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Larval morphology and development of *Neocalanus tonsus*, *Calanoides macrocarinatus*, and *Calanus australis* (Copepoda: Calanoida) in the laboratory

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Abstract *Neocalanus tonsus*, *C. macrocarinatus*, and *C. australis*, three calanids which potentially occur together in New Zealand waters, were raised from eggs and their developmental stages described. All naupliar stages apparently have identical setation. Naupliar stages I–III are very similar. *Neocalanus tonsus* can be easily identified from naupliar stage IV onwards, whereas *C. macrocarinatus* and *C. australis* can be identified with certainty only in the copepodite stages, because their nauplii overlap in size and body proportions. Development at 15 °C from egg to copepodite V took 24 days for *N. tonsus*, 20.2 days for *C. macrocarinatus*, and 23.8 days for *C. australis*. *Neocalanus tonsus* is the smallest species during early developmental stages but by copepodite III stage is larger than the other two species.

Keywords developmental stages; developmental times; *Neocalanus tonsus*; *Calanoides macrocarinatus*; *Calanus australis*

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INTRODUCTION

This study was undertaken to assist in identifying the developmental stages of *Neocalanus tonsus* (Brady, 1883) in field samples. *Neocalanus tonsus* potentially co-occurs off the Otago Peninsula, New Zealand, with two other common calanids, *Calanoides macrocarinatus* (Brodsky, 1972) and *Calanus australis* Brodsky, 1959. Other calanids known to occur in the area (*Calanus simillimus*, *Neocalanus gracilis*, and *Mesocolanus tenuicornis*) are not numerically abundant and their developmental stages are unlikely to be common in field samples.

It is generally thought that the naupliar stages of the Calanidae are very similar, but some authors believe there are distinguishing characteristics. For example, Bjornberg (1972) cites the size of nauplii, shape of the labrum, and the relative size of setae and spines as distinguishing the nauplii of calanids. But Bjornberg's comparison with *C. tonsus* (= *Neocalanus plumchrus* (Marukawa, 1921)) was based on the figures of Campbell (1934) which are now known to be the nauplii of *Metridia pacifica* (Miller et al. 1984). Also Hirche (1980) believes that nauplius VI of *Calanoides carinatus* (Kroyer, 1849) can be distinguished from the same stage in *Calanus* by the presence of 16 setae on the third segment of antenna 1 compared with 17 setae in *Calanus* (Sømme 1934; Ogilvie 1953; Marshall & Orr 1955; Sazhina 1961).

To establish whether or not the developmental stages of *N. tonsus*, *C. macrocarinatus*, and *C. australis* could be distinguished, their young were raised from eggs in laboratory cultures. These experiments also provide information on developmental times and growth increments.

METHODS

Collection and culturing

Calanus australis and *Calanoides macrocarinatus* females were collected on 27 December 1984 in Southland Current water (Jillett 1969) 15 km southeast of Taiaroa Head, Otago Peninsula, South Island, New Zealand. A 1.0 m diameter, 333 µm mesh net with a non-filtering cod end was deployed in the upper 50 m at a station 100 m deep. *Neocalanus tonsus* females were collected on 16 August 1985 in subantarctic water 35 km south-east of Taiaroa Head using a 0.7 m diameter, 202 μm mesh closing net (Brown & Honegger 1978) with a non-filtering cod end, deployed between 1000–500 m at a station 1225 m deep. *Neocalanus tonsus* females were also collected for egg production experiments, but not developmental studies, on 2 November 1984 at the subantarctic station in the upper 150 m.

In the laboratory 10–51 females of each species were sorted into plexiglass cylinders inside 1-litre jars. The floor of each cylinder was 505 μm mesh nylon bolting cloth which permitted eggs to sink below the females and thereby avoid cannibalism. Females and developing larval stages were fed *ad libitum* on a mixture of the diatom *Thalassiosira weissflogii* and the flagellate *Isochrysis galbana* diluted in sea water filtered through Strainrite API filter bags, 1 μm nominal mesh size (New Haven,

Table 1 Time from egg-laying to median occurrence of developmental stages at 15 °C.

	Development time (days)	
	Copepodite I	Copepodite V
Neocalanus tonsus	11.1	24.0
Calanus australis	10.8	23.8
Calanoides macrocarinatus	9.9	20.2

Table 2 Summary of body dimensions (μm) of developmental stages of three calanid species reared at 15 °C. Females of *C. australis* and *C. macrocarinatus* were collected on 27 December 1984 and of *N. tonsus* on 16 August 1985. Eggs from female *N. tonsus*, collected on 2 Nov 1984, had,mean diameter 143 μm (s.d. 8μm). (Body width in ventral view for nauplii; body depth in lateral view for copepodites).

	Neocalanus tonsus					*Calanoides macrocarinatus*					*Calanus australis*				
	Mean	s.d.	*N*	Min	Max	Mean	s.d.	*N*	Min	Max	Mean	s.d.	*N*	Min	Max
Total length															
Egg	139	4	55	130	153	224	23	27	190	261	174	6	68	157	184
NI	137	5	8	126	141	156	2	3	154	158	180	8	30	163	199
NII	165	10	14	150	187	192	9	25	175	207	221	7	26	210	238
NIII	234	10	21	213	249	283		2	247	321	313	12	30	291	337
NIV	295	12	12	270	311	363		2	349	376	387	12	30	369	415
NV	358	11	10	342	376	440	27	20	381	481	456	14	30	412	472
NVI	431	26	6	405	472	514	21	7	480	536	524	21	30	494	558
CI	733	44	65	572	829	798	56	94	608	918	814	45	54	702	878
CII	1082	67	47	934	1284	1086	109	34	932	1377	1094	82	51	864	1235
CIII	1582	116	44	1380	1827	1669	74	27	1479	1785	1337	100	26	1224	1540
CIV	2293	125	26	1989	2436	2157	183	20	1785	2665	1666	102	16	1435	1815
CV	2977	104	3	2859	3055	2774	364	12	2168	3188	2199	191	14	1836	2469
CVI–f						3073		2	3034	3111	2642	263	14	2210	2921
Prosome length															
CI	591	34	65	473	665	652	44	94	526	756	662	40	54	560	728
CII	855	50	47	724	957	884	78	34	756	1094	869	63	51	709	958
CIII	1256	97	44	1096	1462	1380	65	27	1198	1454	1085	80	26	971	1245
CIV	1828	99	26	1583	1959	1765	153	20	1479	2168	1331	72	16	1203	1456
CV	2427	155	3	2272	2581	2311	319	12	1810	2728	1728	165	14	1414	2004
CVI–f						2563		2	2550	2576	2087	198	14	1778	2311
Body "width"															
NI	80	4	8	71	87	90	3	3	88	93	101	4	30	91	111
NII	83	8	14	69	105	98	7	25	85	110	112	6	26	99	122
NIII	113	7	21	103	125	138	10	17	110	152	153	6	30	133	162
NIV	150	8	12	140	160	205		2	200	210	186	8	30	172	204
NV	181	10	10	167	199	212	13	20	194	255	218	10	30	200	239
NVI	192	13	6	173	205	231	12	7	219	250	239	9	30	215	250
CI	195	22	65	119	236	201	23	35	148	256	228	24	44	166	265
CII	255	27	47	189	320	238	28	23	216	319	278	28	40	214	325
CIII	360	49	44	272	480	332	38	27	270	405	305	36	26	256	393
CIV	523	63	26	379	648	455	61	20	338	621	365	38	16	316	422
CV	813		2	750	875	648	92	12	472	756	502	68	14	424	640
CVI–f						776		2	770	783	591	97	14	437	777

