of the two forms, although relatively inconspicuous, do not appear to be size related and, thus, are more likely to be of genetic origin.

My decision to recognize *S. brevispinatus* as a separate species is based on biogeographical, as well as morphological grounds. *S. edwardsii* is restricted to the tropical Atlantic, whereas *S. brevispinatus* is endemic to the eastern tropical Pacific, and thus, there is little likelihood of gene flow between them now or in the recent past. Furthermore, the eastern tropical Pacific supports many endemic pelagic species while excluding many of their more widespread tropical congeners. The region's unique and exclusive pelagic fauna may be a consequence of the extremely low oxygen tensions characterizing its near surface waters (Knauss, 1963), a phenomenon quite possibly requiring special physiological and behavioral adaptations in the mesopelagic species occurring there. For these reasons, I think that it is likely that *S. edwardsii* and *S. brevispinatus* are reproductively isolated and, thus, should be considered separate species.

ETYMOLOGY.—The specific name is derived from the latin *brevis* (short) plus *spinatus* (spined). It refers to the shortness of the outer distal and outer terminal spines on the Mxp3 dactylus of the new species relative to the same spines in *S. edwardsii*.

3. *Sergestes consobrinus* Milne, 1968

FIGURES 9–11, 21b

Sergestes (Sergestes) consobrinus Milne, 1968:26–33, figs. 5–9.

TYPE-LOCALITY.—Great Bear cruise 199, IKMT haul 227 (off southern California: 33°44'N, 124°53'W).

PRELIMINARY REMARKS.—Milne's (1968) description of this species is based on specimens collected from the outer sector of the California Current system. Collections from the central North Pacific examined in the present study contained individuals similar, but not identical, in morphology to *S. consobrinus* from the California Current region.

For reasons discussed below, I am not recognizing these morphologically divergent populations at the present time as separate species but rather as geographical variants, termed the "California Current" and "Central" forms, respectively. The two forms are described separately.

3a. California Current Form

FIGURES 9a–c, g, i, 10, 11, 21b

MATERIAL.—SIO, Pelagic Area Survey: 8(2♂♂, 1♀), 11(1♂, 5♀♀), 14(2♂♂). SIO, Tethys: 4(1♂). SIO, CalCOFI H6204: 60.100(4♀♀), 60.120(1♀), 60.160(4♀♀), 60.180(4♂♂, 1♀), 90.120(5♂♂), 90.160(1♂), 100.80(5♂♂, 3♀♀), 100.90(1♂, 3♀♀), 100.100(6♂♂, 12♀♀), 100.120(4♂♂), 100.120(1♂, 2♀♀), 110.160(1♂), 120.45(1♀), 120.90(1♀), 120.90(1♂, 2♀♀). SIO, CalCOFI 7008: 90.145½(9♂♂, 8♀♀), 120.45(8♂♂, 11♀♀), 120.120(12♀♀), 120.120½(3♂♂, 8♀♀).

The material listed is deposited in the SIO Zooplankton Collections.

DESCRIPTION.—Max1 palp relatively large, with one distal seta (cf. *S. brevispinatus*, Figure 5k).

Mxp3 dactylus (Figure 9g, Table 1) with single mesial spines on outer margins of subsegments 1 and 2. Outer distal spine on subsegment 1 seldom reaching beyond midpoint of subsegment 2; outer distal spine on subsegment 2 seldom reaching much beyond juncture of subsegments 3 and 4; outer distal spine on subsegment 4 very short, seldom reaching to subsegment 5. Outer terminal spine on subsegment 6 typically one-half to two-thirds as long as inner spine. Distal spines on outer margin of subsegments 1, 2, and 4 and outer terminal spine on subsegment 6 tending to be relatively shorter and inner margin spines more numerous in female.

Per3 coxa in female (Figure 9i) with long, broad PP and low, blunt AP; GC broad in ventral view and extending distally to AP.

Petasma (Figure 9a–c) with LI stout, fingerlike, strongly inflected at proximomesial margin. LI lobes both fingerlike; anterior lobe stouter and much longer than posterior lobe, armed both anteriorly and posteriorly with hooks; posterior lobe armed with single terminal hook. LC bilobed: inner lobe low, rounded, armed posteriorly with longitudinal row of large hooks; outer lobe bulbous, directed distolaterally, armed distally and posteriorly with hooks of varying size. LA bilobed: inner lobe low, rounded, covered distally with numerous minute hooks; outer lobe slender, directed

laterally, distally flexed onto anterior face, armed with large terminal hook and lateral row of six to 11 large hooks on proximoanterior margin. PV reaching to level of inflection between LC and LA. PM with three conspicuous lateral projections.

MEASUREMENTS, COUNTS, AND RATIOS

CL	\bar{x} (mm)	95% cl (mm)	R (mm)	N
♂	5.6	±0.2	3.8-6.7	60
♀	6.6	±0.2	4.4-8.1	79

Total number of spines on Mxp3 dactylus inner margin

	\bar{x}	95% cl	R	N
♂	39.8	±2.1	33-41	10
♀	41.3	±2.3	38-47	10

Length of inner/length of outer terminal spines on Mxp3 dactylus

	Md	R	N
♂	0.66	0.49-0.92	10
♀	0.55	0.48-0.72	10

Petasma ratios

	Md	R	N
LI/CL	0.103	0.089-0.119	27
LT anterior/LI	0.79	0.69-0.86	27
LT posterior/LI	0.66	0.55-0.77	27
LC outer/LI	0.69	0.57-0.87	27
LA/LI	0.56	0.48-0.52	27

DISTRIBUTION.—This geographical form of *S. consobrinus* appears to be restricted to the outer sector of the California Current region.

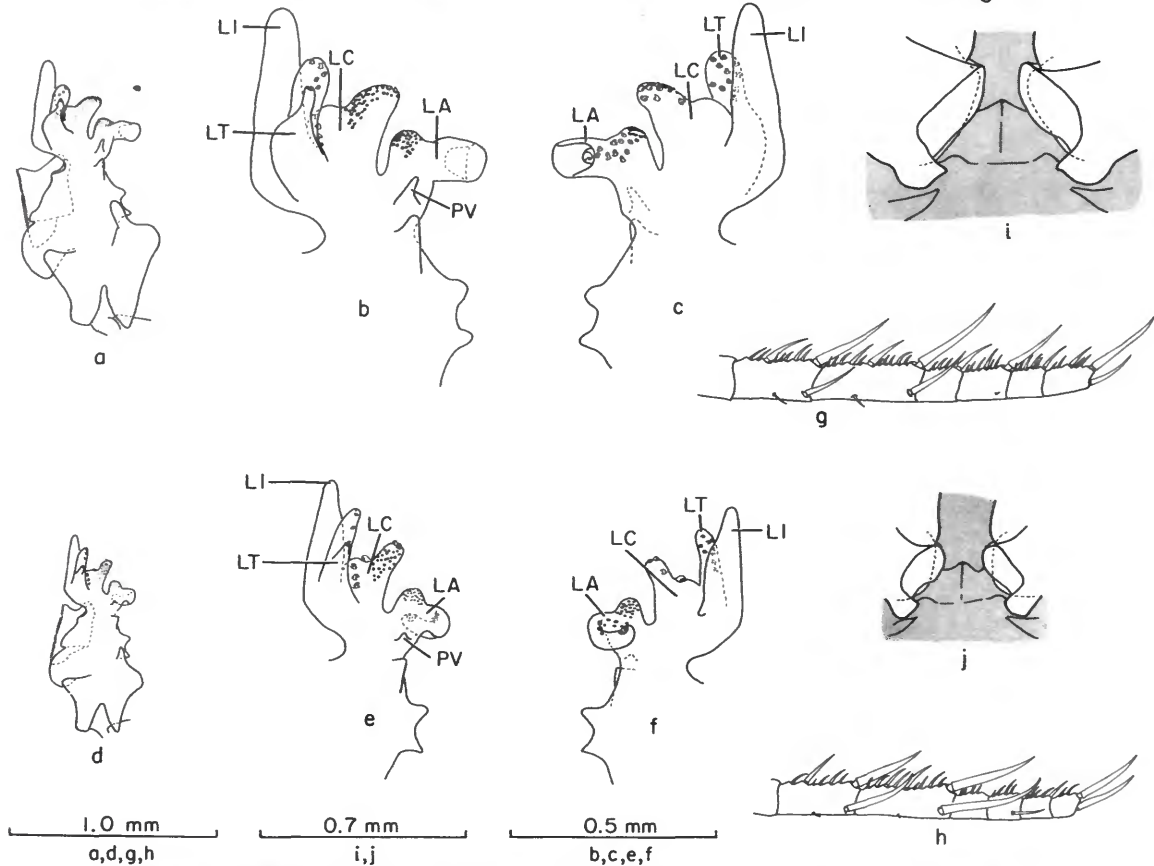


FIGURE 9.—*Sergestes consobrinus*, California Current form, ♂, 6.1 mm CL: a, left petasma, posterior; b, c, capitulum of left petasma, posterior and anterior. Central form, ♂, 4.9 mm CL: d, left petasma, posterior; e, f, capitulum of left petasma, posterior and anterior. California Current form, ♂, 6.0 mm CL: g, left Mxp3 dactylus, mesial. Central form, ♂, 4.4 mm CL: h, left Mxp3 dactylus, mesial. California Current form, ♀, 6.2 mm CL: i, thelycum, posteroventral. Central form, ♀, 4.3 mm CL: j, thelycum, posteroventral.

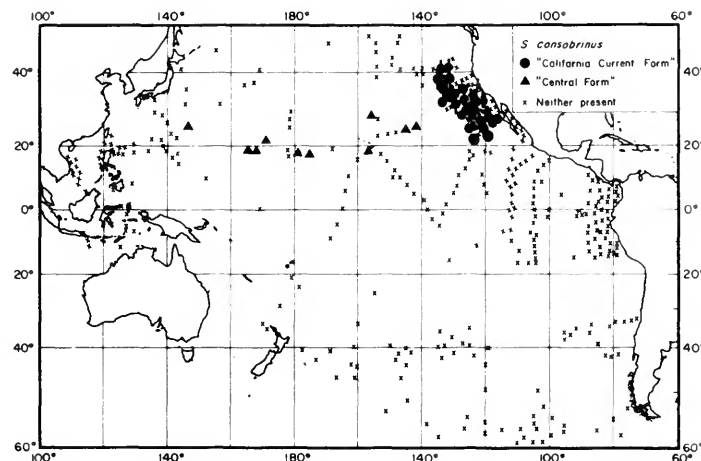


FIGURE 10.—Geographical distribution of records of the California Current and Central forms of *Sergestes consobrinus* (line through solid circle = literature record of the California Current form; see Milne, 1968).

