

To Ernie
with best wishes!
Jim

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DESCRIPTION OF A NEW SPECIES, *CRANGON HANDI*, AND NEW
GENUS, *LISSOCRANGON*, OF CRANGONID SHRIMPS
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COAST, WITH NOTES ON ADAPTATION IN BODY
SHAPE AND COLORATION

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Shrimps of the genus *Crangon* occurring in shallow waters of the Californian coast have been known taxonomically for 75 to 120 years. Although they are an abundant and important element of the inshore epibenthic fauna, contribute to a minor fishery in San Francisco Bay (Israel, 1936; Skinner, 1962; personal observations), and are common in museum collections, they have been infrequently studied. In the only major studies since Schmitt's (1921) taxonomic monograph of the decapod Crustacea of California, Israel (1936) detailed the growth, reproduction, and fisheries statistics for *Crangon franciscorum* and *C. nigricauda* in San Francisco Bay; and Krygier and Horton (1975) considered growth, reproduction, and local distribution for the same species in Yaquina Bay, Oregon.

A distinctive species of *Crangon* from Californian nearshore waters, *Crangon handi* n. sp. is described in this study. It first came to our attention in Horseshoe Cove, Bodega Head, Sonoma County, California, where it is remarkably camouflaged on coarse-grained, sandy substrates. In order to effect proper subgeneric placement, Zarenkov's (1965) *Crangon* subgenera are evaluated and a new genus is proposed. Adaptation in body shape and color pattern among *Crangon* of the central California coast are further discussed.

Four related species of the genus *Crangon* have long been known from shallow waters of the central California coast: *C. nigricauda* Stimpson, 1856, *C. franciscorum* Stimpson, 1856, *C. nigromaculata* Lockington, 1877, and *C. alaskensis* Lockington, 1877 (= *C. alaskensis elongata* Rathbun, 1902). These species, along with *Crangon handi*, have carapace spination limited to one median gastric spine and one pair of hepatic spines and further differ from other Pacific coast *Crangon* by having a short unornamented rostrum and a sixth abdominal segment lacking a pair of prominent dorsal keels (carinae) but having a sulcate ventral surface. These are termed the *smooth, sulcate species group*. "*Crangon*" *stylirostris* Holmes, 1900, is also included in the analyses and discussion, as it is ecologically and geographically sympatric with species of the smooth, sulcate group. Other Pacific coast *Crangon* have a convex ventral surface on the sixth abdominal segment, possess dorsal abdominal carinae, or have additional carapace spines.

MATERIALS AND METHODS

Although the first specimen from Horseshoe Cove was captured in 1965, we were unable to obtain more than a few additional specimens until 1975, when the first

specimen from Shell Beach, Sonoma Coast State Beach, north of Bodega Head was collected from a low intertidal tidepool. Specimens can now be collected at will from this locality with a long-handled dipnet.

All measurements were done with a vernier caliper to 0.1 mm. Carapace length was measured from the posterior margin of the orbit to the dorsal midline of the posterior margin of the carapace. Total length was taken from the anterior tip of the spine of the antennal scale to the posterior margin of the uropods with the shrimp extended flat on its dorsal surface. Repeated readings within 0.1 mm showed this measurement to be a very precise estimator of overall length. The curve of the body and the presence of eggs on ovigerous females do not permit comparable precision for measurements of the usual "tip of rostrum to tip of telson" total length dimension of shrimp systematics. Israel (1936) reported 6-8% variation from tip of rostrum to tip of telson depending on how the specimen was held. Thus, the measurement inclusive of antennal scales and uropods is used for the morphometric studies, while the usual tip of rostrum to tip of telson measurement is given in the species description of *C. handi* for comparative purposes. Length of the antennal scale was measured along the lateral margin from its basal articulation to the tip of the spine. Antennal scale width was measured at the widest point and included the spine. Chela length was measured along the lateral margin of the propodus. Chela width was taken at the widest point. Length of the sixth abdominal segment was measured along the dorsal midline.

Relative growth is described here by the power function $y = \beta x^\alpha$, where x is the reference dimension, y is the dependent variable and β and α are constants. This curvilinear relationship becomes linear on logarithmic coordinates, such that $\log y = \alpha \log x + \log \beta$, where β represents the size of y when $x = 1$, α is the slope of the logarithmically transformed equation and describes the rate of growth of the dependent variable in comparison to the reference dimension. Allometric growth is positive if $\alpha > 1$, and negative if $\alpha < 1$. The growth relationship is isometric if $\alpha = 1$ (Teissier, 1960; Gould, 1966). Growth is considered isometric if $0.9 < \alpha < 1.1$. This is analogous to the definition of arithmetic growth (as opposed to progressive and regressive growth) used by Kurata (1962) and Hepper (1967).

Frequently, the greatest linear dimension (in this case total length) is chosen as the reference dimension. However, this measurement is notoriously variable in flexible animals such as shrimp. Carapace length is used here as the reference dimension, because it is the greatest measurement possible on a relatively rigid cuticle and relates to overall body size.

For color and background pattern adaptation, animals were placed in containers with either Shell Beach or Horseshoe Cove substrate for 14 days prior to photography. Sediment samples collected in mid-summer were analyzed, and mean grain size (based on graphical phi percentile measures) was determined following methods given by Folk (1968), involving sorting dry sand through a consecutive graded series of Tyler sieves using a mechanical shaker.

Specimens examined are on deposit at the National Museum of Natural History (NMNH), California Academy of Sciences (CAS), Allan Hancock Foundation, University of Southern California (AHF), Santa Barbara Museum of Natural History (SBMNH), and Bodega Marine Laboratory Synoptic Collection (BMLSC).