CT). Phytoplankton cultures were grown under continuous illumination at 15 °C in f/2 medium (Guillard & Ryther 1962). Females were transferred to successive jars after about 1 day's egg production to initiate synchronously developing cohorts. Cultures were sampled with 51 µm mesh nylon bolting cloth, faecal pellets removed, and phytoplankton replenished daily until cultures had progressed to copepodite stages II–III, after which the interval was changed to every second day to minimise depletion of animals. Half the water in each culture was replaced at about 4-day intervals. Copepod cultures were maintained in diffuse, dim illumination at 15 ± 0.4 °C. This temperature was

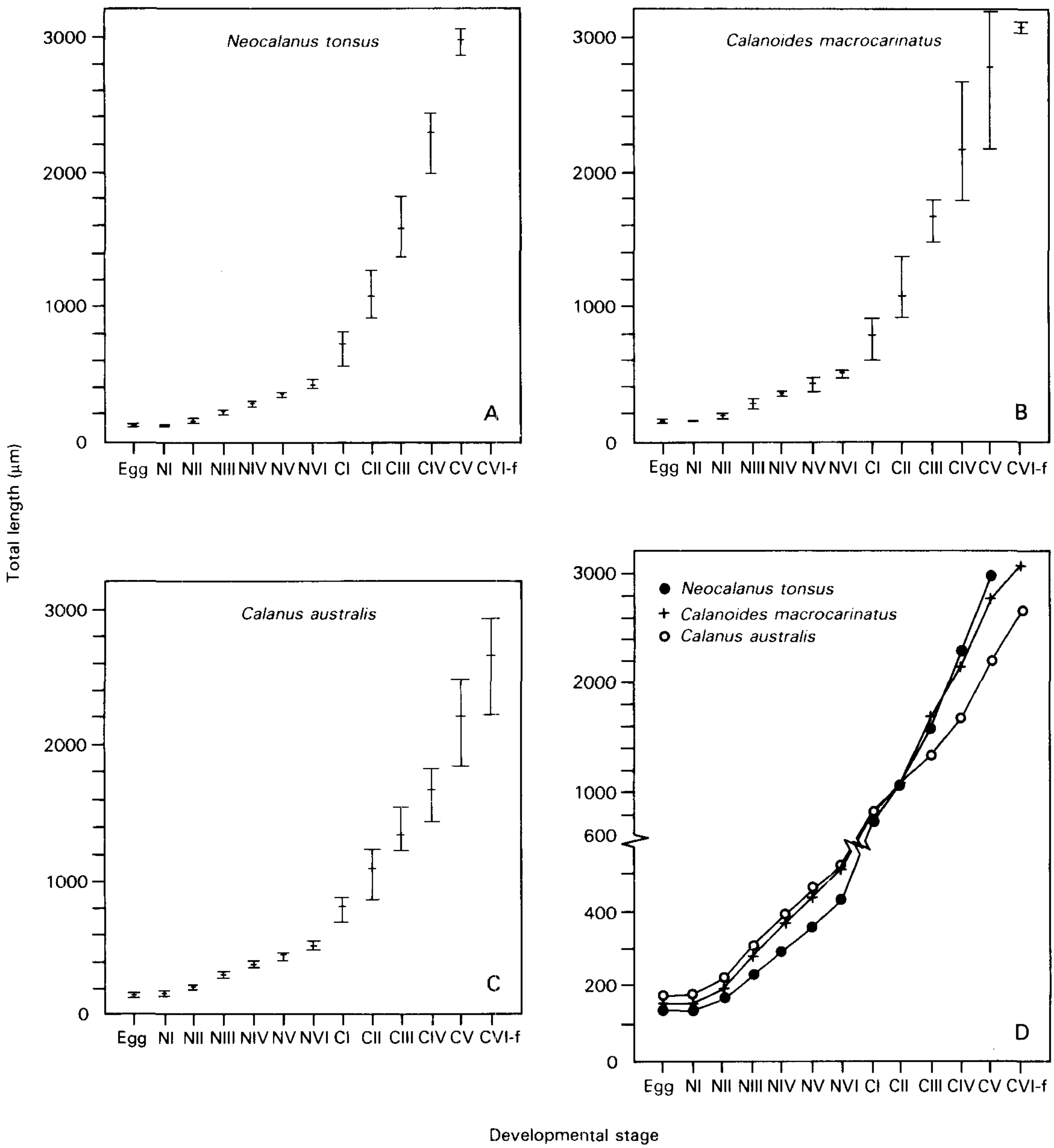


Fig. 1 Total length (mean, range) of copepod developmental stages in culture at 15 °C. A, *Neocalanus tonsus*; B, *Calanoides macrocarinatus*; C, *Calanus australis*; D, comparative means for the three species. Note the change of scale in total length in panel D. *Calanoides macrocarinatus* egg dimensions exclude the outer membrane.