3b. Central Form

FIGURES 9d-f, h, j, 10, 11, 21b

MATERIAL.—SIO, Tethys: 27(1 ♀), 28(1 ♂). SIO, Naga: 61-341 (1 ♂, 2 ♀). SIO, Styx VII: 68-447(2 ♀), 68-451(2 ♂), 68-468(1 ♂, 1 ♀), 68-471(1 ♂, 9 ♀), 68-478(2 ♂, 1 ♀). SIO, Climax II: A6(1 ♂, 1 ♀), A7(5 ♂, 1 ♀), A9(2 ♂, 2 ♀). SIO, FCRG 71-2: 68(1 ♂, 1 ♀).

The material listed is deposited in the SIO Zooplankton Collections.

DESCRIPTION.—Max1 palp vestigial and without setae, or sometimes entirely absent (cf. *S. edwardsii*, Figure 5j).

Mxp3 dactylus (Figure 9h) with single mesial spines on outer margins of subsegments 1 and 2. Outer distal spine on subsegment 1 usually reaching well beyond midpoint of subsegment 2; outer distal spine on subsegment 2 usually reaching to or beyond subsegment 5; outer distal spine on subsegment 4 long, usually reaching beyond midpoint of subsegment 5. Outer terminal spine on subsegment 6 at least three-fourths as long as, sometimes longer than, inner terminal spine.

Per3 coxa in female (Figure 9j) very similar to that in California Current form.

Petasma (Figure 9d-f) very similar to that in California Current form but differing in following features: all distal lobes tending to be slenderer; LA outer lobe with flexure occurring proximally

rather than distally and with only five to eight hooks on anterior face; PV a mere bud, not extending to inflection between LA and LC.

MEASUREMENTS, COUNTS, AND RATIOS

CL	\bar{x} (mm)	95% cl (mm)	R (mm)	N
♂	4.1	±0.2	3.6-4.8	15
♀	4.8	±0.3	4.2-6.7	18
Total number of spines on Mxp3 dactylus inner margin				
	\bar{x}	95% cl	R	N
♂	33.0	±3.7	27-41	10
♀	36.9	±3.1	29-41	10
Length of inner/length of outer terminal spines on Mxp3 dactylus				
	Md	R	N	
♂	1.02	0.75-1.10	10	
♀	1.01	0.77-1.30	10	
Petasma ratios				
	Md	R	N	
LI/CL	0.108	0.091-0.126	16	
LT anterior/LI	0.84	0.74-0.94	16	
LT posterior/LI	0.74	0.62-0.89	16	
LC outer/LI	0.73	0.62-0.86	16	
LA/LI	0.51	0.39-0.75	16	

DISTRIBUTION.—The Central form of *S. consobrinus* occurs widely throughout the vast expanse of the subtropical North Pacific (Figure 10). Unfor-

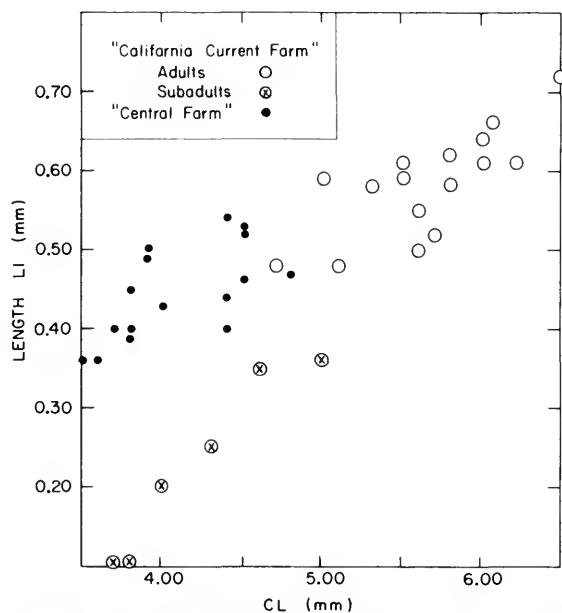


FIGURE 11.—Relationship between LI length and CL in the California Current and Central forms of *Sergestes consobrinus*.

tunately, this region of the Pacific is poorly represented by the collections examined, and, hence, the range of the Central form is imprecisely known. The area in the eastern Pacific (ca. 15°–30° N, 130°–140° W) where the two forms of *S. consobrinus* are most likely to co-occur and perhaps intergrade is especially poorly sampled.

REMARKS.—A striking difference between the California Current and Central forms of *S. consobrinus* is the conspicuously smaller size of the Central variety. Judging from development of the petasma, California Current males reach sexual maturity when they are about the size of the largest Central males (cf. Figure 11). It is noteworthy that subadult California Current individuals are quite similar to adult Central specimens in development of the Max1 palp and spination of the Mxp3 dactylus. The possibility that these differences may be caused by differing food levels in their respective environments must be given consideration.

Although the differences distinguishing the Central and California Current forms of *S. consobrinus* closely parallel those separating *S. edwardsii* and *S. brevispinatus*, I am not recognizing the two

forms as separate species, at least at the present time. I have not done so because I have not had the opportunity to examine any specimens from the northeast Pacific where the two forms are likely to co-occur and may intergrade. A definitive study based on adequate material from the region of presumed overlap may yield insight into the relative importance of heredity and environment in bringing about the observed differences between the two forms and, thus, permit taxonomic treatment more satisfactory than is now possible.

4. *Sergestes tantillus* Burkenroad, 1940

FIGURES 7, 12, 13, 21b

Sergestes tantillus Burkenroad, 1940:42.

Sergestes (Sergestes) tantillus.—Yaldwyn, 1957:8.

TYPE-LOCALITY.—Dana sta 3556 II (eastern tropical Pacific: 2°52'N, 82°38'W).

TYPES.—The holotype male, the only specimen cited by Burkenroad (1940) in his description of this species, apparently has been lost. I have deposited the following neotype in NMNH: USNM 155585, adult ♂, 6.1 mm CL, sorted from a micronekton collection taken at ETP 12 sta 252 (8°25'N, 112°07'W; 17 Mar 1967; nighttime oblique tow with BMN from ca. 200 m).

REFERENCE SPECIMENS.—I have deposited the following reference specimens in NMNH: USNM 168089: 4 adult ♂♂, 5.5, 6.0, 6.1, 6.1 mm CL, and 3 adult ♀♀, 5.8, 6.0, 6.0 mm CL; sorted from same micronekton collection as neotype.

ADDITIONAL MATERIAL.—SIO, Shellback: 13(1♂). SIO, East-tropic: 2(1♂), 4(4♂♂, 5♀♀), 5(2♂♂), 6(1♂, 1♀). SIO, Tethys: 5(1♂), 6(3♀♀), 7(34♂♂), 8(21♂♂, 1♀), 9(2♂♂, 2♀♀), 11(1♀), 17(1♀), 18(1♂, 10♀♀), 19(20♂♂, 42♀♀), 20(17♂♂, 42♀♀), 21(1♂, 4♀♀). SIO, Styx VI: 2(2♂♂), 5(34♂♂, 2♀♀), 6(3♂♂). SIO, Aries I: E(1♂), G(22♂♂). SWFC, ETP 12: 084(1♂), 106(1♂), 235(17♂♂, 1♀), 244(3♂♂), 260(16♂♂). SWFC, ETP 14: 199(6♂♂, 1♀), 206(1♂), 213(1♂), 232(5♂♂), 240(2♂♂). SOS, USARP *Eltanin* 31: 67-39(1♂).

The material listed is deposited in the SIO Zooplankton Collections.

DESCRIPTION.—Max1 palp relatively large, distally with one or two setae (cf. *S. gibbilobatus*, Figure 2g).

Mxp3 dactylus (Figure 12d, Table 1) with single mesial spines on outer margins of subsegments 1 and 2. Outer distal spine on subsegment 1 usually

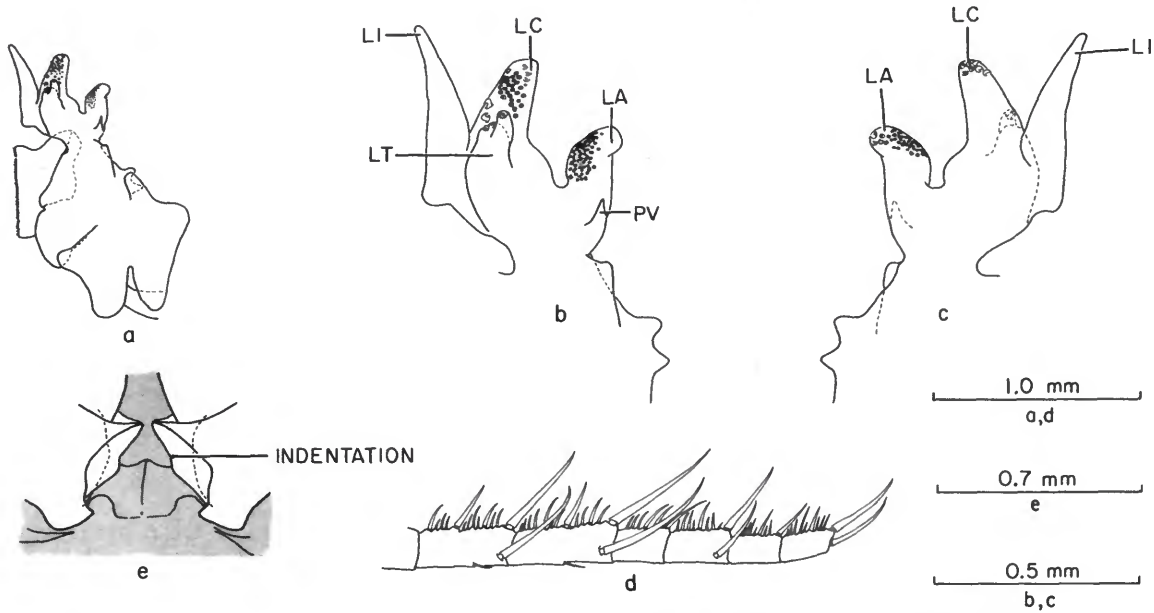


FIGURE 12.—*Sergestes tantillus*, ♂, 6.3 mm CL: a, left petasma, posterior; b, c, capitulum of left petasma, posterior and anterior. ♂, 7.1 mm CL: d, left Mxp3 dactylus, mesial. ♀, 6.1 mm CL: e, thelycum, posteroventral.

reaching to origin of outer distal spine on subsegment 2; outer distal spine on subsegment 2 usually reaching to origin of distal spine on subsegment 4; outer distal spine on subsegment 4 usually reaching beyond midpoint of subsegment 5; outer terminal spine on subsegment 6 typically subequal to

inner terminal spine. Outer distal spines on subsegments 1, 2, and 4, and outer terminal spine on subsegment 6 tending to be relatively shorter in female.