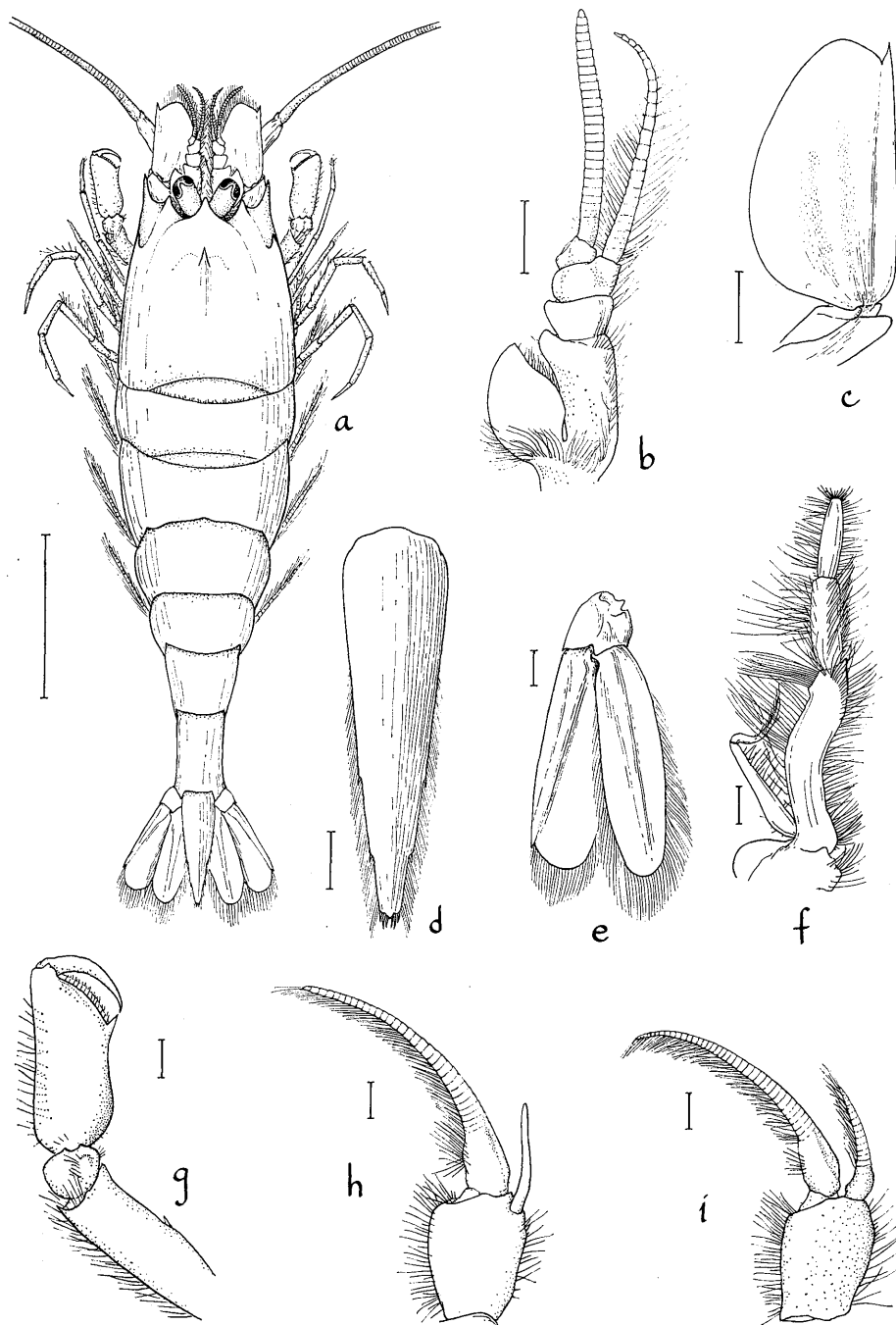


FIGURE 1. *Crangon handi*, new species: a, adult ovigerous female, total length 51 mm; b, antennule (first antenna) and antennular scale; c, antennal scale (scaphocerite); d, telson; e,

TAXONOMY

Crangon handi new species (Figure 1 a-i, Figure 2, a, d, g)

Crangon sp., Carlton and Kuris, 1975: 388, 404

Diagnosis

Antennal scale short, one-half length of carapace or less, and very broad (length less than or about equal to two times width), acicle not exceeding blade; flagella of first antenna equal in length; sixth abdominal segment very short, dorsum smooth; first pleopod lacking spine on anterodistal corner.

Description (adult ovigerous female, Fig. 1a)

Antennule (first antenna) (Fig. 1b) with flagella extending beyond antennal scale; flagella equal in length, the inner (lower) flagellum not as robust as outer; peduncle about one-half length of antennal scale, approximately one-half length of antennal peduncle. Antenna with peduncle about two-thirds length of antennal scale; antennal flagella about three-fifths body length. Antennal scale (scaphocerite) (Fig. 1c) short, one-half length of carapace or less, and broad, length generally less than two times width; spine (acicle) and anterointernal (anteromesial) margin of blade codistant. Eye stalk and ocellus reaching well beyond rostrum. Carapace with one medial gastric spine and one pair of hepatic spines. Rostrum short, straight, unornamented, grooved above, round at tip. Abdomen with segments typical, unornamented, except for very weak medial monocarination; abdominal segment very short, about two-thirds length of telson, smooth dorsally, sulcate ventrally but not deeply so. Telson (Fig. 1d) smooth dorsally with lateral spination typical: a single tiny spine on each margin about one-seventh the distance from tip and again about one-third the distance from tip; tip acute, flanked on each side by three tiny spines. Uropods (Fig. 1e) subequal, as long as telson, spine of exopod without setae or spines on margin. Maxilliped 3 (Fig. 1f) typical. Cheliped (Fig. 1g) with chela stout, dactyl turned down at approximately 45° angle; spine short, acute, margin of propodus lightly setose. Pereopods typical. Pleopods (first, Fig. 1h; second, Fig. 1i) normal, except that first pleopod lacks a spine on the anterodistal corner.

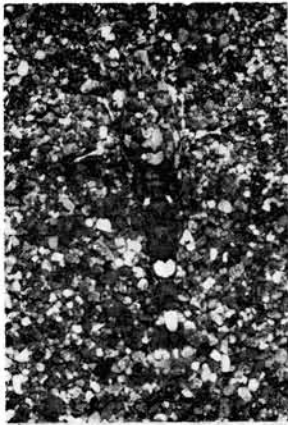
Size

Largest specimen examined (holotype), total length, 50.3 mm; carapace length, 10.7 mm (from Horseshoe Cove, Bodega Head). Range: male carapace length 6.1 mm; females, ovigerous, 10.2-10.7 mm, not ovigerous, 8.1-9.6 mm; small, unsexed, 3.2-3.8 mm.

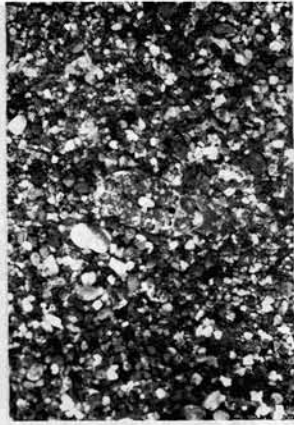
Color in life (adult female)

The dorsal surface presents a complex pattern of almost a dozen colors. On the antennal scale are cloudy-white patches anteriorly and posteriorly, separated by a

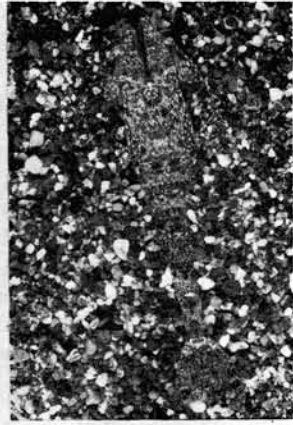
uropods; f, maxilliped 3; g, cheliped; h, pleopod 1; and i, pleopod 2. All are left, except for c. Scale on a = 1 cm; others = 1 mm.