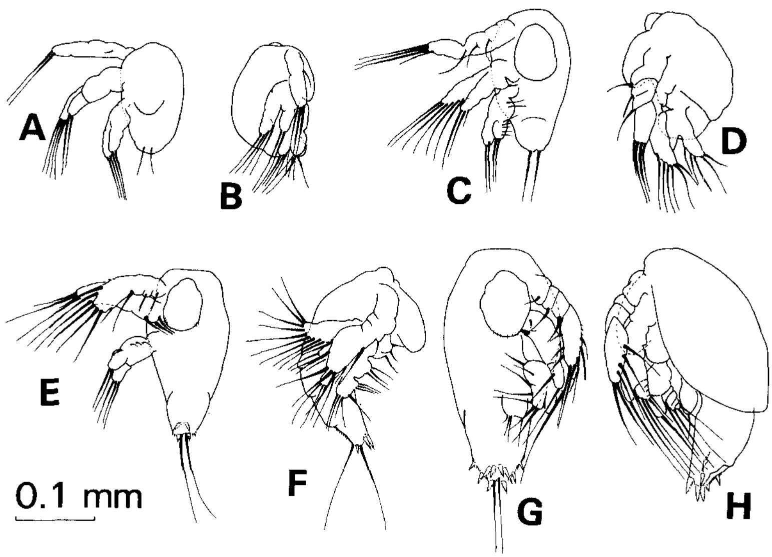


Fig. 2 *Neocalanus tonsus* naupliar stages: A, I ventral; B, I lateral; C, II ventral; D, II lateral; E, III ventral; F, III lateral; G, IV ventral; H, IV lateral.

Table 3 Segmentation and setation of naupliar appendages of *Neocalanus tonsus*. s, spine; mp, masticatory process; ms, minute spines. A "+" separates different tufts or types of setae or spines. Numbers alone = setae; * 4 incipient segments.

	Stage					
	I	II	III	IV	V	VI
Antenna 1						
No.of segments	0*	0*	4	4	4	4
Segment 1	1	1	1	1	1	1
Segment 2	1	1	1	1	1	1
Segment 3	1	1	1	1	1	1
Segment 4						
ventral	0	0	1	3	4	5
dorsal	0	0	2+3ms	4+2-4ms	6+2-3ms	8+3-4ms
terminal	3	4	4	4	4	4
Antenna 2						
basipod 1	1mp	1mp	2mp+1	2mp+1	2mp+1	2mp+1
basipod 2	1mp	1mp+1	1mp+2	1mp+2	1mp+2	1mp+2
endopod 1	1s	1	1	2	2	2
endopod 2						
lateral	2s	1	3	3	3	4
terminal	2	3	4	4	5	5
exopod	6	7	9	10	11	12
Mandible						
basipod 1	1s	1	1	1	1	1
basipod 2	2s	2	3	5	5	5
endopod	2s+1s+2	2+2+1+3	2+2+2+4	3+2+2+4	3+2+2+4	3+2+2+4
exopod	5	5	6	6	6	6
Caudal armature						
setae	2	2	2	2	2	2
ventral hooks	–	–	2	4	4	4
terminal hooks	–	–	2	2	2	2
lateral hooks	–	–	–	4	6	6

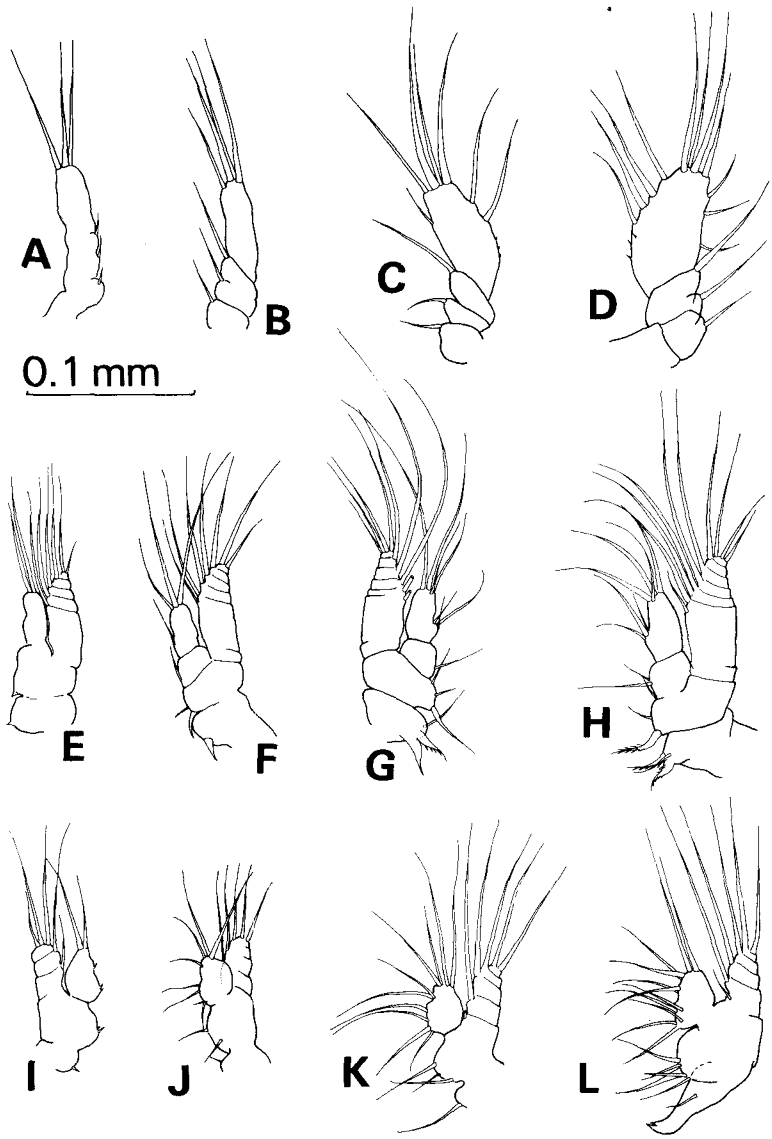


Fig. 3 *Neocalanus tonsus*, limbs of naupliar stages: antenna 1 (A,B,C,D), antenna 2 (E,F,G,H), mandible (I,J,K,L); nauplius I (A,E,I), nauplius II (B,F,J), nauplius III (C,G,K), nauplius IV (D,H,L).

selected to encourage development during the time available for experiments (M.D.O.'s time at University of Otago was limited), although 15 °C is higher than temperatures typically encountered in subantarctic water.

Measurements

Eggs (collected from these and other experiments) were measured live. Nauplii and copepodites (total length, prosome length, and body width) were measured in a glycerine/seawater mixture after preservation in formalin. Sample size decreased with increasing developmental stage, as the population was reduced by sampling. The mean, standard deviation, and range of body sizes is reported (see Table 2).