Per3 coxa in female (Figure 12e) with short PP, low, rounded AP, and distinct indentation at mid-

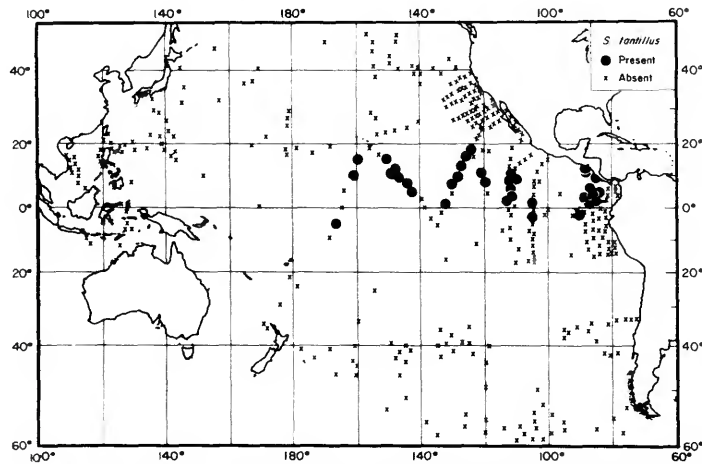


FIGURE 13.—Geographical distribution of records of *Sergestes tantillus* (line through solid circle = literature record; see Burkenroad, 1940).

point of dorsal lip of GC; GC extending distally to AP.

Petasma (Figure 12a-c) with LI distinctly tapered, mesially slightly concave, bearing slight projection immediately beyond acute proximomesial inflection. LI lobes both fingerlike; anterior lobe shorter and stouter than posterior lobe, distally armed with several small hooks; posterior lobe armed with single large terminal hook. LC single, thumblike, distally directed lobe armed with numerous hooks of varying size on posterior and distal margins. LA single, thumblike lobe directed distally with end bent laterally and somewhat anteriorly, armed with numerous minute hooks on upper surface. PV not reaching to inflection between LC and LA. PM with three conspicuous lateral projections.

MEASUREMENTS, COUNTS, AND RATIOS

CL				
	\bar{x} (mm)	95% <i>cl</i> (mm)	<i>R</i> (mm)	<i>N</i>
♂	5.5	±0.1	3.6-7.0	202
♀	6.2	±0.2	4.3-7.5	83
Total number of spines on Mxp3 dactylus inner margin				
	\bar{x}	95% <i>cl</i>	<i>R</i>	<i>N</i>
♂	55.0	±3.9	50-68	10
♀	56.2	±1.6	53-59	10
Length of inner/length of outer terminal spines on Mxp3 dactylus				
	<i>Md</i>	<i>R</i>	<i>N</i>	
♂	1.00	0.86-1.15	10	
♀	0.91	0.77-1.00	21	
Petasma ratios				
	<i>Md</i>	<i>R</i>	<i>N</i>	
LI/CL	0.091	0.067-0.111	21	
LT anterior/LI	0.69	0.57-0.111	11	
LT posterior/LI	0.79	0.63-1.06	21	
LC outer/LI	0.96	0.80-1.22	21	
LA/LI	0.43	0.35-0.56	21	

DISTRIBUTION.—*Sergestes tantillus* is indigenous to the eastern and central equatorial Pacific (Figure 13). Its range is obviously centered north of the equator, with most records falling between 0° and 20°N. It occurred most frequently in ETP collections farthest from the Central and South American land masses (Figure 7a) and, thus, appears to be more oceanic in distribution than either *S. brevispinatus* or *S. geminus*.

5. *Sergestes semissis* Burkenroad, 1940

FIGURES 14, 15, 21b

Sergestes semissis Burkenroad, 1940:42-43.*Sergestes (Sergestes) semissis*.—Yaldwyn, 1957:8.

HOLOTYPE.—Dana 3905 I, 1 ♂, 4.0 mm CL (deposited in UZM).

TYPE-LOCALITY.—Dana sta 3905 I (northwestern Indian Ocean: 4°44'N, 89°06'W); 1929.

ADDITIONAL MATERIAL.—SOSC, IIOE *Anton Bruun* 3: 1A (10 ♂♂, 15 ♀♀), 1B (4 ♂♂, 1 ♀), 2 (1 ♂), 3A (1 ♂, 1 ♀), 3B (3 ♂♂), 4B (1 ♀). SOSC, IIOE *Anton Bruun* 6: 328A (3 ♂♂, 2 ♀♀), 328B (5 ♂♂, 13 ♀♀), 329B (47 ♂♂, 26 ♀♀), 330B (2 ♂♂, 2 ♀♀), 331A (2 ♂♂, 2 ♀♀), 331B (1 ♂, 2 ♀♀), 335A (3 ♂♂, 1 ♀). SOSC, IIOE *Kristna* 26: 703 (1 ♂).

All specimens other than holotype are deposited in NMNH.

DESCRIPTION.—Max1 palp relatively large, with one or two distal setae (cf. *S. gibbilobatus*, Figure 2g).

Mxp3 dactylus (Figure 14e, Table 1) with single mesial spines on outer margins of subsegments 1 and 2. Outer distal spine on subsegment 1 usually not reaching beyond midpoint of subsegment 2; outer distal spine on subsegment 2 usually not reaching much beyond juncture of subsegment 3 and 4. In male, outer terminal spine on subsegment 6 usually subequal to inner terminal spine; in female, outer terminal spine only one-half to three-fourths as long as inner spine.

Per3 coxa in female (Figure 14g) with broad, blunt PP and low, rounded DP; GC not extending to AP.

Petasma (Figure 14a-d) with LI stout, directed distomesially, with small projection at about midpoint of mesial margin but without strong proximomesial inflection. LT situated posteriorly to LI; anterior lobe cylindrical, elongate, directed distomesially, armed distally with single, large exposed hook; posterior lobe stout, thumblike, unarmed, directed posteriorly. LC single, thumblike, laterally directed lobe armed distally with small number of minute hooks and anteriorly with lateral row of large hooks. LA bilobed; inner lobe with lower margin elongate, projecting below origin of PV, covered distally with numerous minute hooks; outer lobe flexed back onto anterior face of inner lobe, armed with large terminal hook and lateral

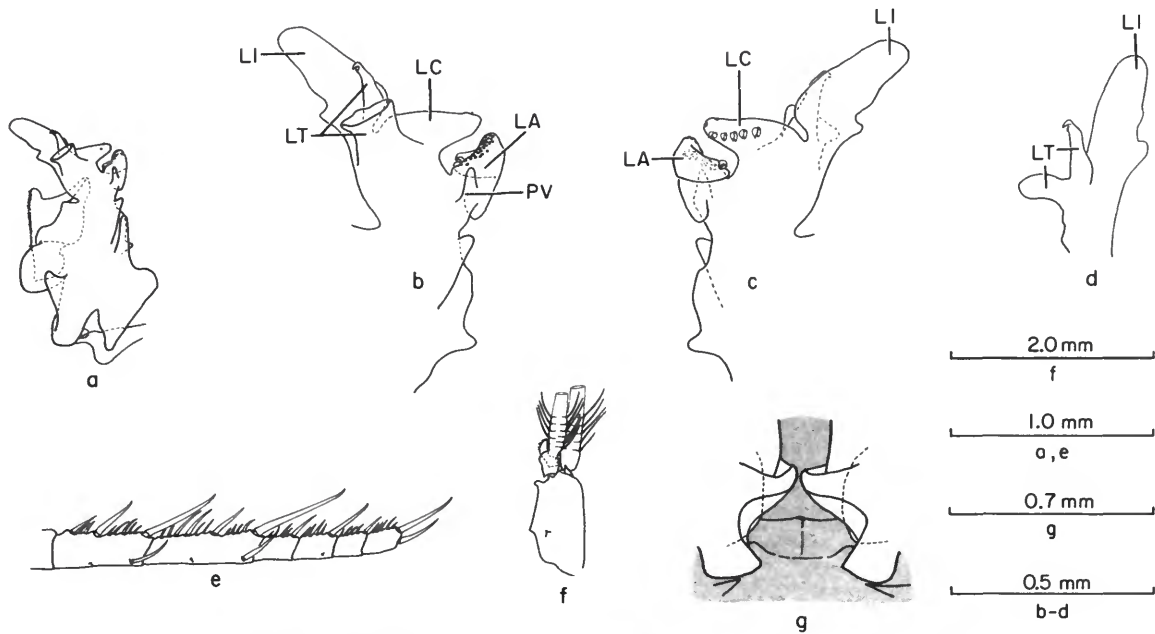


FIGURE 14.—*Sergestes semissis*, ♂, 5.5 mm CL: a, left petasma, posterior; b, c, capitulum of left petasma, posterior and anterior; d, LI and LT, lateral; e, left Mxp3 dactylus, mesial; f, ♂ left pleopod 2 (endopod and exopod incomplete), mesial. ♀, 6.3 mm CL: g, thelycum, posteroventral.

row of small hooks on proximoanterior margin. PV reaching distally to or beyond inflection between LA and LC. Middle projection on PM low, rounded.

Pleopod 2 in male (Figure 14f) with two denticles, instead of one (cf. Figure 3i,j), on midmesial margin of propodus.

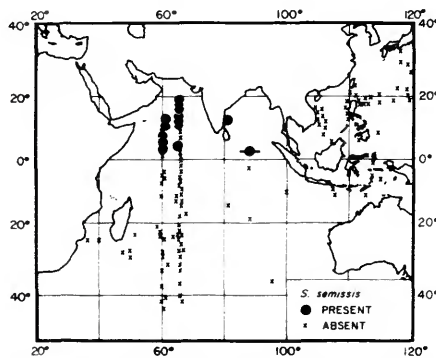


FIGURE 15.—Geographical distribution of records of *Sergestes semissis* (line through solid circle = literature record; see Burkenroad, 1940).