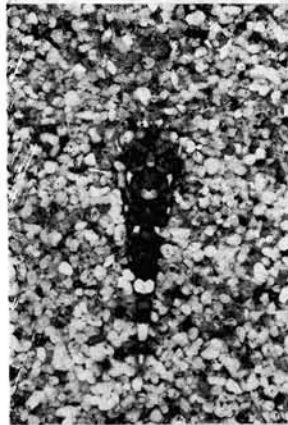
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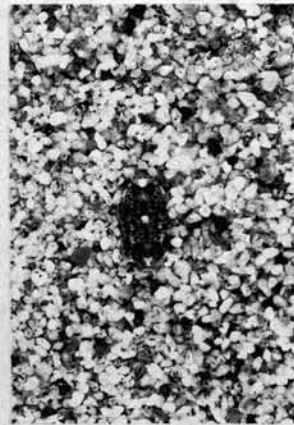
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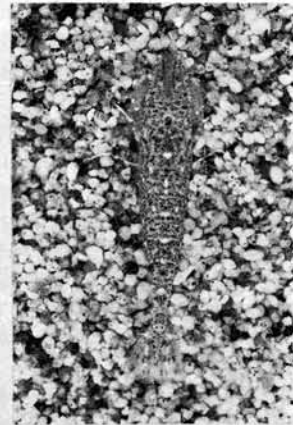
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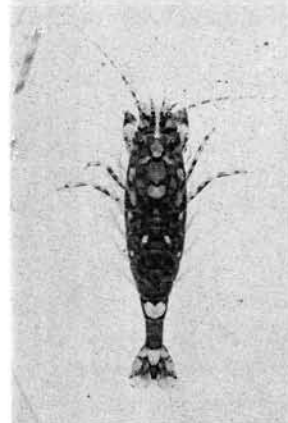
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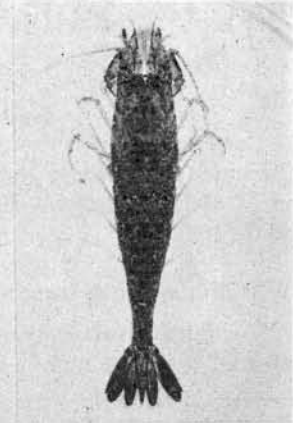
F



G



H



I

black band; another black bar is at the base of the scale. The peduncle of the first antenna is brown, black, and white-marked; the flagella are green, brown and/or black-marked. The peduncle of the second antenna is black and orange, with the flagella black-and-green banded with alternating white areas. On the carapace there is an anterior irregular white patch, and on most specimens a small notch at the base of this patch which conforms to the tip of the median gastric spine. The rostrum is white, and may or may not be black-tipped. The remainder of the carapace pattern is complex, with regions of purple, black, brown, white, and orange. The gastric spine is brown, with a distal brown band below a white tip. Hepatic spines are translucent. The posterior margin of the carapace is marked by a subrectangular white patch.

Abdominal segments are generally translucent with brown, white, red, black, and green markings. Notable and generally consistent on the abdominal segments are two gently sloping white marks on either side of the medial line of the second segment; a brown-black dot on the posterior medial margin of the third segment, and a very conspicuous heart-shaped white patch, generally with a central black dot, on the fifth abdominal segment. The anterior half of the telson consists of an elongate pink-white patch; the central area of the telson is black with a pink-white patch; the posterior area of the telson is white. On the uropods distally and proximally are broad white bands, separated by brown and orange bars and markings. Abdominal coxae are brown with black and/or yellow marks.

The cheliped hand is distally black and proximally white, marked here and there with white and green markings. Remaining articles are black-spotted. Pleopods have brown markings, the lateral surface with a long yellow line or a line of yellow spots; pereopods are variously translucent, or with yellow, orange, and black spots. The carpus of pereopods 4 and 5 has a white line or a line of white spots medially.

Crangon handi presents, then, a highly disruptive pattern blending in superbly with its surrounding coarse sand substrate (Fig. 2a, d). On or near the medial dorsal line of the shrimp, there are a series of approximately equally-spaced conspicuous white marks: white patches on the antennal scale, white areas anteriorly and posteriorly on the carapace, two white marks on the second abdominal segment, a white heart-shaped patch on the fifth segment, and white patches anteriorly and posteriorly on the telson and uropods.

Etymology

We are pleased to name this species in honor of Dr. Cadet H. Hand, Jr., founder and Director of the Bodega Marine Laboratory and a keen student of the central California invertebrate fauna. Dr. Hand took an interest in this work and other projects, provided a model for sharp-eyed field work, and encouraged Robert Sikora's exploratory sampling of Horseshoe Cove.

Type locality and type material

Horseshoe Cove, Bodega Head, Sonoma County (38° 18' 30" N, 123° 4' W). Holotype, adult ovigerous female (Fig. 1a), total length 50.3 mm, total carapace

FIGURE 2. a, d, g: *Crangon handi*, new species; b, e, h: the isopod *Tecticeps convexus*; c, f: *Lissocrangon stylirostris*; i: *Crangon nigricauda*; a-c are on coarse substrate from Shell Beach, d-f are on coarse substrate from Horseshoe Cove, and g-i are on smooth white backgrounds.

length 10.7 mm, length from tip of rostrum to tip of telson 43.2 mm, collected 1965, R. Sikora, deposited at NMNH, no. 169870. Paratypes deposited at CAS, and AHF; additional material at NMNH, CAS, AHF, SBMNH and BMLSC.

Geographic range and bathymetry

Crangon handi occurs from the intertidal zone to 55 m from Shell Beach, Sonoma County, to Bahia Colnett, northern Baja California. North of Point Conception, collections are centered around Sonoma County (Shell Beach, Carmet, Horseshoe Cove), and Monterey Bay (Santa Cruz, Pacific Grove, Monterey), with one collection in San Luis Obispo County. In southern California several subtidal collections were from the Channel Islands.

Habitat

With the possible exception of a "shore" record at Corona del Mar, Orange County, all specimens south of Sonoma County have been dredged or lack detailed habitat notes.

All Sonoma County specimens of *C. handi* have been collected from beach wrack, tidepools or shallow water over a very coarse to coarse sand substrate typical of small beaches, coves, and surge channels along the Marin, Sonoma, and Mendocino County rocky coasts of California. Most of this coast lies east of the San Andreas Fault. Here, such as at Shell Beach, the sands are dark, consisting largely of chert, graywacke, greenstone and serpentine clasts derived from the Franciscan Formation which lies along the fault zone. West of the fault zone, beach sands may be light and granitic, such as the beach at Horseshoe Cove on Bodega Head (which also has a small amount of Franciscan sediments washed around Mussel Point on Bodega Head).

Sand size analyses from Horseshoe Cove and from Shell Beach show that these habitats have a much larger mean grain size (approximately 1.45 mm and 0.92 mm, respectively) than the sandy or muddy substrates over which other species of *Crangon* considered here normally occur (for example, Campbell Cove, Bodega Harbor, a medium-sand sandflat, with aeolian-deposited sediments derived largely from local sand dunes, has a mean grain size of 0.35 mm).

Co-occurring with *C. handi* in Sonoma County are cottid fish, polychaete worms, and the sphaeromatid isopod *Tecticeps convexus* Richardson. To the south, *C. handi* has been recorded regularly over sand, gravel, and "shell" bottoms with a number of associated species including *C. nigricauda*, *C. alaskensis*, *C. alba*, *C. holmesi*, the echinoid *Dendraster* and the brachyuran *Pugettia*.

Epizoics, food, and predators

Specimens of *C. handi* examined were almost always free of epibiotic organisms. A specimen of the foraminifer *Rosalina columbiensis* was noted on the left third maxilliped of an adult female from Shell Beach (July 11, 1975).