Descriptions

Drawings were made from whole specimens on a cavity slide in a glycerine/seawater mixture and with the assistance of a Zeiss drawing apparatus. Naupliar and copepodite limbs were drawn from whole preparations and dissected specimens respectively.

RESULTS

Development times

Calanus australis and *Calanoides macrocarinatus* progressed to the adult female stage but adult males were not observed. *Neocalanus tonsus* developed to copepodite V in the time available for this experiment. Development times are reported as the time for 50% of the population to reach the stated stage, estimated graphically from a plot of stage frequency *versus* time (Table 1). Development times to copepodite I were similar for all three species but *C. macrocarinatus* developed to copepodite V faster than *N. tonsus* and *C. australis.*

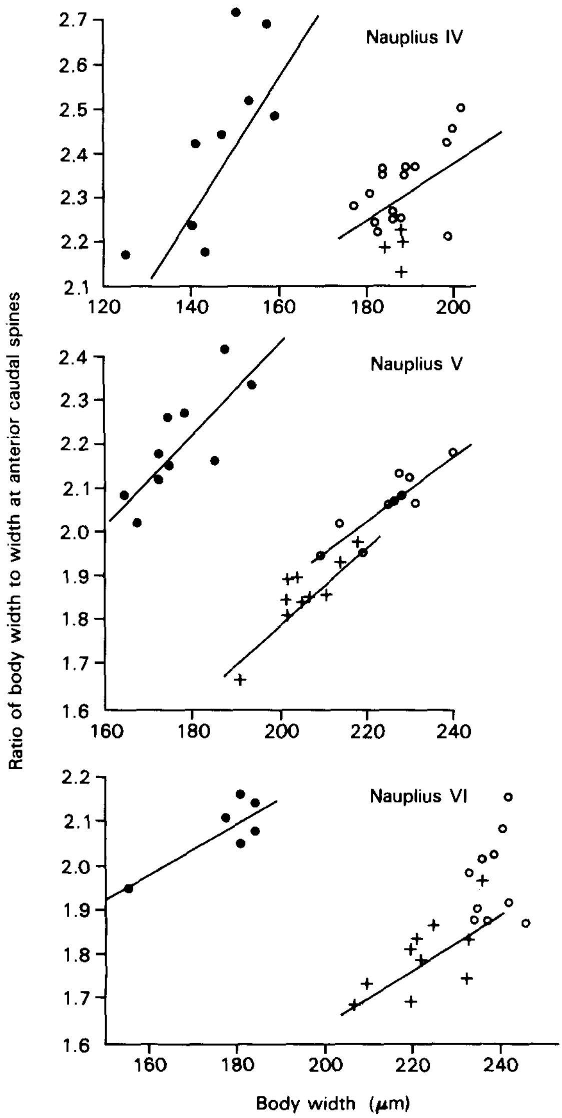


Fig. 4 Relationship between body width and the ratio of body width to width at the anterior caudal spines for nauplius IV, V, and VI for *N. tonsus* (●), *C. macrocarinatus* (+), and *C. australis* (○).

Table 4 Armature of antenna 2 to maxilliped of copepodite stages of *Neocalanus tonsus*. * deformed.

	I	II	III	IV	V
Antenna 2					
basipod 1	1	1	1	1	1
basipod 2	2	2	2	2	2
endopod 1	2	2	2	2	2
endopod 2	4/6	5/6	6/7	7/7	8/7
exopod 1	2	2	2	2	2
exopod 2	2	2	2	2	2
exopod 3	1	1	1	1	1
exopod 4	1	1	1	1	1
exopod 5	1	1	1	1	1
exopod 6	1	1	1	1	1
exopod 7	4	4	4	4	4
Mandible					
basipod	4	4	4	4	4
endopod 1	4	4	4	4	4
endopod 2	6	7	8	9	10
exopod 1	1	1	1	1	1
exopod 2	1	1	1	1	1
exopod 3	1	1	1	1	1
exopod 4	1	1	1	1	1
exopod 5	2	2	2	2	2
Maxilla 1					
inner lobe 1	10	11	13	15	15
inner lobe 2	4	4	4	4	4
inner lobe 3	4	4	4	4	4
outer lobe 1	4	6	8	9	9
outer lobe 2	0	1	1	1	1
exopod	7	7	8	9	10
basipod	3	3–4	4	4	5
endopod 1					
median	2	2	3	3	4
distal	2	2	3	3	4
endopod 2	5	5	6	6	7
Maxilla 2					
lobe 1	3	5	5	6	6
lobe 2	3	3	3	3	3
lobe 3	3	3	3	3	3
lobe 4	3	3	3	3	3
lobe 5	4	4	4	4	4
endopod	8	8	9	10	10
Maxilliped					
basipod 1	5	9	11*	11	11
basipod 2	3	4	5	5	5
endopod 1	1	1	1	2	3
endopod 2	–	–	1	2	2
endopod 3	–	–	–	1	2
endopod 4	–	1	1–2	1–2	1
endopod 5	4	4	4	4	4

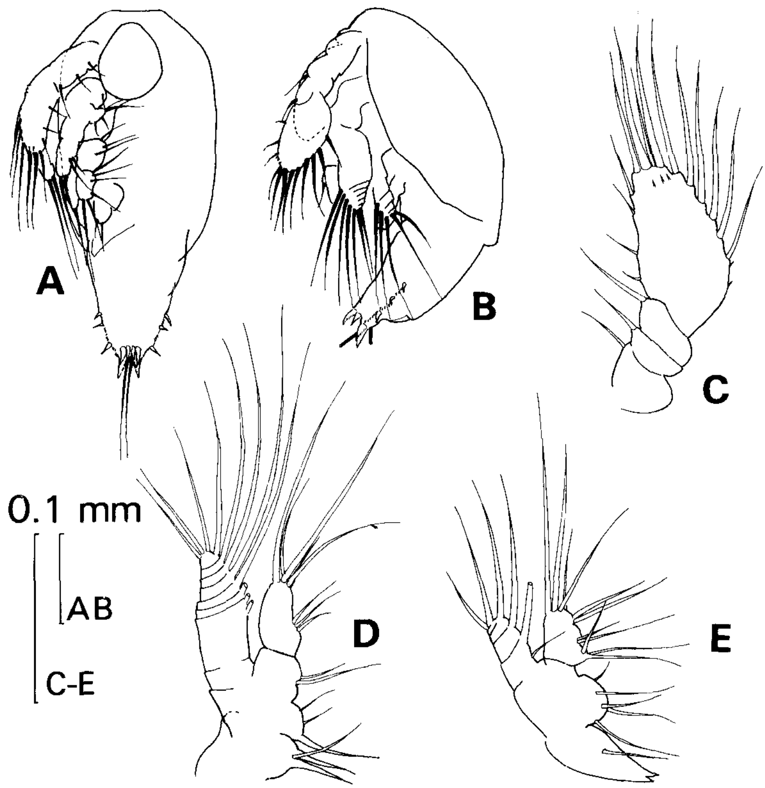


Fig. 5 *Neocalanus tonsus* nauplius V. A, ventral; B, lateral; C, antenna 1; D, antenna 2; E, mandible.