MEASUREMENTS, COUNTS, AND RATIOS

CL				
	\bar{x} (mm)	95% cl (mm)	R (mm)	N
♂	5.1	±0.2	3.6-6.7	84
♀	6.5	±0.3	4.4-7.9	66
Total number of spines on Mxp3 dactylus inner margin				
	\bar{x}	95% cl	R	N
♂	43.8	±3.3	36-49	10
♀	48.5	±2.8	46-57	10
Length of inner/length of outer terminal spines on Mxp3 dactylus				
	Md	R	N	
♂	1.00	0.76-1.19	15	
♀	0.74	0.44-0.95	10	
Petasma ratios				
	Md	R	N	
LI/CL	0.105	0.094-0.108	13	
LT anterior/LI	0.81	0.77-0.90	13	
LT posterior/LI	0.58	0.55-0.63	13	
LC outer/LI	0.60	0.52-0.64	13	
LA/LI	0.51	0.45-0.60	13	

DISTRIBUTION.—*Sergestes semissis* inhabits the northern Indian Ocean, the Arabian Sea, and the Bay of Bengal (Figure 15).

6. *Sergestes orientalis* Hansen, 1919

FIGURES 16a-e,k,l, 17, 18, 21a

Sergestes orientalis Hansen, 1919:22-26, pl. 2: fig. 2.
Sergestes (Sergestes) orientalis.—Yaldwyn, 1957:8.—Kensley, 1971:238, fig. 12.

TYPES.—Although Hansen did not designate type specimens in his publication, individuals from Siboga stations 148 and 230 have been labeled, perhaps by Hansen himself, as "Types" and "Cotypes," respectively. Data on these specimens, which were loaned to me by UZM and ITZ, respectively, are summarized below. I have designated the male labelled "cotype" as the lectotype.

"Types": 5 ♂♂, 4.0, 4.4, 5.1, 5.4, 5.4 mm CL; 3 ♀♀, 4.9, 5.1, 6.0 mm CL; 1 juvenile, 2.4 mm CL; from Siboga sta 148 (0°17.6'S, 129°14.5'E); 9 Aug 1899; tow with Hensen vertical net from 1000 m to the surface; deposited in ITZ.

"Cotypes": 1 ♂, 6.5 mm CL; 1 ♀, 6.5 mm CL; from Siboga sta 230 (3°58'S, 128°20'E); 14 Nov 1899; tow with Hensen vertical net from 2000 m to the surface; deposited in UZM.

ADDITIONAL MATERIAL.—SIO, Monsoon: 2(3 ♂♂, 6 ♀♀), 3(1 ♀), 4(1 ♂, 3 ♀♀), 5(2 ♂♂, 12 ♀♀), 7(1 ♂, 3 ♀♀). SIO, Fazor II: Plum-28(1 ♂), Quince-29(2 ♀♀). SIO, Styx VI: 4(4 ♂). SIO, Circe: 15(4 ♂♂), 20(2 ♂♂, 3 ♀♀), 63(1 ♂), 80(1 ♂), 96(2 ♂♂), 129(2 ♂♂). SIO, Scan: 41(2 ♂♂, 7 ♀♀), 55(5 ♂♂, 3 ♀♀). SIO, Antipode IV: 11(3 ♀♀), 12(2 ♂♂, 2 ♀♀), 13(1 ♂, 1 ♀), 14(1 ♀), 15(1 ♀), 16(1 ♂, 3 ♀♀), 17(1 ♂, 5 ♀♀), 18(2 ♂♂, 5 ♀♀), 20(2 ♂♂, 4 ♀♀), 21(2 ♂♂, 1 ♀), 22(1 ♂), 23(2 ♂♂, 1 ♀), 24(2 ♂♂, 3 ♀♀), 25(2 ♀♀), 26(2 ♂♂, 1 ♀), 27(1 ♂), 28(1 ♂). SIO, Naga: 60-215(2 ♀♀), 60-219a(2 ♂♂, 3 ♀♀), 60-226d(1 ♂), 60-244(2 ♂♂), 60-248(1 ♂), 61-060(3 ♀♀), 61-065(1 ♀), 61-208(1 ♀), 61-271(1 ♀), 61-282(1 ♀), 61-296(1 ♀), 61-299(1 ♂), 61-309(3 ♂♂, 5 ♀♀), 61-312(2 ♀♀), 61-316(3 ♀♀), 61-321(3 ♀♀), 61-323(1 ♂), 61-324(3 ♂♂, 4 ♀♀), 61-326(2 ♀♀), 61-328(1 ♀), 61-329(2 ♂♂, 5 ♀♀), 61-331(5 ♂♂, 13 ♀♀). SIO, Antipode IX: 71-71(38 ♂♂, 49 ♀♀). SOSC, HIOE *Anton Bruun* 3: 3A(147-7013(1 ♀)), 3A(147-7016(2 ♂♂)), SOSC, *Anton Bruun* 6: 338A(7220(2 ♂♂)), 339A(7228(1 ♂, 2 ♀♀)), 340A(7238(1 ♂)), 340B(7242(3 ♂♂)), 342B(7258(2 ♂♂)), 343A(7263(1 ♂)). UH, Blind Faith: 6(9 ♂♂).

Also examined were the Siboga Expedition collections (deposited in ITZ) cited by Hansen (1919) in the original description of the species. SIO and UH specimens are deposited in the SIO Zooplankton Collections. SOSC material is deposited in NMNH.

DESCRIPTION.—Max1 palp relatively large, with one or two distal setae (cf. *S. gibbilobatus*, Figure 2g).

Mxp3 dactylus (Figure 16k) usually with two, but occasionally only one, mesial spines on outer mar-

gins of subsegments 1 and 2. Outer distal spines on subsegments 1 and 2 very short, outer distal spine on subsegment 4 minute, often little more than seta. Inner terminal spine on subsegment 6 thicker and about twice as long as outer terminal spine.

Per3 coxa in female (Figure 16l) with long, broad, distally acute PP with distinct bulge on anterior margin; AP acute; GC very broad viewed ventrally, extending distally to AP.

Petasma (Figure 16a-e) with LI gently inflected at proximomesial margin, distally bearing variable number of irregular protuberances. LT with pronounced proximoposterior ledge; anterior lobe lamellar, twisted, distally armed with large exposed hook; posterior lobe cylindrical, elongate, distally armed with large recessed hook. LC usually (71% of males examined) with three, but sometimes only two, low rounded lobes armed with numerous hooks; middle lobe largest, outer and inner lobes about equal in size. LA bilobed; inner lobe low, rounded, covered distally with numerous minute hooks; outer lobe short, thumblike, directed laterally and somewhat anteriorly, armed on anterior face with numerous hooks increasing in size distally. PV reaching to or beyond inflection between LA inner and outer lobes. Middle projection on PM low, rounded.

MEASUREMENTS, COUNTS, AND RATIOS

CL	\bar{x} (mm)	95% cl (mm)	R (mm)	N
♂	6.0	±0.1	4.2-8.0	112
♀	6.6	±0.2	4.6-8.9	140

Total number of spines on Mxp3 dactylus inner margin

	\bar{x}	95% cl	R	N
♂	37.3	±1.7	33-40	10
♀	39.4	±1.2	36-42	10

Length of inner/length of outer terminal spines on Mxp3 dactylus

	Md	R	N
♂	0.54	0.37-1.00	15
♀	0.54	0.40-0.89	10

Petasma ratios

	Md	R	N
LI/CL	0.116	0.107-0.134	52
LT anterior/LI	0.85	0.77-0.98	51
LT posterior/LI	0.67	0.51-0.76	51
LC outer/LI	0.44	0.37-0.53	51
LA/LI	0.33	0.21-0.45	51