A single specimen of a small gammarid amphipod, *Hyale frequens* (Stout, 1913), along with numerous sand fragments, was found in the stomach of a *Crangon handi* collected at Shell Beach (July 10, 1975). A specimen of an oedicerotid gammaridean amphipod and sand particles were also found in the buccal region of a *C. handi* from beach drift on Horseshoe Cove (June 27, 1968).

Predators upon *C. handi* in the northern half of its range are unknown. However, five specimens were removed from the stomach of a thornback skate, *Platyrrhinoides triseriata*, collected on Naples Reef, 11 km north of Santa Barbara, California, over a coarse sand substrate. The thornback skate occurs in shallow water to 46 meters from near Thurloe Head, Baja California to San Francisco (Miller and Lea, 1972).

Comparison with related species and morphometrics

A new key to the five *Crangon* species of Schmitt's (1921) Group I, A and B1, and to *C. handi* follows. Distinctions between two often misidentified species, *C. nigricauda* and *C. alaskensis*, are clarified.

1. No gastric spine; rostrum narrow, tip pointed, curving strongly downward; telson shorter than uropods; first (antepenultimate) article of third maxilliped broadly expanded *stylirostris*
- One gastric spine; rostrum relatively broad, tip round, straight; telson equal to or longer than uropods; first article of third maxilliped narrow, not dilated 2
2. Finger of hand (dactyl of chela) turned down almost parallel (180°) to hand; an acute spine on posterodorsal corner of fifth abdominal segment; inner flagellum of first antenna more than two times as long as outer flagellum *franciscorum*
- Finger of hand at a 45° angle, or less, to hand; no spine on posterodorsal corner of fifth abdominal segment; inner flagellum of first antenna distinctly less than two times as long as outer flagellum 3
3. Flagella of first antenna equal in length; length of antennal scale about equal to or less than two times width; spine of antennal scale not exceeding blade; anterodistal corner of first pleopod without a spine *handi*
- Inner flagellum of first antenna distinctly longer than outer flagellum; antennal scale length always greater than two times width; spine of antennal scale almost always distinctly exceeding blade (common exception is *nigricauda*); anterodistal corner of first pleopod with a spine 4
4. Tip of telson without three small spines flanking each side (but with a single small spine on each side slightly proximal to tip); dorsum of sixth abdominal segment smooth, without a distinct row of small setae; antennae as long or longer than body; finger of hand at about a 30° angle to hand [*in living specimens*, always distinguished by one prominent circular spot (blue center with a blue and then a yellow ring) on side of sixth abdominal segment; this often fading in preservative] ... *nigromaculata*
- Tip of telson with three spines on each side; dorsum of sixth abdominal segment slightly grooved, with a distinct row of central setae (may be worn) (*living specimens* never with colored spot on sixth abdominal segment) 5
5. Antennal scale blade tip narrow, spine long, much exceeding blade; scale greater than two-thirds length of carapace; finger of hand at about 45° angle to hand; antennae about two-thirds body length *alaskensis*
- Antennal scale blade tip broad, spine generally short, hardly exceeding blade; scale about two-thirds length of carapace; finger of hand tending toward transverse, at about 30° angle to hand; antennae from two-thirds body length to as long as body (a variable species) *nigricauda*

In Schmitt's key (1921, p. 82) *C. handi* keys as far as I-B-1-a-ii, but will not key to species. *Crangon handi* lacks the large circular spot on the much longer sixth abdominal segment of *C. nigromaculata*, which also possesses a much longer antennal scale. *Crangon handi* possesses only a very weakly monocarinate fifth abdominal segment; the "carina" is weaker than that of *C. nigricauda*. *Crangon handi* is further distinguished from *C. alaskensis* and *C. nigricauda* by the distinctly shorter and broader antennal scale of the former, and by the more elongate chelae of both species. *Crangon handi* is keyed in *Light's Manual* (Carlton and Kuris, 1975) as *Crangon* sp. In Kozloff (1974, p. 164) *C. handi* will key (13a) to *Crangon nigricauda*, but can be distinguished from that species by the characters noted above.

When log total length is compared with the reference dimension log carapace length (Fig. 3), *Crangon handi* is the most robust species, followed closely by "*C.*" *stylirostris*. *Crangon nigromaculata* and *C. alaskensis* are similar and most attenuate. *Crangon nigricauda* and *C. franciscorum* are similar and intermediate.

Relative length of log sixth abdominal segment, when compared to log carapace

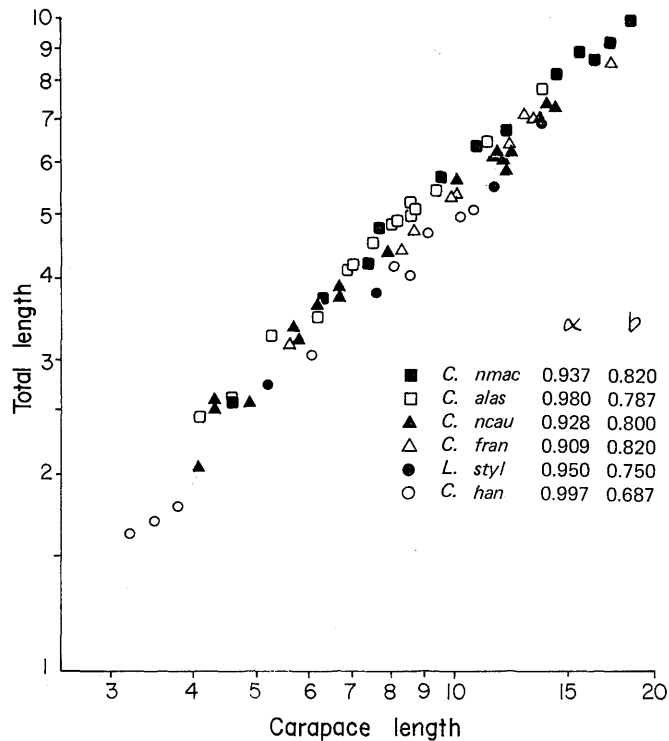


FIGURE 3. Relative growth of log total length compared with log carapace length for six crangonid shrimp; abbreviations and sample sizes (N) include *C. nigromaculata* = *C. nmac.*, N = 13; *C. alaskensis* = *C. alas.*, N = 15; *C. nigricauda* = *C. ncau.*, N = 19; *C. franciscorum* = *C. fran.*, N = 10; *L. stylirostris* = *L. styl.*, N = 5; and *C. handi* = *C. han.*, N = 9. Pearson product-moment correlation coefficients (r) were uniformly very high with a range of 0.980–0.999, for all groups in Figures 3–8.