Size of developmental stages

Although *N. tonsus* produced smaller eggs and nauplii than *C. macrocarinatus* and *C. australis* (Table 2, Fig. 1), a cross-over point in lengths occurred at copepodite stages II–III (Fig. 1D). Beyond copepodite III the developmental stages of *N. tonsus* were longer than those of the other two species. The same cross-over point occurred in body depth (data not illustrated).

Description of developmental stages

Neocalanus tonsus (Brady)

Fig. 2-11, Table 2, 3 (nauplii), 4 (copepodites)

Egg spherical, unpigmented, lacking surface ornamentation.

Nauplius I–III General body shape as for the family (Fig. 2), becoming more elongate with age. Nauplius III with a pair of terminal and a pair of posteroventral hooks.

Antenna 1, Antenna 2, and Mandible (Fig. 3) have segmentation and setation as in Table 3.

Nauplius IV–VI General body shape of nauplius IV distinctly separated into cephalosome and posterior narrower region which is terminated by a pair of terminal hooks, four posteroventral hooks, and two pairs of lateral hooks (Fig. 2G, H). Body of nauplius V tapering posteriorly with two terminal hooks, four posteroventral hooks, and three pairs of lateral hooks (Fig. 5A, B). Body of nauplius VI more elongate than nauplius V, posterior hooks as in nauplius V (Fig. 6A, B).

The results of the relationship between the ratio of body width to the width at the anterior caudal spines (y) and body width (x) confirm that the former varies directly with body size in nauplius IV–VI. Equations for these relationships for nauplius VI–VI are respectively (Fig. 4):

$y = 0.015\,x + 0.157$ $r = 0.77, P < 0.01$
$y = 0.0102\,x + 0.378$ $r = 0.79, P < 0.01$
$y = 0.0057x + 1.078$ $r = 0.83, P < 0.05$

Antenna 1, Antenna 2, and Mandible of nauplius IV–VI (Fig. 3D, H, L; 5 C–E; 6 C–E) have segmentation and setation as in Table 3.

Maxilla 1 rudiment present in nauplius IV–VI, rudiment of Maxilla 2 present in nauplius VI.

Copepodite I Body with three free pedigerous segments. In dorsal view mandibular swelling on cephalosome slight; anal segment about as wide as long (Fig. 7A, B).

Antenna 1 (Fig. 7B) ten-segmented, extending beyond the caudal rami by one segment.

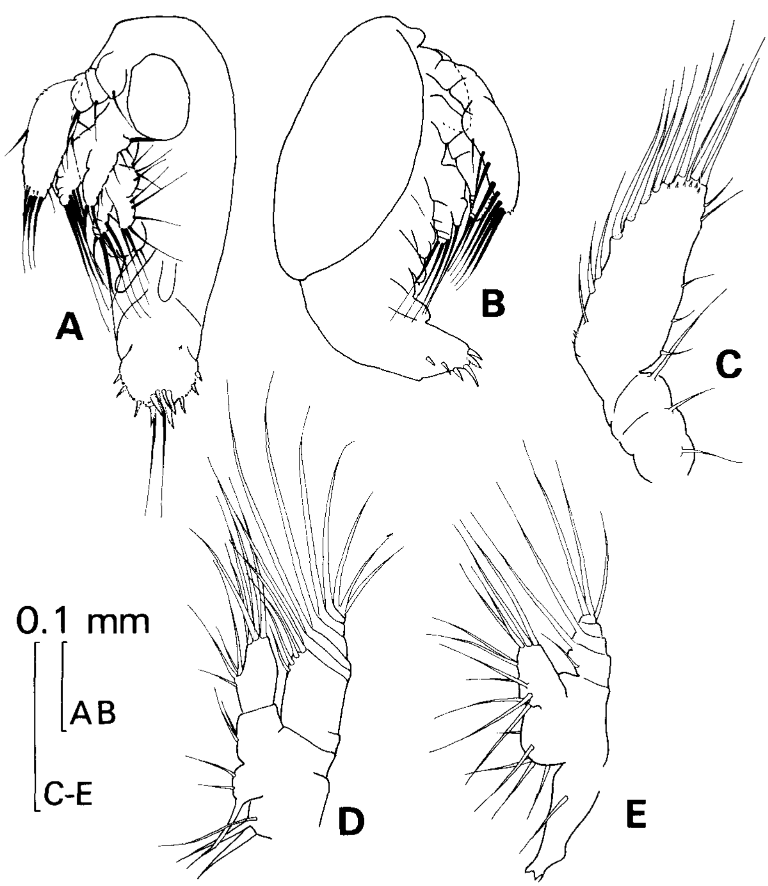


Fig. 6 *Neocalanus tonsus* nauplius VI. A, ventral; B, lateral; C, antenna 1; D, antenna 2; E, mandible.

Swimming leg 1 (Fig. 7H) with one-segmented rami; endopod with seven setae, exopod with four outer edge spines, long terminal spine, and three inner edge setae; basipods 1 and 2 naked.

Swimming leg 2 (Fig. 7I) with one-segmented rami; endopod with six setae, exopod with three outer edge spines, long, terminal, serrated spine (7–11 teeth) and three inner edge setae; basipod 2 with small outer distal edge spinule.

Copepodite II Body with four free pedigerous segments. In dorsal view, anal segment length 1.33 times width (Fig. 8A, B).

Antenna 1 (Fig. 8B) 16-segmented, extending beyond caudal rami by at least two segments. Setation of remaining mouthparts as in Table 4.

Swimming leg 1 (Fig. 8I) rami two-segmented; endopod 1 with one inner edge seta, endopod 2 with seven setae; exopod 1 with one outer edge spine, exopod 2 with three outer edge spines, one long terminal spine, and four inner edge setae; basipods 1 and 2 with one inner distal seta each.