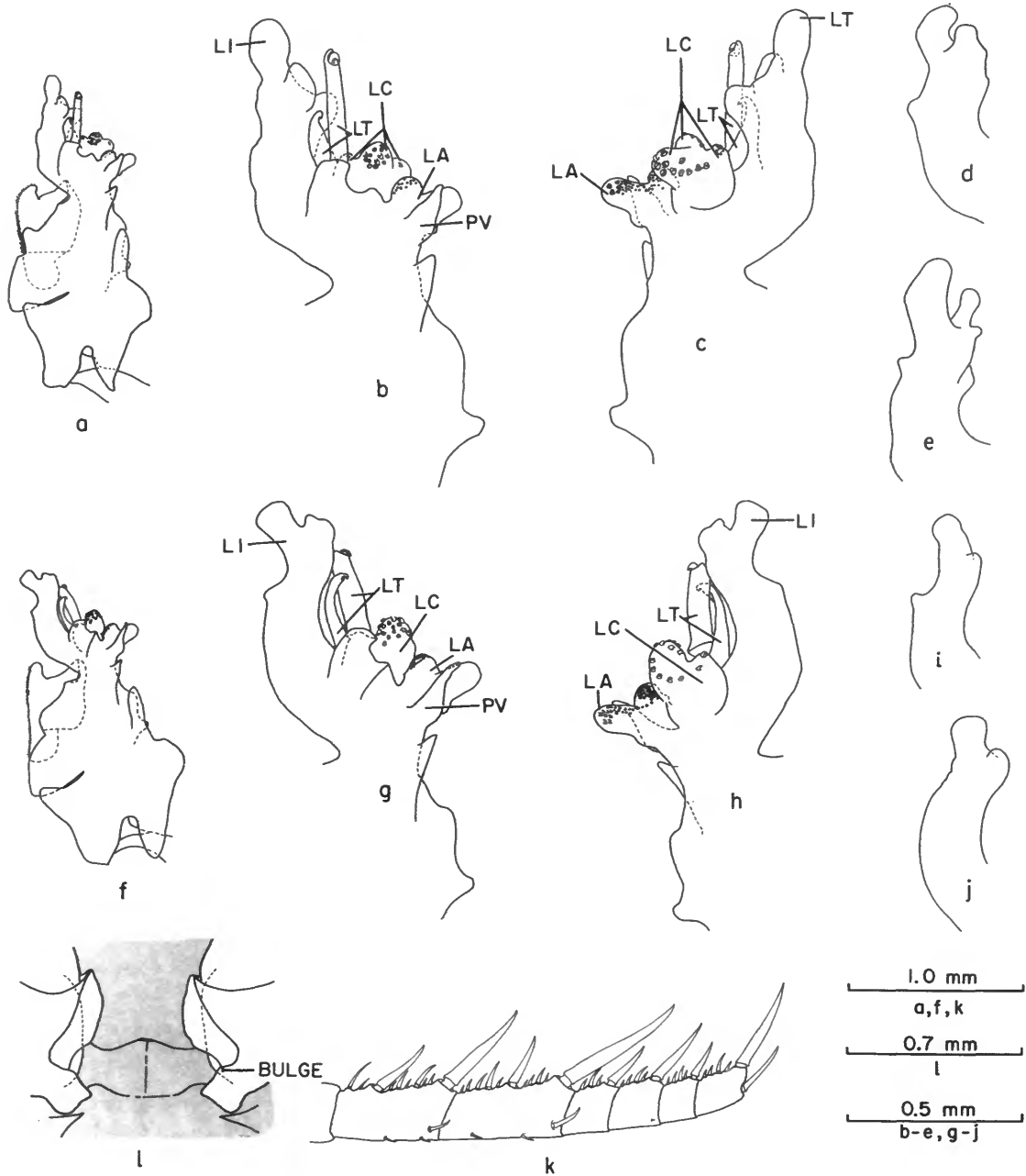


FIGURE 16.—*Sergestes orientalis*, ♂, 7.4 mm CL: a, left petasma, posterior; b, c, capitulum of left petasma, posterior and anterior. *S. orientalis*, ♂, 7.1 mm CL: d, distal LI, posterior. *S. orientalis*, ♂, 6.5 mm CL: e, distal LI, posterior. *S. geminus*, ♂, 7.7 mm CL: f, left petasma, posterior; g, h, capitulum left petasma, posterior and anterior. *S. geminus*, ♂, 7.1 mm CL: i, distal LI, posterior. *S. geminus*, ♂, 6.9 mm CL: j, distal LI, posterior. *S. orientalis*, ♂, 7.1 mm CL: k, left Mxp3 dactylus, mesial. *S. orientalis*, ♀, 7.9 mm CL: l, thelycum, posterior.

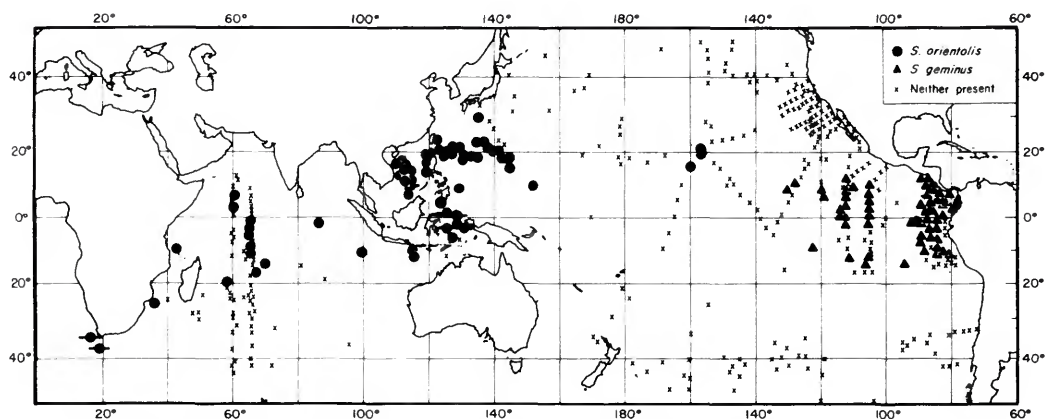
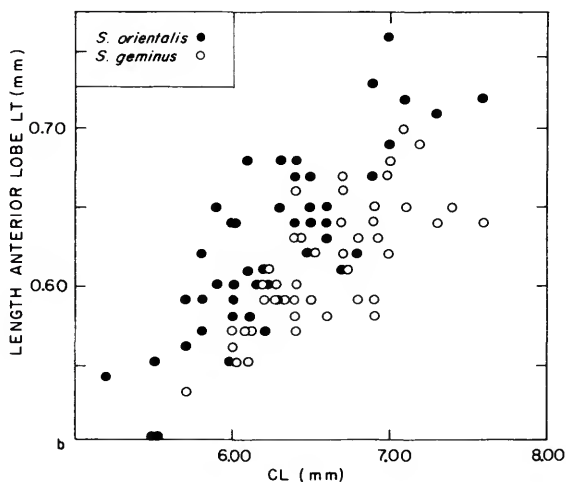
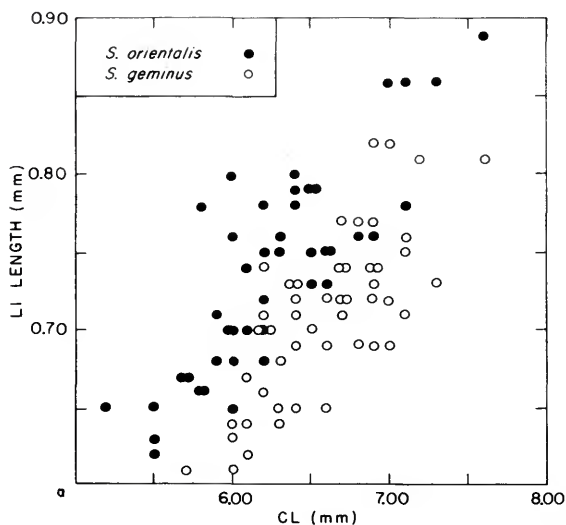


FIGURE 17.—Geographical distribution of records of *Sergestes orientalis* and *S. geminus* (line through solid circle = literature record of *S. orientalis*; see Hansen, 1919, Kensley, 1971).



DISTRIBUTION.—*Sergestes orientalis* occurs throughout the tropical Indian Ocean, the Indo-Australian Archipelago, and the western tropical Pacific (Figure 17). The few specimens reported by Kensley (1971) off southern Africa are probably “waifs” advected into the region by the Agulhas Current. A possibly isolated population of *S. orientalis* occurs in the vicinity of the Hawaiian Islands.

REMARKS.—Examination of taxonomically useful features revealed no evidence of geographic variation in *S. orientalis*. Samples from the Indian Ocean, Indo-West Pacific, and Hawaiian Islands were found by analysis of covariance not to differ significantly ($p > 0.20$) in length of the LI or LT anterior lobe relative to CL. However, additional specimens from the vicinity of the Hawaiian Islands will have to be examined before a final determination of that population's relationships can be made.

7. *Sergestes geminus*, new species

FIGURES 2a-c, 7, 16f-j, 17, 18, 21a

HOLOTYPE.—USNM 155060, adult ♂, 7.1 mm CL.

FIGURE 18.—*Sergestes orientalis* and *S. geminus* compared for certain relationships: a, LI length and CL; b, LT anterior lobe length and CL.

TYPE-LOCALITY.—Sorted from micronekton collection taken at ETP 14 sta 326 (4°48'N, 83°38'W); 1 Apr 1967; nighttime oblique tow with BMN from ca. 200 m depth.

ALLOTYPE.—USNM 155061, adult ♀, 8.9 mm CL; sorted from micronekton collection taken at ETP 14 sta 037 (0°46'N, 80°42'W); 8 Feb 1967; nighttime oblique tow with BMN from ca. 200 m depth.

PARATYPES.—USNM 155063, 1 adult ♂, 7.1 mm CL; sorted from micronekton collection taken at ETP 14 sta 138 (7°55'S, 88°46'W); 2 Mar 1967; nighttime oblique tow with BMN from ca. 200 m depth. USNM 155062, 4 adult and subadult ♂♂, 6.2, 6.4, 7.0, 7.3 mm CL, and 5 adult and subadult ♀♀, 6.8, 8.5, 8.7, 9.3, 9.4 mm CL; from same collection as allotype.

ADDITIONAL MATERIAL.—SIO, Shellback: 2(1 ♂), 6(2 ♂♂, 2 ♀♀), 10(1 ♂, 3 ♀♀), 11(1 ♂, 3 ♀♀), 13(1 ♀). SIO, Eastropic: 3(3 ♀♀), 4(6 ♂♂, 5 ♀♀), 5(4 ♂♂, 8 ♀♀), 6(2 ♂♂, 3 ♀♀), 8(1 ♂, 1 ♀), 9(15 ♂♂, 18 ♀♀), 11(17 ♂♂, 1 ♀), 12(1 ♂), 13(2 ♂♂, 6 ♀♀), 14(2 ♂♂, 4 ♀♀), 15(5 ♀♀). SIO, Tethys: 8(2 ♂♂, 6 ♀♀), 9(4 ♀♀). SIO, Anton Bruun 12: 65-606(1 ♂). SIO, Piquero: 29(1 ♂), 32(1 ♀), 43(2 ♂♂), 8-2(1 ♂). SIO, Quebrada: 16(2 ♂♂), 21(10 ♂♂). SIO, Aries I: E(1 ♂), 2(1 ♂), 3(2 ♂♂). SWFC, ETP 12: 059 (9 ♂♂, 4 ♀♀), 067(5 ♂♂, 4 ♀♀), 075(1 ♀), 084(4 ♂♂, 14 ♀♀), 094(2 ♂♂, 3 ♀♀), 106(4 ♂♂), 142(1 ♂), 212(1 ♂), 224(1 ♀), 235(4 ♂♂, 4 ♀♀), 244(1 ♂, 1 ♀), 252(22 ♂♂), 260(3 ♀♀). SWFC, ETP 14: 001(2 ♀♀), 014(1 ♂), 018(11 ♂♂, 1 ♀), 022(14 ♂♂), 027(2 ♂♂), 031(3 ♂♂, 1 ♀), 037(6 ♂♂, 17 ♀♀), 043(7 ♂♂), 081(1 ♂), 132(3 ♂♂), 138(4 ♂♂, 1 ♀), 154(2 ♂♂, 1 ♀), 199(2 ♂♂, 2 ♀♀), 206(1 ♂, 1 ♀), 213(4 ♂♂, 3 ♀♀), 232(11 ♂♂, 1 ♀), 240(9 ♂♂, 3 ♀♀), 255(1 ♂), 263 (17 ♂♂), 280(1 ♂), 287(6 ♂♂, 1 ♀), 303(2 ♂♂), 310(3 ♂♂, 3 ♀♀), 326(4 ♂♂).

The material listed is deposited in the SIO Zooplankton Collections.

DESCRIPTION.—Max1 palp, Mxp3 dactylus, and thelycum as in *S. orientalis* (cf. Figure 16*k,l*)

Petasma (Figure 16*f-g*) very similar to that in *S. orientalis* but differing in following features: LC usually bilobed (59% of males examined), third lateral lobe, when present, tending to be smaller than either inner lobe; LI and LT anterior lobe tending to be shorter relative to CL (Figure 18*a,b*).