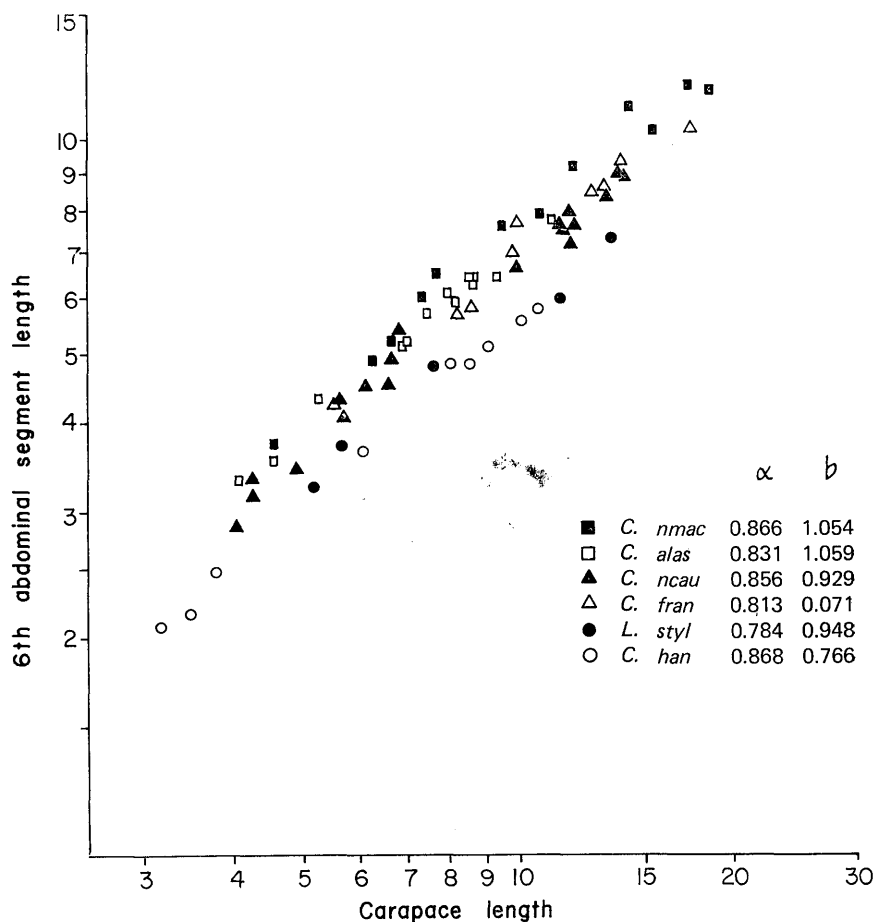


FIGURE 4. Relative growth of log sixth abdominal segment length compared with log carapace length for six crangonid species. See Figure 3 for key to species, abbreviations and sample sizes, except for *C. nigromaculata*, $N = 12$.

length (Fig. 4), varies between species more than does log total length *versus* log carapace length. *Crangon handi* has the shortest sixth abdominal segment, followed by "*C.*" *stylirostris*. *Crangon nigricauda* and *C. franciscorum* are similar, while *C. nigromaculata* has the longest sixth abdominal segment.

Log chela length *versus* log carapace length shows the least variation between species (Fig. 5). "*Crangon*" *stylirostris* has the shortest chela; *C. franciscorum*, the longest. The remaining four species are similar and intermediate.

Log chela length *versus* log chela width shows more between-species variation than do the three allometric relationships considered above (Fig. 6). *Crangon franciscorum* has very narrow chelae. *Crangon nigromaculata* and *C. alaskensis* are similar and have the next most elongate chelae. *Crangon nigricauda* and *C. handi* are similar with rather wide chelae, while "*C.*" *stylirostris* has the widest

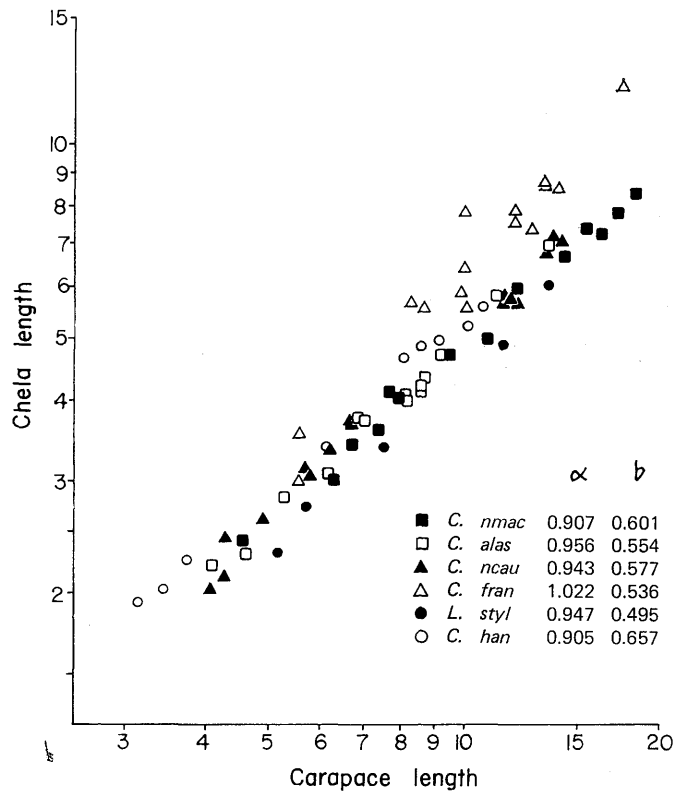


FIGURE 5. Relative growth of log chela length compared with log carapace length for six crangonid species. See Figure 3 for key to species, abbreviations and sample sizes, except for *C. alaskensis*, $N = 14$.

chela of these six species. The slope of the *C. franciscorum* regression is 0.768, the other five species have similar slopes, between 0.948 and 1.082.

Log antennal scale length *versus* log carapace length exhibits greater between-species variation than do the four preceding relationships (Fig. 7). Antennal scale length of *C. handi* is considerably shorter and has a lower slope than the other five species. *Crangon nigricauda* and *C. franciscorum* are similar and have the next shortest antennal scale length. *Crangon alaskensis* and "*C.*" *stylirostris* have distinctly longer antennal scales compared to the three previous species. *Crangon nigromaculata* has a slightly longer antennal scale than the preceding two species, but the relationship between log antennal scale length and log carapace length may be curvilinear for *C. nigromaculata*. Large and small individuals of *C. nigromaculata* approximate the *C. alaskensis* and "*C.*" *stylirostris* relationship.

Between species, variation in the log antennal length-width relationship is similar to the variation in the preceding relationship (Fig. 8). *Crangon handi* has much the widest antennal scales, showing no overlap with the species having the next widest antennal scale, *C. nigricauda*. The remaining four species have a

similar antennal scale length-width relationship, all being distinctly narrower than *C. nigricauda*. *Crangon nigromaculata* appears to have a slightly curvilinear relationship with the largest specimens having relatively wide antennal scales.

Generic revisions

An attempt to assign *C. handi* to a proper subgenus, as defined by Zarenkov (1965), has led us to propose the following partial revision of crangonid taxa falling within Schmitt's (1921) group I, those species with the gastric region of the carapace not depressed. Species here appear to fall into three natural groups, not previously defined as such: a genus lacking gastric spines (*Lissocrangon*, new genus), a genus with one median gastric spine (*Crangon*) and a genus with two gastric spines (*Neocrangon*). These three genera may be distinguished by several features in addition to gastric spination.