Swimming leg 2 (Fig. 8J) rami two-segmented; endopod 1 with one inner edge seta, endopod 2 with seven setae; exopod 1 with one outer edge spine and an outer distal recurved hook; exopod 2 with two outer edge spines, one long, naked terminal spine, and four inner edge setae; basipod 1 with one inner edge seta; basipod 2 with one outer edge spine.

Swimming leg 3 (Fig. 8K) rami one-segmented; endopod with six setae; exopod with three outer edge spines, long terminal spine, three inner edge setae; basipods 1 and 2 naked.

Copepodite III Body with five free pedigerous segments (Fig. 9A). Cephalosome in lateral view sloping from region of mandibles to anterior head so that the head appears flattened (Fig. 9B). Anal segment in dorsal view with length more than 1.25 times its width.

Antenna 1 (Fig. 9B) 13-segmented, extending beyond the caudal rami by three segments. Setation of remaining mouthparts as in Table 4.

Swimming leg 1 (Fig. 9H) with segmentation and setal numbers as in stage II except that exopod 1 has one inner edge seta, and endopod 2 has eight setae.

Swimming leg 2 (Fig. 9I) with segmentation and setal numbers as in stage II except that exopod 1

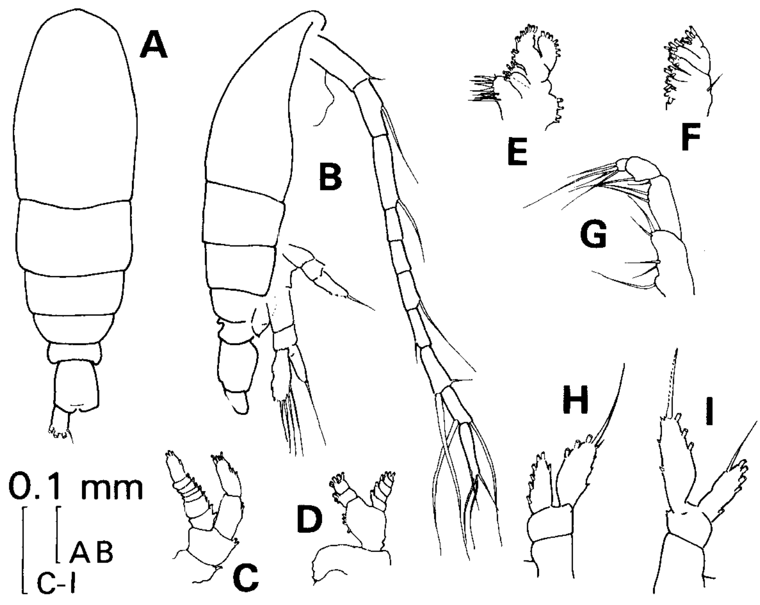


Fig. 7 *Neocalanus tonsus* copepodite I. A, dorsal; B, lateral; C, antenna 2; D, mandible; E, maxilla 1; F, maxilla 2; G, maxilliped; H, leg 1; I, leg 2.

has one inner edge seta, exopod 2 has three outer edge spines and five inner edge setae, and endopod 2 has eight setae; exopod 1 also with recurved outer distal hook.

Swimming leg 3 (Fig. 9J) rami two-segmented; endopod 1 with one inner edge seta, endopod 2 with seven setae, exopod 1 with one outer edge spine, exopod 2 with two outer edge spines, one long, naked, terminal spine, and four inner edge setae; basipod 1 with one inner edge seta, basipod 2 with one outer edge spine.

Swimming leg 4 (Fig. 9K) rami one-segmented; endopod with six setae, exopod with three rudimentary spine-like processes, one terminal spine, and three inner edge setae; basipods 1 and 2 naked.

Copepodite IV Body (Fig. 10A) with five free pedigerous segments. Cephalosome in lateral view sloping from region of mandibles to anterior head so that the head appears to be flattened (Fig. 10B).

Antenna 1 (Fig. 10B) 23-segmented, extending beyond caudal rami by two segments. Setation of remaining mouthparts as in Table 4.

Swimming leg 1 (Fig. 10H) segmentation and setation as in stage III; lobe present on proximal part of posterior surface of exopod 1.

Swimming leg 2 (Fig. 10I) as in stage III except that endopod 2 has nine setae, outer edge exopod spines larger, posterior surface spines on inner distal part of basipod 2; recurved hook on outer distal edge of exopod 1.

Swimming leg 3 (Fig. 10J) as in stage III except that endopod 2 has eight setae, exopod 1 with one inner edge seta, exopod 2 with three outer edge spines, one long naked terminal spine, five inner edge setae; basipod 2 with posterior surface spines on inner distal part of segment.

Swimming leg 4 (Fig. 10K) rami two-segmented; endopod with one outer edge seta, endopod 2 with seven setae, exopod 1 with one outer edge spine, exopod 2 with three outer edge spines, one long, naked terminal spine (deformed in illustrated specimen), five inner edge setae; basipod 1 with one inner edge seta, basipod 2 with one outer distal edge setule, posterior surface has spines on inner distal part.

Swimming leg 5 (Fig. 10L) with one-segmented rami; endopod with six setae, exopod with three outer edge spines, one long, naked, terminal spine, three inner edge setae; basipod 1 naked, basipod 2 with one outer distal edge setule, small spines on distal, posterior surface.

Copepodite V Body (Fig. 11A) with five free pedigerous segments. Cephalosome in lateral view less flattened along dorsoanterior surface than in copepodite IV (Fig. 11B).

Antenna 1 (Fig. 11B) 23-segmented, extending to the caudal rami. Setation of remaining mouthparts as in Table 4.

Swimming leg 1 (Fig. 11H) rami three-segmented; number of spines and setae as in stage IV except that exopod 3 has four inner edge setae, endopod 3 has seven setae.

Swimming leg 2 (Fig. 11I) rami three-segmented; number of spines and setae as in stage IV except that exopod 3 has five inner edge setae, endopod 3 with eight setae.