MEASUREMENTS, COUNTS, AND RATIOS

CL	\bar{x} (mm)	95% <i>cl</i> (mm)	R (mm)	N
♂	6.4	±0.1	5.0-7.7	239
♀	7.4	±0.2	4.9-9.8	147

Total number of spines on Mxp3 dactylus inner margin

	\bar{x}	95% <i>cl</i>	R	N
♂	38.5	±2.3	33-45	10
♀	38.1	±1.8	35-42	10

Length of inner/length of outer terminal spines on Mxp3 dactylus

	<i>Md</i>	R	N
♂	0.50	0.38-0.72	15
♀	0.45	0.40-0.59	15

Petasma ratios

	<i>Md</i>	R	N
LI/CL	0.108	0.96-0.119	46
LT anterior/LI	0.86	0.79-0.97	46
LT posterior/LI	0.68	0.58-0.78	46
LC outer/LI	0.43	0.33-0.51	46
LA/LI	0.33	0.23-0.44	46

DISTRIBUTION.—Like *S. brevispinatus*, *S. geminus* is clearly indigenous to the eastern tropical Pacific (Figure 17), differing in distribution from the former species primarily by its greater abundance in the western part of that region (Figure 7*a,b*).

REMARKS.—Because of their close similarity in all features, it is difficult to defend my separation of *S. geminus* from *S. orientalis* on strictly morphological grounds. However, *S. geminus* and the main population of *S. orientalis* appear to be separated by a large expanse of water in the central Pacific (a hiatus occupied by *S. gibbilobatus* and *S. tantillus*), and, thus, it does not seem likely that there is gene flow between them. The Hawaiian population of *S. orientalis* also appears to be isolated from *S. geminus*. Moreover, morphometric differences in the petasmata of the two forms, although apparently minor, do indicate that they clearly have diverged genetically. Furthermore, there are numerous examples in other pelagic taxa of closely related yet distinct species having disjunct distributions in the eastern and western equatorial Pacific (cf. Fleminger and Hulsemann, 1973). Because of these parallel examples in other taxa, as well as the morphological evidence of genetic divergence, I prefer to recognize *S. geminus* as a species distinct from *S. orientalis*.

ETYMOLOGY.—The name *geminus* ("twin" in Latin) connotes the obvious similarities existing between the new species and *S. orientalis*.

8. *Sergestes gibbilobatus*, new species

FIGURES 2g, 4c, 7, 19a-h, 20, 21a

HOLOTYPE.—USNM 155064, adult ♂, 5.6 mm CL.

TYPE-LOCALITY.—Sorted from micronekton collection taken at Styx VI sta 3 (0°0'S, 165°42'W); 11–12 Sep 1968; nighttime oblique tow with IKMT, 2550 m maximum warp out.

ALLOTYPE.—USNM 155065, adult ♀, 8.0 mm CL; from same collection as holotype.

PARATYPES.—USNM 155066, 5 adult ♂♂, 5.7, 5.8, 5.9, 6.1, 6.1 mm CL, and 5 adult ♀♀, 6.2, 6.3, 6.3, 7.2, 7.5 mm CL; from same collection as holotype and allotype.

ADDITIONAL MATERIAL.—SIO, Capricorn: 41(2♂♂, 6♀♀). SIO, Tethys: 11(1♂, 2♀♀), 12(1♂), 14(1♂, 1♀), 15(1♂), 16(1♂, 1♀), 17(4♀♀). SIO, Piquero: 29(18♂♂, 2♀♀), 39(2♂♂, 6♀♀), 43(1♂), 49(3♂♂, 2♀♀). SIO, Styx VI: 2(2♂♂), 3(15♂♂, 24♀♀), 4(2♂♂, 2♀♀). SWFC, ETP 12: 126(2♂♂), 134(4♂♂), 142(6♂♂), 192(4♀♀). SWFC, ETP 14: 124(1♂), 128(1♀), 132(4♂♂), 280(1♂).

The material listed is deposited in the SIO Zooplankton Collections.

DESCRIPTION.—Max1 palp (Figure 2g) relatively large, with one or two distal setae.

Mxp3 dactylus (Figure 19g) similar in spination to that in *S. orientalis* and *S. geminus* but tending to have more spines on inner margin.

Per3 coxa in female (Figure 19h) similar to that

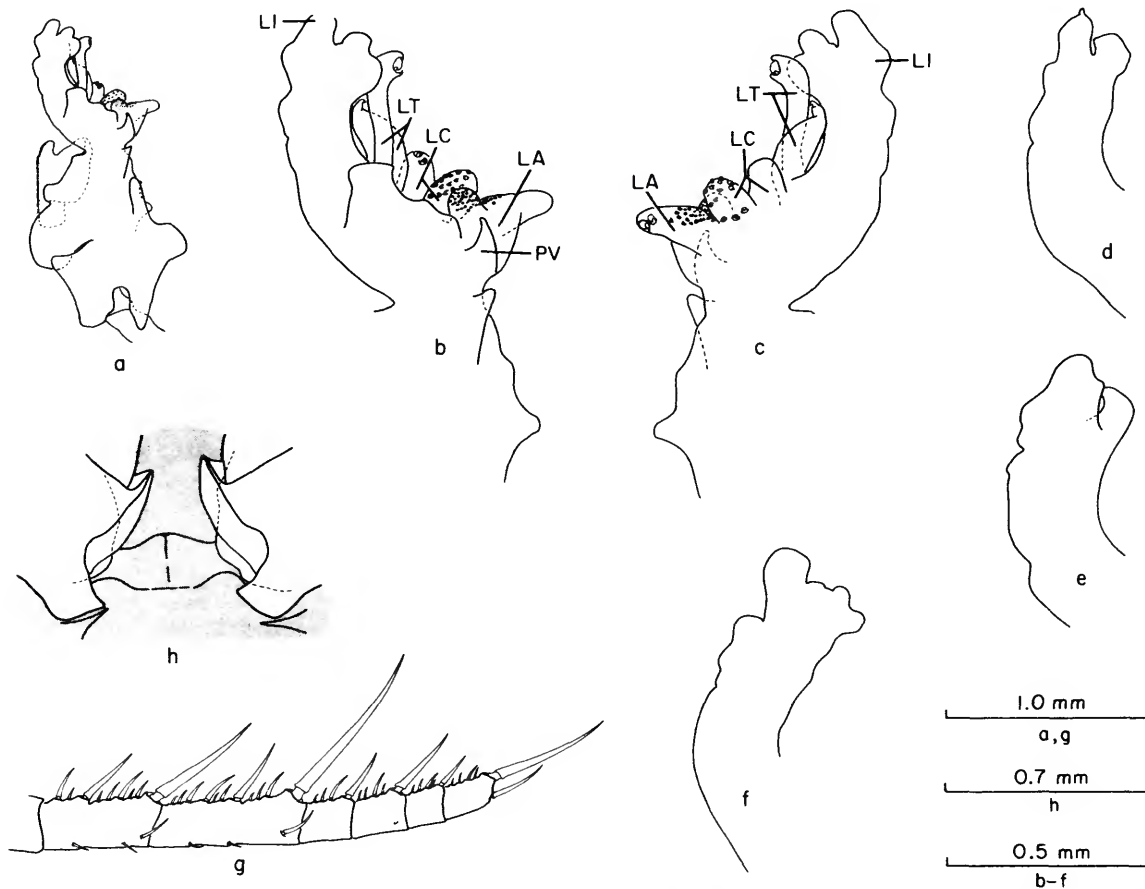


FIGURE 19.—*Sergestes gibbilobatus*, ♂, 6.9 mm CL: a, left petasma, posterior; b, c, capitulum of left petasma, posterior and anterior. ♂, 6.6 mm CL: d, distal LI, posterior. ♂, 7.5 mm CL: e, distal LI, posterior. ♂, 7.4 mm CL: f, distal LI, posterior. ♂, 6.9 mm CL: g, left Mxp3 dactylus, mesial. ♀, 7.8 mm CL: h, thelycum, posteroventral.

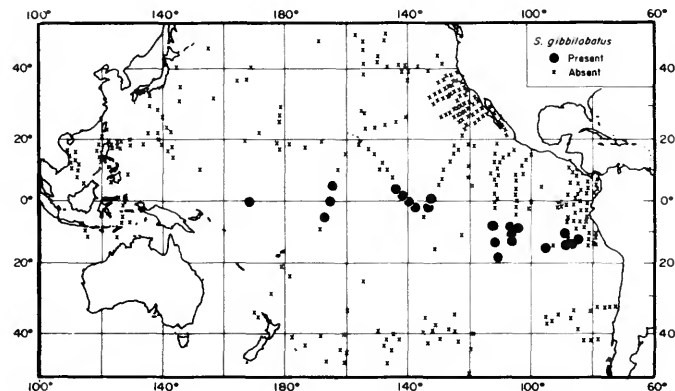


FIGURE 20.—Geographical distribution of records of *Sergestes gibbilobatus*.

in *S. orientalis* and *S. geminus* but lacking distinct bulge on anterior margin of PP and having somewhat narrower GC.

Petasma (Figure 19a-f) similar to that in *S. orientalis* and *S. geminus* but differing in following features: LT posterior lobe with laterally directed flexure at distal end; LC bilobed, never trilobed, inner lobe longer than outer lobe; PV seldom reaching to inflection between LA inner and outer lobes.

MEASUREMENTS, COUNTS, AND RATIOS

CL

	\bar{x} (mm)	95% cl (mm)	R (mm)	N
♂	6.1	±0.2	4.9-7.4	62
♀	6.6	±0.2	5.0-8.1	57

Total number of spines on Mxp3 dactylus inner margin

	\bar{x}	95% cl	R	N
♂	42.5	±2.0	39-48	10
♀	44.3	±2.7	40-48	10

Length of inner/length of outer terminal spines on Mxp3 dactylus

	Md	R	N
♂	0.56	0.43-0.80	15
♀	0.50	0.40-0.71	13

Petasma ratios

	Md	R	N
LI/CL	0.120	0.093-0.139	20
LT anterior/LI	0.86	0.78-0.98	20
LT posterior/LI	0.72	0.64-0.88	20
LC outer/LI	0.44	0.38-0.52	20
LA/LI	0.30	0.25-0.38	20

DISTRIBUTION.—*Sergestes gibbilobatus* inhabits the equatorial Pacific between approximately 80°W

and 170°E (Figure 20). In the western part of its range, *S. gibbilobatus* occurs in the immediate vicinity of the equator, but to the east it appears to be absent from equatorial waters, occurring no farther north than 8°S in material examined. A factor which may contribute to the apparent exclusion of *S. gibbilobatus* from the more equatorial portions of the eastern tropical Pacific are the persistently low oxygen tensions characterizing those regions (Knauss, 1963).