Family Crangonidae Bate

Lissocrangon, new genus

Type species: *Crangon stylirostris* Holmes, 1900.

Generic diagnosis: No gastric spines on carapace. Rostrum long, narrow, tip pointed, sharply decurved. Telson shorter than uropods. Sixth abdominal segment without a pair of dorsal carinae.

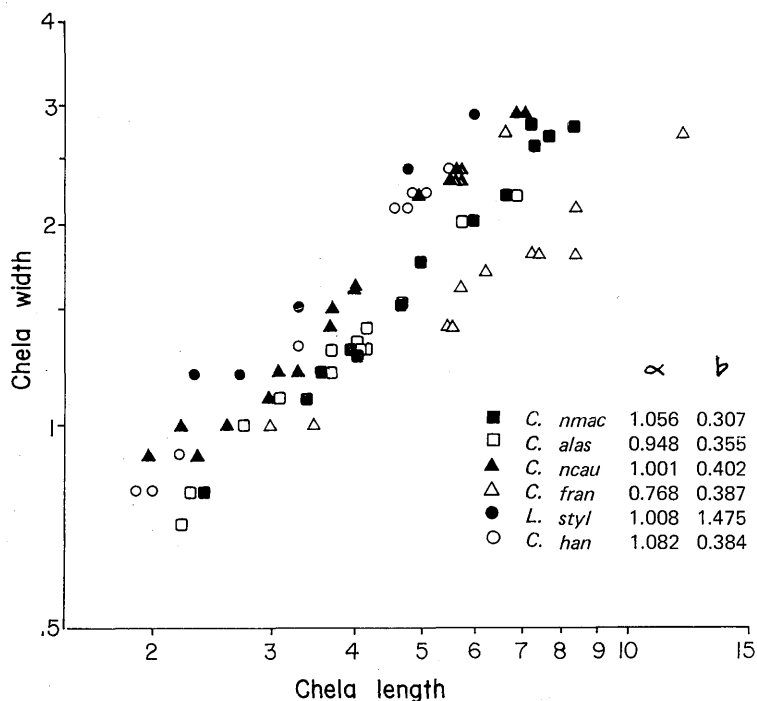


FIGURE 6. Relative growth of log chela width compared with log chela length for six crangonid species. See Figure 3 for key to species, abbreviations and sample sizes, except for *C. alaskensis*, N = 14.

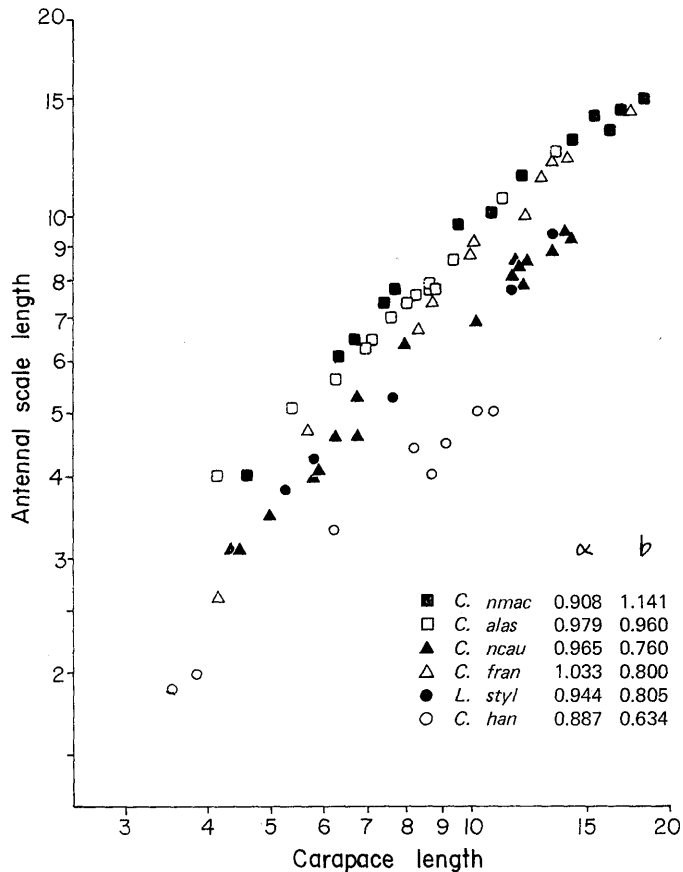


FIGURE 7. Relative growth of log antennal scale length compared with log carapace length for six crangonid species. See Figure 3 for key to species, abbreviations and sample sizes.

Etymology: From the Greek *lissos*, smooth, and *crangon*.

Remarks: Monotypic. Members of *Crangon* and *Neocrangon* possess a straight or upturned rostrum and a telson as long as or longer than the uropods, further separating them from this group. *Lissocrangon stylirostris* also possesses a broadly dilated first article of the third maxilliped, a character shared with *Crangon* (*Crangon*) *alba* Holmes, 1900.

Crangon Fabricius, 1798

Generic diagnosis: We here restrict *Crangon* to those shrimp with one medial gastric spine, straight or upturned rostrum, and a telson equal in length to or longer than the uropods. Other characters are those previously established for the genus. Two subgenera are distinguishable:

(*Crangon*) Fabricius, 1798

Type species: *Cancer crangon* Linnaeus, 1758.

Subgeneric diagnosis: Sixth abdominal segment smooth, lacking prominent dorsal carinae.

Remarks: Two groups of *Crangon* (*Crangon*) are apparent, a *sulcate* group, with the ventrum of the sixth abdominal segment sulcate (*C. nigricauda*, *C. franciscorum*, *C. nigromaculata*, *C. alaskensis*, *C. handi*, *C. crangon*, and *C. septemspinosa* Say, 1818, and perhaps *C. affinis* de Haan, 1849), and a *convex* group, with the ventrum of the sixth abdominal segment convex (*C. alba* and *C. holmesi* Rathbun, 1902). The anterolateral angle of the antennal scale blade, where it joins the antennal scale spine, is adnate in the convex group but not in the sulcate group. The convex species also do not appear to reach as large a body size as do species of the sulcate group.

(*Steiracrangon*) Kinahan, 1862, revived and amended

Type species: *Crangon allmanni* Kinahan, 1857.

Subgeneric diagnosis: Sixth abdominal segment with two prominent dorsal carinae.