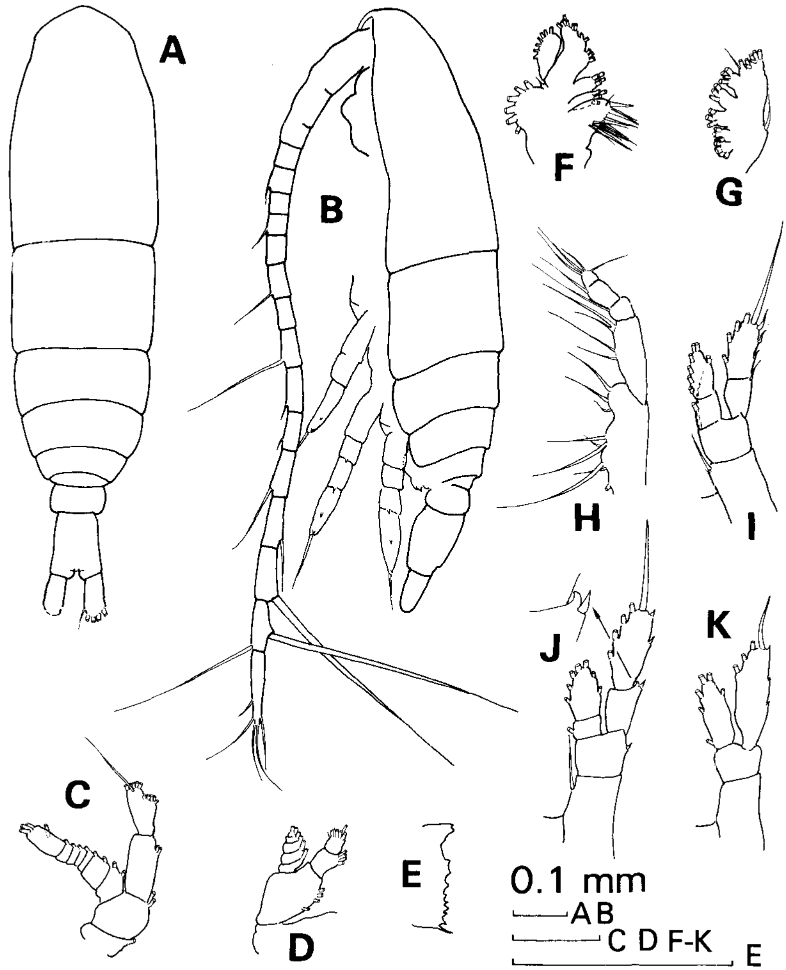


Fig. 8 *Neocalanus tonsus* copepodite II. A, dorsal; B, lateral; C, antenna 2; D, mandibular palp; E, distal part of mandibular blade; F, maxilla 1; G, maxilla 2; H, maxilliped; I, leg 1; J, leg 2; K, leg 3.

Swimming leg 3 (Fig. 11J) deformed as endopod 1 and exopod 1 fused. This was so for both specimens which were in good condition.

Swimming leg 4 (Fig. 11K) rami three-segmented; number of spines and setae as in stage IV except endopod 3 with seven setae; exopod 3 appeared to be slightly deformed.

Swimming leg 5 (Fig. 11L) rami two-segmented; legs asymmetrical and apparently deformed; exopod 2 with two or five outer edge spines and four or five inner edge setae, endopod 2 with six setae; otherwise generally similar to stage IV.

Adult female Development did not proceed to this stage in the time available.

Calanoides macrocarinatus (Brodsky)

Fig. 12–15, Table 2

Egg spherical (156 ± 18 μm), surrounded by a transparent region (34 ± 15 μm thick) with a slightly wrinkled surface similar to that reported by Hirche (1980) for *C. carinatus*. Refractile yellow-orange droplets usually visible within the egg. Occasionally eggs were observed with a smaller transparent zone but unchanged ovum diameter, with the resultant total egg diameter averaging 178 μm rather than 224 μm.

Nauplius I–VI General body shape as in *N. tonsus* (Fig. 12A–F). The results of the relationship between the ratio of body width to the width at the anterior caudal spines (y) and body width (x) confirms that the former varies directly with body size in nauplius V and VI (there are too few data for a trend to be evident in nauplius IV). Equations for these relationships for nauplius V and VI are respectively (Fig. 4):

$y = 0.0093\,x - 0.071$ $r = 0.89, P < 0.001$

$y = 0.0061\,x + 0.425$ $r = 0.69, P < 0.02$

Limbs have segmentation and setation as in *N. tonsus* (Table 3).

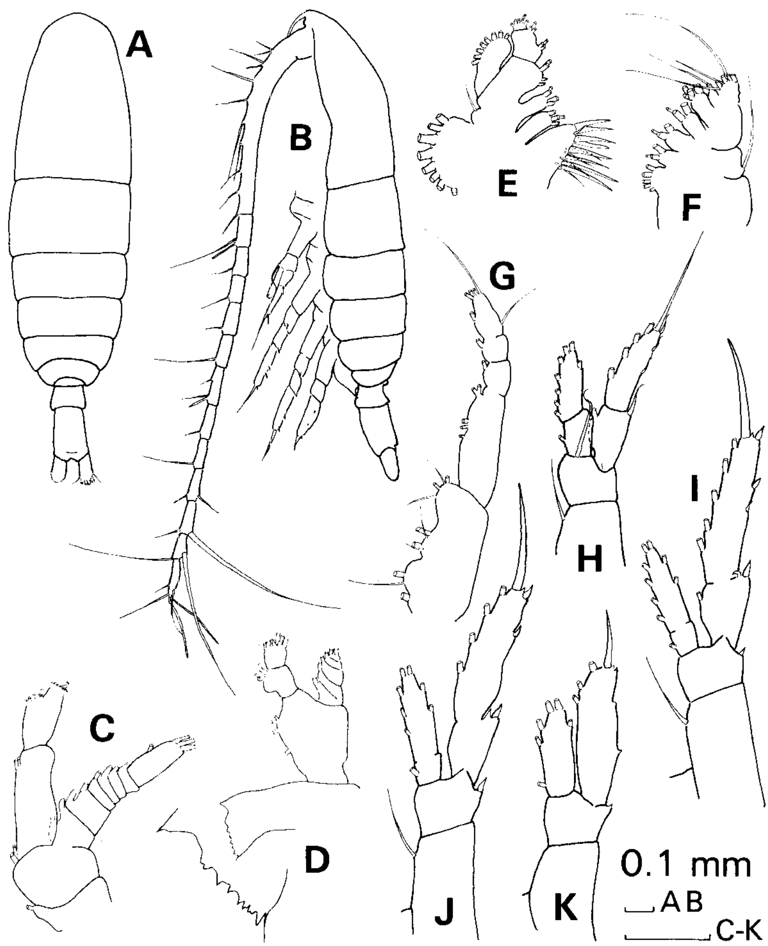


Fig. 9 *Neocalanus tonsus* copepodite III. A, dorsal; B, lateral; C, antenna 2; D, mandible; E, maxilla 1; F, maxilla 2; G, maxilliped; H, leg 1; I, leg 2; J, leg 3; K, leg 4.