REMARKS.—The similarity of *S. gibbilobatus* to *S. geminus* and *S. orientalis* is obvious, the former differing from the latter two species in only a few features of the petasma and female genital coxa. I found no evidence, however, of intergradation between *S. gibbilobatus* and *S. geminus* in sectors of the eastern tropical Pacific where the two species overlap, and, hence, I have no doubts that *S. gibbilobatus* is a separate species.

ETYMOLOGY.—The specific name, from the Latin *gibbus* (bent) plus *lobatus* (lobed), refers to the distal flexure of the LT anterior lobe in the new species.

Phylogenetic Relationships

Morphological separation of species of the *edwardsii* group is concentrated in the male copulatory apparatus, the petasma. Species differ to a much lesser degree in development of the palp on the first maxilla, in spination of the third maxilliped, in shape of the female genital coxa, and in carapace length. My discrimination of relationships within the group is based in part on conventional

TABLE 2.—Character states in the *edwardsii* group (species are listed in parentheses after the character states they exhibit: E = *S. edwardsii*; B = *S. brevispinatus*; CL = *S. consobrinus*, California Current Form; C2 = *S. consobrinus*, Central Form; T = *S. tantillus*; S = *S. semissis*; O = *S. orientalis*; Ge = *S. geminus*; Gi = *S. gibbilobatus*)

Character	Character States
1. Palp on Max1	a. Prominent, bearing one or two setae (B,Cl,T,S,O,Ge,Gi) b. Reduced, lacking setae (E,C2)
2. LI distal protuberances	a. Present (O, Ge,Gi) b. Absent (E,B,Cl,C2,T,S)
3. LI proximomesial margin	a. Strong inflection at juncture with PM (E,B,Cl,C2,T,O,Ge,Gi) b. Nearly straight (S)
4. LT posterior lobe	a. Tapered, fingerlike (E,B,Cl,C2,T) b. Cylindrical, distal end bent laterally (Gi) c. Cylindrical, distal end not bent (O,Ge) d. Thumblike, directed posteriorly (S)
5. LT anterior lobe	a. Tapered, fingerlike (E,B,Cl,C2,T) b. Twisted, lamellar (S,O,Ge,Gi)
6. LC	a. Single lobed (T,S) b. Always, or usually, bilobed (E,B,Cl,C2,Ge,Gi) c. Usually trilobed (O)
7. Lobe(s) of LC	a. Low, rounded (O,Ge,Gi) b. Projecting, fingerlike (E,B,Cl,C2,T,S)
8. LA	a. Single lobed (T) b. Bilobed, inner lobe projecting distally (E,B,Cl,C2,O,Ge,Gi) c. Bilobed, inner lobe projecting laterally (S)
9. LA outer lobe	a. Distal end straight, or slightly recurved (E,B,T,O,Ge,Gi) b. Distal end strongly flexed anteriorly (Cl,C2,S)
10. PV	a. Projects to or beyond depression between lobes of LA (Gi) b. Does not project beyond any part of distal margin of LA (E,B,Cl,C2,T,S,O,Ge)
11. PM mesial projection	a. Projects beyond adjacent projections (E,B,Cl,C2,T) b. Does not project beyond adjacent projections (S,O,Ge,Gi)
12. LI length/CL	a. < 0.100 (T) b. 0.100 - 0.120 (B,Cl,C2,S,O,Ge,Gi) c. > 0.120 (E)
13. LT anterior lobe length/LI	a. < 0.70 (E,B,T) b. > 0.70 (Cl,C2,S,O,Ge,Gi)
14. LT posterior lobe length/LI	a. < 0.60 (E,S) b. 0.61 - 0.70 (Cl,O,Ge) c. ≥ 0.71 (B,C2,T,Gi)
15. LC outer lobe length/LI	a. < 0.50 (O,Ge,Gi) b. 0.51 - 0.75 (E,B,Cl,C2,S) c. > 0.75 (T)
16. LA length/LI	a. < 0.35 (O,Ge,Gi) b. > 0.35 (E,B,Cl,C2,T,S)
17. GC of female genital coxa	a. Extends to AP (S) b. Does not extend to AP (E,B,Cl,C2,T,O,Ge,Gi)
18. GC of female genital coxa	a. Dorsal margin with distinct indentation (T) b. Dorsal margin without indentation (E,B,Cl,C2,S,O,Ge,Gi)
19. PP of female genital coxa	a. Anterior margin with bulge (O,Ge) b. Anterior margin lacks bulge (E,B,Cl,C2,T,S,Gi)
20. Outer distal spine on subsegment 1 of Mxp3 dactylus	a. < ½ length subsegment 2 (O,Ge,Gi) b. ≥ ½ length subsegment 2 (E,B,Cl,C2,T,S)
21. Outer distal spine on subsegment 2 of Mxp3 dactylus	a. < length subsegment 3 (O,Ge,Gi) b. ≥ length subsegment 3 (E,B,Cl,C2,T,S)
22. Outer mesial spines on subsegments 1 and 2 of Mxp3 dactylus	a. 1 (E,B,Cl,C2,T,S) b. 2 (O,Ge,Gi)
23. Outer distal spine on subsegment 4 of Mxp3 dactylus	a. Prominent (E,C2,T) b. Very short (B,Cl,S,O,Ge,Gi)
24. Ratio outer : inner terminal spines of Mxp3 dactylus in male	a. < 0.60 (O,Ge,Gi) b. 0.61 - 0.80 (B,Cl) c. > 0.80 (E,C2,T,S)
25. Ratio outer : inner terminal spines of Mxp3 dactylus in female	a. < 0.60 (Cl,O,Ge,Gi) b. 0.61 - 0.80 (B,S) c. > 0.80 (E,C2,T)
26. Number spines on inner margin of Mxp3 dactylus in male	a. < 50 (E,B,Cl,C2,S,O,Ge,Gi) b. > 50 (T)
27. Number spines on inner margin of Mxp3 dactylus in female	a. < 50 (E,B,Cl,C2,S,O,Ge,Gi) b. > 50 (T)
28. Protopodite of 2nd pleopod in male	a. 1 mesial projection (E,B,Cl,C2,T,O,Ge,Gi) b. 2 mesial projections (S)
29. Mean CL (mm) in male	a. 4.0 - 4.5 (C2) b. 4.6 - 5.4 (E,B,S) c. 5.5 - 5.9 (Cl,T) d. 6.0 - 6.4 (O,Ge,Gi)
30. Mean CL (mm) in female	a. 4.5 - 5.0 (C2) b. 5.1 - 6.0 (E) c. 6.0 - 7.0 (B,Cl,T,S,O,Ge) d. 7.1 - 7.5 (Ge)

considerations of petasma morphology and in part on 30 equally weighted characters drawn from all aforementioned features. These characters and their expression ("character state") in different species of the group are listed in Table 2.

To assess phenetic similarities within the *edwardsii* group, I used the 30 characters in calculations of an index of affinity between all possible pairs of geographic populations. The two forms of *S. consobrinus* are considered separately in this analysis. In its present usage, the index of affinity is defined as $\frac{J}{C} - \frac{1}{2\sqrt{C}}$, where C is the number of characters examined in the analysis and J is the number of character states which are identical in the pair of populations being compared. Values of the index greater than 0.5 have been found empirically to provide objective groupings of species (Fager, 1969; Fleminger and Hulsemann, 1974).

Examination of the index of affinity matrix (Table 3) reveals two mutually exclusive assemblages of species. Within either assemblage all values of the index exceed 0.5. One assemblage comprises *S. edwardsii*, *S. brevispinatus*, and *S. consobrinus*; the other comprises *S. orientalis*, *S. geminus*, and *S. gibbilobatus*. Both of these assemblages (or "lineages") are easily recognizable through subjective evaluation of diagnostic characters, particularly the petasma.

Although *S. tantillus* did not show high numerical affinities with every member of the *S. edwardsii* assemblage (Table 3), obvious similarities in petasma structure strongly suggest that it is a member of that lineage, although apparently a diver-

gent one. *S. semissis* does not show particularly high affinities with either of the two major lineages, and judging from certain unique features in its petasma, male second pleopod, and female genital coxa, it seems likely that this species represents a third, independent lineage within the *edwardsii* group.

On the basis of similarities in petasma morphology, *S. edwardsii* and *S. brevispinatus*, on the one hand, and the two geographical forms of *S. consobrinus*, on the other hand, would appear to comprise distinct, although closely related, pairs of populations within their lineage. In the numerical analysis (Table 3), these similarities are to a large extent obscured by the inclusion of other, less complex features. Within the other major lineage, comparison of petasma structure reveals that *S. orientalis* and *S. geminus* comprise a sibling pair distinct from *S. gibbilobatus*.

Although morphological separation of geographical populations within the *edwardsii* group is concentrated in the petasma, similarities in this structure should not be used as absolute indicators of genealogical (i.e., "cladistic") relationships. It is likely that interspecific differences in the petasma serve to reproductively isolate closely related, sympatric forms. There is growing evidence that selection against the wastage of gametes in hybrid mating between related but genetically divergent species builds pre-mating isolating mechanisms (Dobzhansky, 1970:376-382). Thus, it is significant that closely related *edwardsii* species that overlap in distribution, however slightly, (e.g., *S. geminus* - *S. gibbilobatus*) tend to be much more divergent in petasma structure than closely related pairs which appear to be allopatric (e.g., *S. geminus* - *S. orientalis* and *S. edwardsii* - *S. brevispinatus*). On the basis of available data, the Central and California Current forms of *S. consobrinus* appear to be contiguous in distribution, and, hence, appear not to conform to the morphological-distributional pattern observed between other closely related members of the group. However, final judgment on this must await examination of material from the zone of potential overlap between the two forms.