Remarks: *Crangon dalli* Rathbun, 1902, *C. sagamiense* Balss, 1913, and *C. geniculata* Yokoya, 1933 are also included here. Kinahan (1862) originally re-

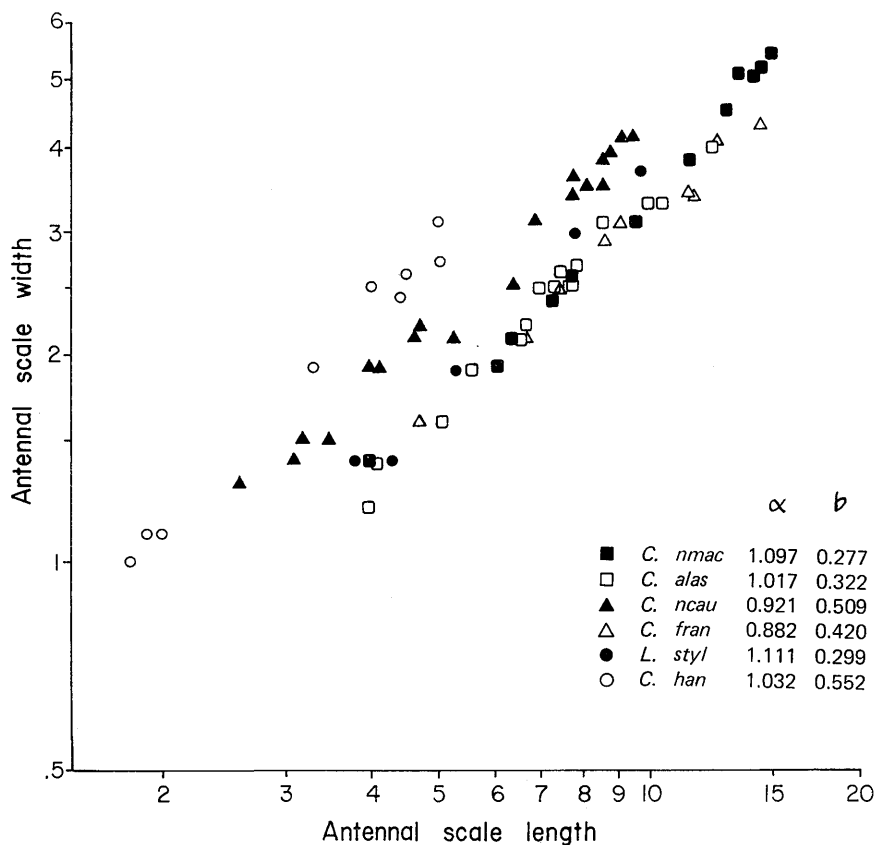


FIGURE 8. Relative growth of log antennal scale width compared with log antennal scale length for six crangonid species. See Figure 3 for key to species, abbreviations and sample sizes.

served this genus for species with either one or two dorsal keels and a sulcate dorsal surface of the telson. The name remains available for *C. allmanni* as the rest of Kinahan's listed species are included in the subgenus *Crangon* as defined above.

Neocrangon Zarenkov, 1965

Type species: *Crangon communis* Rathbun, 1899.

Generic diagnosis: Two medial gastric spines on carapace. Sixth abdominal segment with two prominent dorsal carinae. Rostrum long (extending beyond eyes), or short recurved (ascending), sometimes ornamented with a compressed ventral process.

Remarks: *Neocrangon resima* (Rathbun, 1902), *N. abyssorum* (Rathbun, 1902), *N. joloensis* (De Man, 1929), and *N. zacaе* (Chace, 1937) are also included here.

Acceptance of Zarenkov's *Neocrangon* (originally proposed as a subgenus of *Crangon*), which he based upon *Crangon communis*, requires that the genus be recognized as having two gastric spines (possessed by *communis*) rather than one as Zarenkov indicated. All other species placed in *Neocrangon* by Zarenkov (and accepted without comment by Squires and Figueira, 1974), other than those noted above, must be reassigned.

DISCUSSION

The functional significance of body proportion and of body shape of shrimp is poorly understood. Shrimp anatomy may be considered through analogy with fish functional anatomy, which is relatively well-known (Marshall, 1966; Alexander, 1967; Gosline, 1971). A fast swimming fish is elongate, has a streamlined head, long, narrow caudal peduncle and lunate tail. The power stroke is delivered through the alternate contraction of the body musculature which whips the caudal fin in alternating lateral directions. Slow swimming fishes have squat bodies with short, wide caudal peduncles and a fan-shaped tail.

Shrimp swim in two different ways. Slow swimming, head-first, is achieved through the sculling action of the natatory pleopods and will not be considered further here. Rapid swimming is backwards, functioning as an escape response. The motive force here is delivered through the dorsoventral flexure of the abdominal musculature. The expanded fanshaped uropods and telson, and the sixth (last) abdominal segment, are analogous to the caudal fin and caudal peduncle, respectively, of fishes.

When carapace length is compared simultaneously with total length and with the length of the sixth abdominal segment (Figs. 3, 4) *Crangon handi* and, to a lesser extent, *Lissocrangon stylirostris* are more robust than the remaining four species. These two species also have the shortest sixth abdominal segments. Thus *C. handi* and perhaps *L. stylirostris* would seem less capable of rapid, sustained swimming than the other four species. These two squat shrimp appear to be built like sculpins (Cottidae) designed for quick short bursts of movement. Such adaptations may be related to the specialized habitats of these two species. *Crangon handi* appears to be largely restricted to intertidal and shallow shelf coarse-grained sediments. *Lissocrangon stylirostris* is also a habitat specialist, occurring as a

common inshore species along high energy sandy beaches; infrequently it is captured over mud or coarse sand (Schmitt, 1921; personal observations). For both species, a squat body form with a resultant short-distance escape response and rapid reburial may be efficient to elude predators, presumably fishes.

The remaining four species with relatively attenuate body shapes are habitat generalists, found over sand and mud with a wide depth range (Schmitt, 1921; personal observations). All frequent bays, but *C. franciscorum* is rarely taken offshore, where *C. alaskensis*, *C. nigricauda* and *C. nigromaculata* are commonly taken. *Crangon nigromaculata* is the most elongate of these four species and also reaches the largest body size (based on examination of several thousand specimens at CAS and BMLSC).

When chela length and width are considered with reference to carapace length *C. franciscorum* and *L. stylirostris* represent the morphological extremes (Figs. 5, 6). The remaining four species are similar and intermediate with regard to chela size and shape. *Crangon franciscorum* has the longest and narrowest chela. The subchelate appendage is also the most extremely reflected; when closed, the dactyl is directed posteriorly considerably more than 45°. *L. stylirostris* has the shortest and widest chela. The anterior margin of this appendage is also the most transverse. Although the function of these appendages in *Crangon* is unknown, they may be used in feeding. If so, *C. franciscorum* and *L. stylirostris* are predicted to be feeding specialists when compared to the other four species.

The relationships between carapace length and antennal scale length and width show considerable variability between species (Figs. 7, 8). *Crangon handi* differs considerably from the other five species in having short, wide antennal scales. *Crangon nigricauda* has the next shortest and widest antennal scale. However, the slopes of the *C. handi* relationships show that the relative length of the antennal scale decreases with increasing size, while the relative width increases. The slope of the carapace length-antennal scale length relationship ($\alpha = 0.887$) falls short of the 0.9 to 1.1 range defined above as isometric and thus is characterized as negatively allometric. *Crangon nigricauda* on the other hand shows a tendency to have relatively narrow antennal scales with increasing size ($\alpha = 0.921$) and a carapace length-antennal scale length relationship that approaches perfect isometry ($\alpha = 0.965$). Of the remaining species, *C. franciscorum* has short but narrow antennal scales; antennal scale width shows a negative allometric relationship to antennal scale length ($\alpha = 0.882$). Thus the antennal scale of *C. franciscorum* is increasingly slender at larger sizes, while the scale of *C. handi* becomes increasingly wider.

Crangon alaskensis and *L. stylirostris* have relatively long and narrow antennal scales. While both relationships for *C. alaskensis* are isometric (Figs. 7, 8), the antennal scales of *L. stylirostris* are positively allometric ($\alpha = 1.111$) for the latter relationship. *Crangon nigromaculata* is similar to the two preceding species; however, visual inspection of both relationships suggests that they are curvilinear. Large specimens of *C. nigromaculata* (> 10.0 mm carapace length) have shorter and wider antennal scales than would be predicted by extrapolation from smaller specimens.

The variability in shape of the antennal scales within and between species suggests that these are important adaptive structures. Unfortunately the function of the antennal scales is so poorly understood that further discussion is not possible.

Crangon handi is remarkably cryptic when observed over the coarse grained sandy substrates that characterize the two localities where it has been observed in the field (Fig. 2a, d). This adaptation is shared by another epibenthic macrocrustacean common over the coarse-grained substrate of these localities, *Tecticeps convexus*, a sphaeromatid isopod (Fig. 2b, e). *Lissocrangon stylirostris* (Fig. 2c) and *C. nigricauda* (Fig. 2f) are normally taken over sandy or muddy substrates. These latter species are unable to match the degree of crypsis achieved by the coarse-grained specialists *C. handi* and *Tecticeps*. The black and white chromatophores of the fine-grained species are evenly distributed over their dorsal surface, creating a salt-and-pepper effect (Fig. 2c, f, i). *Crangon handi* and *Tecticeps* have a wider range of colored spots with an uneven distribution over their dorsal surface, suggesting the irregular blotchy pattern of the coarse sandy beach (Fig. 2a, b, d, e). Figure 2a and b show that this color pattern is particularly effective in disrupting the body outline, an important predator avoidance color adaptation (Wickler, 1968).

Specimens of *C. handi* and *Tecticeps* captured at Horseshoe Cove show a degree of crypsis on the light-colored coarse-grained granitic sand of the cove that is comparable to the Shell Beach specimens (Fig. 2a, b). Efforts to obtain these species from Horseshoe Cove for photographic purposes in the summer of 1975 were unsuccessful. Shell Beach specimens were placed in aquaria containing Horseshoe Cove sand 14 days prior to photography. Figure 2g and h show that adaptation to the light-colored substrate with similar grain size was only partially successful. *Lissocrangon stylirostris* collected from Horseshoe Cove does not show any ability to mimic the coarse-grain size (Fig. 2i) retaining its salt-and-pepper coloration.

Interestingly, *C. nigromaculata* is the only species considered here that presents a single distinctive lateral color spot on the posterior portion of the sixth abdominal segment. This prominent circular spot has a blue center surrounded by a black ring and then a peripheral yellow ring. On morphological evidence *C. nigromaculata* may spend more time in sustained swimming or in exposed crawling over sandy and muddy substrates. If so, it may be prone to predation from pelagic fishes (which are predators of *Crangon* spp., Skogsberg, 1939; Boothe, 1957; McKechnie and Fenner, 1971; Prince and Gotshall, 1976) in addition to bottom feeders such as flounder (also important predators of *Crangon* spp., A.M.K., personal observations; Gordon, 1974; Kosaka, 1970; see also references in Zarenkov, 1965). The lateral caudal eyespot may function as a predator shock signal or a target decoy as suggested for similar color markings on fishes (Wickler, 1968). The adaptive function of this prominent color marking in the caudal region of a posteriorly directed swimmer (while in the escape response) must be considered speculative until subjected to behavioral analysis.

Based on field and laboratory observations, it can be suggested that *Crangon handi* has adopted two distinctive adaptations compared to those of its four congeneric species. To escape detection, at least in its coarse-grained environment of the central California coast, it utilizes a squat body form to effect short distance movement in rapid bursts, followed by rapid reburial combined with crypsis, in the form of camouflaging coloration to effect body outline disruption (Fig. 2a, d). The isopod *Tecticeps convexus*, which co-occurs with *Crangon handi* in Horseshoe

Cove and at Shell Beach, appears to have adopted an even broader suite of presumed predator avoidance mechanisms. Besides a squat body form for quick bursts of movement and rapid reburial and crypsis (like *C. handi*, also remarkable camouflaging coloration on a coarse-grained background), *Tecticeps* is also capable of: modified conglobation, the isopod curling response, modified in *Tecticeps* for folding only in half, rather than into a complete ball, as in some other sphaeromatids; a probable allelochemic response, dramatic release of a cucumber (*Cucumis*)-like scent upon being handled (an allomone and/or kairomone, or depressant—see Whittaker and Feeny, 1971); spine display, the lateral protrusion of the exopod of the uropod to form protective spines when the animal is folded (Richardson, 1899); and escape maneuvering, sudden and rapid turning of direction with circular movements before reburial. Sculpins (cottids) are also common epibenthic organisms in these habitats and exhibit comparable modifications: they are squat with short, wide caudal peduncles and a fan-shaped tail; and they swim in short, quick bursts and often exhibit strong cryptic coloration. This broad suite of mechanisms suggests that predation pressure upon epibenthic fish and macrocrustaceans over exposed coarse-grained flat bottoms may be relatively high.

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SUMMARY

1. *Crangon handi*, new species, is described and compared with five other California crangonid shrimps; it occurs from the littoral zone to 55 m from Sonoma County to Bahia Colnett, northern Baja California. *Crangon handi* is a specialist for shallow-water coarse sand substrates and here exhibits remarkable crypsis. *Crangon handi* eats small gammarid amphipods and has in turn been found in the stomach of the thornback skate.

2. *Lissocrangon*, new genus, is proposed to accommodate *C. stylirostris*, a species lacking gastric spination; *Crangon* is restricted to shrimp with one gastric spine; *Steiracrangon* Kinahan, is revived for shrimp with bicarinate sixth abdominal segments; and *Neocrangon* Zarenkov is revised and amended to include shrimp with two gastric spines and bicarinate sixth abdominal segments.

3. Morphological analyses and relative growth are presented and discussed for all six crangonids considered. *Crangon handi* and *L. stylirostris* are squat shrimps in restricted habitats probably adapted for short quick bursts of movement followed by rapid reburial; the remaining four species are relatively elongate and habitat generalists.

4. *Crangon* species normally occurring on finer mud and sand bottoms are unable to achieve the degree of crypsis of the coarse-grained species, *Crangon handi*. *Crangon handi* from dark coarse-grained sediments is only partially able to adapt to light coarse-grained sediments.

5. *Crangon nigromaculata* is the only species with a lateral color spot, and it is suggested that this may serve as a predator shock signal or target decoy analogous to similar markings in some fish.

6. Fish, such as cottids, and macrocrustaceans, including *C. handi* and the sphaeromatid isopod, *Tecticeps convexus*, sympatric with it on coarse sand bottoms, exhibit a wide range of mechanisms apparently to escape detection and avoid predation. *Tecticeps* alone has at least six such mechanisms. This suggests that predation pressure in such habitats may be relatively high.

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