To summarize, the *edwardsii* species group, although of monophyletic origin, appears to have diverged early in its history into two, or possibly three, separate lineages. Judging from interspecific differences in petasma structure, more than one epi-

TABLE 3.—Morphological similarity of species of the *edwardsii* group, as estimated by the index of affinity (values ≥ 0.50 underlined)

Species	Species									
	<i>S. gibbilobatus</i>	<i>S. geminus</i>	<i>S. orientalis</i>	<i>S. semissis</i>	<i>S. tantillus</i>	<i>S. consobrinus</i> , Central Form	<i>S. consobrinus</i> , California Current Form	<i>S. brevispinatus</i>		
<i>S. edwardsii</i>	0.24	0.24	0.21	0.44	0.58	0.71	0.58	0.68		
<i>S. brevispinatus</i>	0.41	0.34	0.34	0.48	0.54	0.64	0.74	0.68		
<i>S. consobrinus</i> , California Current Form	0.41	0.41	0.44	0.51	0.47	0.68	0.74	0.68		
<i>S. consobrinus</i> , Central Form	0.28	0.28	0.24	0.48	0.54					
<i>S. tantillus</i>	0.18	0.14	0.14	0.31						
<i>S. semissis</i>	0.28	0.28	0.31							
<i>S. orientalis</i>	0.83	0.90								
<i>S. geminus</i>	0.74									

sode of speciation has occurred in the two major lineages. Separation of the morphologically most similar pairs of species within the group (i.e., *S. edwardsii*–*S. brevispinatus* and *S. orientalis*–*S. geminus*) would appear to be the result of the most recent episode(s). This interpretation is, of course, tentative, and the actual genealogical sequence of speciation may be obscured by character divergence (Mayr, 1970:51–53) resulting from selection against the wastage of gametes during hybridization.

Comments on Distribution

Although the *edwardsii* species group is represented throughout all tropical and in certain sub-

tropical regions of the world ocean, individual species have rather restricted ranges (Figure 21a,b): *S. edwardsii* is indigenous to the tropical Atlantic; *S. orientalis* and *S. semissis* inhabit contiguous sectors of the tropical Indo-West-Pacific region; *S. brevispinatus*, *S. tantillus*, *S. geminus*, and *S. gibbilobatus* occupy adjacent regions in the eastern and central tropical Pacific; the larger form of *S. consobrinus* inhabits the outer portion of the California Current region whereas the smaller form appears to occur throughout most of the central North Pacific.

On the basis of collections examined in this study, the vertical distribution of the *edwardsii* group cannot be described in any detail. However, recently acquired, but incompletely analyzed, data

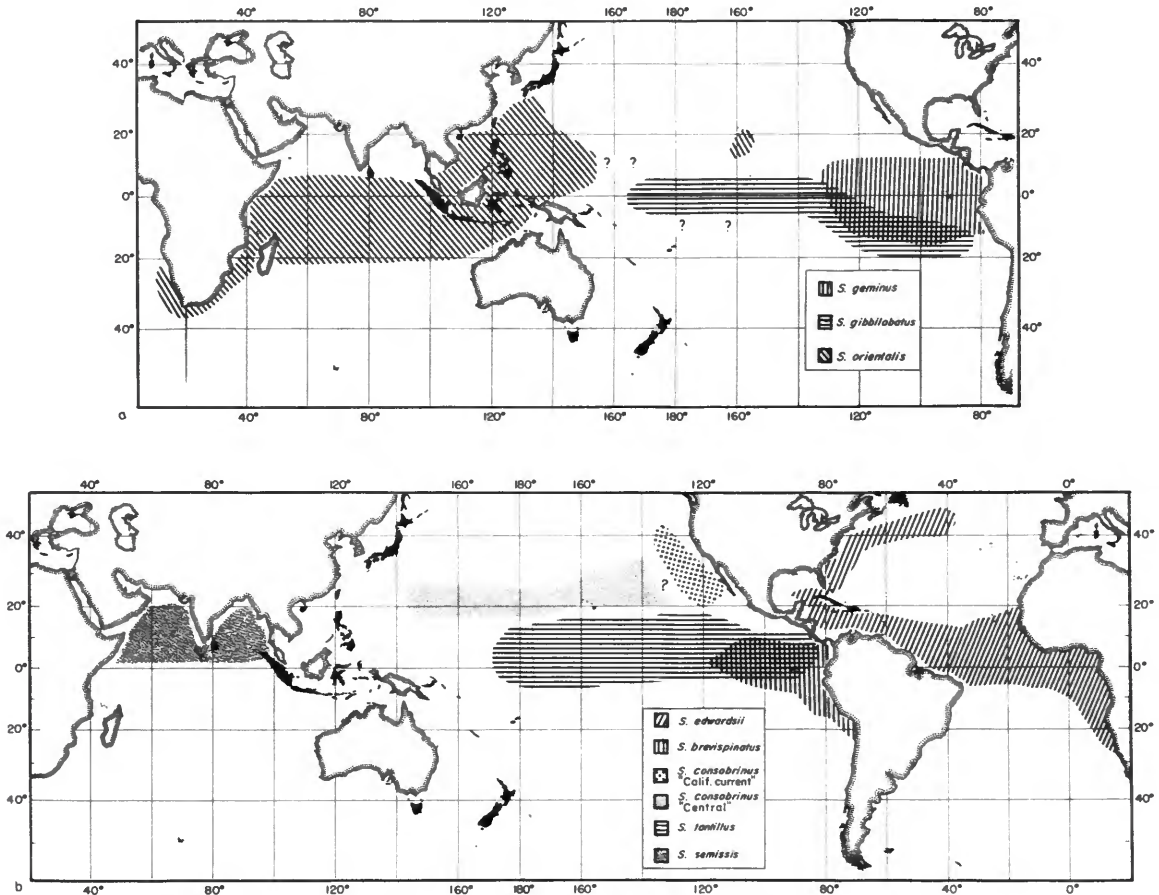


FIGURE 21.—Probable distributions of related species of the two major lineages within the *Sergestes edwardsii* group: a, *S. orientalis*, *S. geminus*, and *S. gibbilobatus*; b, *S. edwardsii*, *S. brevispinatus*, *S. consobrinus*, *S. tantillus*, also *S. semissis*, a divergent species within the *edwardsii* group.

from the Atlantic indicates that *S. edwardsii* concentrates within the upper 125 m at night but reveals little about its daytime range (Judkins, unpubl.). Similar epipelagic habits are suggested for *S. orientalis*, *S. brevispinatus*, and *S. geminus* by their frequent occurrence in extensive series of shallow (<200 m) nighttime tows made within their respective ranges. Furthermore, published records (Hansen, 1919, 1922; Sund, 1920; Gurney and Lebour, 1940) suggest that, as larvae and postlarvae, *S. edwardsii* and *S. orientalis* occur in the upper few tens of meters, and it is probable that the early developmental stages of other species of the group are epipelagic, as is generally the case throughout the genus *Sergestes* (Gurney and Lebour, 1940; Omori, 1974).

If the above suppositions concerning the vertical distribution of species of the *edwardsii* group are correct, it is likely that their geographical distributions are profoundly affected by conditions in the surface layers. A conspicuous feature of tropical regions of the world oceans are their systems of zonally arranged eastward and westward flowing surface currents and near-surface undercurrents (Knauss, 1963). The restriction of *S. brevispinatus*, *S. geminus*, *S. tantillus*, and *S. gibbilobatus* to distinct, limited sectors of the tropical Pacific (Figure 21a,b) is perplexing in view of the strength and complexity of the equatorial current system in that region (Wyrski, 1967). These species may be adapted behaviorally to seek vertical strata where currents serve to maintain them in, or return them to, favored geographical regions. The contiguous, but essentially nonoverlapping Indian Ocean distributions of *S. orientalis* and *S. semissis* possibly are maintained by similar behavioral patterns in conjunction with the extensive monsoonal reversals in circulation which typify that ocean (Taft, 1971). However, these explanations are hypothetical and must remain so until a fuller understanding of the ecology and behavior of these species is achieved.

Within the *edwardsii* group, species appear to exhibit relatively little overlap in their geographical ranges (Figure 21a,b). Co-occurrences of two or more species in the same collection were restricted to two regions: the Indian Ocean and the eastern tropical Pacific (Table 4). To assess the degree of overlap within these regions co-occurrences were analyzed by means of the index of affinity (Fager and McGowan, 1963). In this usage, the

index is the geometric mean of the proportion of joint occurrences corrected for sample size; i.e., $\frac{J}{\sqrt{A \times B}} - \frac{1}{2\sqrt{B}}$, where A and B are the numbers of collections in which the two species respectively occur, $B \leq A$, and J is the number of joint occurrences.

In only two comparisons did the index exceed 0.1 and in none did it exceed 0.5 (Table 4), a value chosen by Fager and McGowan (1963) to signify association in the same community. The largest values of the index occurred between *S. geminus* and *S. brevispinatus* (0.40) and between *S. geminus* and *S. tantillus* (0.33). Significantly, *S. geminus* appears to be of a lineage distinct from that of the two species with which it occurs most frequently. Values of the index found between species of the same lineage (i.e., *S. geminus* - *S. gibbilobatus*, *S. brevispinatus* - *S. tantillus*) were low, corroborating the subjective impression of a tendency towards allopatry-parapatry within lineages.

TABLE 4.—Extent of overlap of co-occurring species in the *edwardsii* group

Co-occurring species	Number of Co-occurrences	Index of Affinity
Eastern tropical Pacific		
<i>S. tantillus</i> - <i>S. brevispinatus</i>	5	0.07
<i>S. tantillus</i> - <i>S. gibbilobatus</i>	3	0.03
<i>S. tantillus</i> - <i>S. geminus</i>	18	0.33
<i>S. brevispinatus</i> - <i>S. gibbilobatus</i>	2	0.01
<i>S. brevispinatus</i> - <i>S. geminus</i>	22	0.40
<i>S. geminus</i> - <i>S. gibbilobatus</i>	5	0.07
Indian Ocean		
<i>S. orientalis</i> - <i>S. semissis</i>	2	0

Closely related groups of species within other well studied pelagic taxa also tend to be allopatric (cf. Ebeling, 1962; Ebeling and Weed, 1963; Frost and Fleminger, 1968; Gibbs, 1969; Baird, 1971; Fleminger, 1973; Fleminger and Hulsemann, 1974; Johnson, 1974), supporting the idea that the prevailing mode of speciation in sexually reproducing animals begins with genetic divergence of spatially separated stocks (Mayr, 1970). Unfortunately, pelagic metazoans lack the fossil record necessary for direct determination of the events leading to their present day distribution. I am of the opinion, however, that valuable insights into the evolution and zoogeography of these groups will result from a better understanding of the factors determining their present day distributions.

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