Copepodite I General body shape (Fig. 13A) as in *N. tonsus* except length of anal segment is about 0.75 times width and mandibular swelling on cephalosome, viewed dorsally, conspicuous. *Antenna 1* (Fig. 13B) shorter than caudal rami. Setation of the limbs as in *N. tonsus* (Table 4).

Copepodite II General body shape (Fig. 13D) as in *N. tonsus* except length of anal segment approximately equal to its width. Setation of limbs as in *N. tonsus* (Table 4).

Antenna 1 (Fig. 13E) does not extend beyond caudal rami.

Swimming leg 2 (Fig. 13F) exopod 1 with outer distal extension normal, i.e., not recurved as in *N. tonsus.*

Copepodite III General body shape (Fig. 14A, B) as in *N. tonsus* except that the anterior head is pointed in lateral view; anal segment length approximately equals width. Setation of limbs as in *N. tonsus* (Table 4).

Antenna 1 (Fig. 14B) does not extend beyond caudal rami.

Swimming leg 2 (Fig. 15A) exopod 1 with outer distal extension normal, i.e., not recurved as in *N. tonsus.*

Copepodite IV General body shape (Fig. 14C, D) as in *N. tonsus* except that the anterior head is pointed in lateral view, and the posterior margin of the last metasomal segment is angular in lateral view.

Antenna 1 (Fig. 14D) does not extend beyond anal segment. Setation of limbs as in *N. tonsus* (Table 4) except that swimming leg 2 (Fig. 15B) exopod 1 outer distal extension is normal; i.e., not recurved as in *N. tonsus*, swimming leg 5 (Fig. 15C) endopod with five setae; basipod 2 of legs 2–5 with naked posterior surfaces.

Copepodite V General body shape (Fig. 14G, H) as in *N. tonsus* except that the anterior head is pointed in lateral view, and the posterior margin

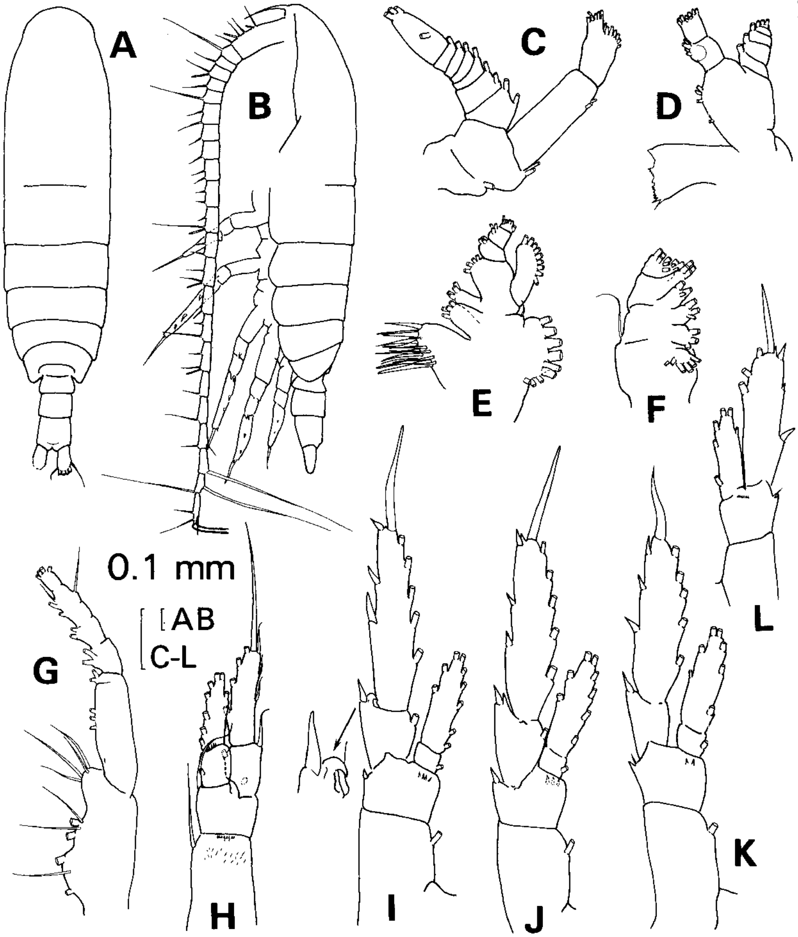


Fig. 10 *Neocalanus tonsus* copepodite IV. A, dorsal; B, lateral; C, antenna 2; D, mandible; E, maxilla 1; F, maxilla 2; G, maxilliped; H, leg 1; I, leg 2; J, leg 3; K, leg 4; L, leg 5.

of the last metasomal segment is angular in lateral view.

Antenna 1 (Fig. 14H) does not extend to the anal segment.

Setation of limbs as in *N. tonsus* (Table 4) except that swimming leg 2 (Fig. 15D) exopod 1 outer distal extension is normal (i.e., not recurved as in *N. tonsus*), swimming leg 5 (Fig. 15E) endopod with five setae, basipod 2 of legs 2–5 with posterior surfaces naked.

Adult General body shape (Fig. 14E, F) as in *N. tonsus* except that the anterior head is pointed in lateral view (illustrated specimen deformed), and the posterior margin of the last metasomal segment is angular in lateral view. The description conforms to that of the genus given by Bradford & Jillett (1974) and species by Brodsky (1972).

Calanus australis Brodsky
Fig. 16–19, Table 2

Egg is spherical, unpigmented, lacking surface ornamentation.

Nauplius I–VI General body shape as in *N. tonsus* (Fig. 16A–F). The results of the relationship between the ratio of body width to width at the anterior caudal spines (y) and body width (x) confirms that the former varies directly with body size in nauplius IV and V (the relationship is not significant for nauplius VI on the data at hand). Equations for these relationships for nauplius IV and V are respectively (Fig. 4):

$y = 0.0066\,x + 1.053 \qquad r = 0.53, P < 0.05$

$y = 0.0077\,x + 0.334 \qquad r = 0.89, P < 0.001$

Limbs with segmentation and setation as in *N. tonsus* (Table 3).

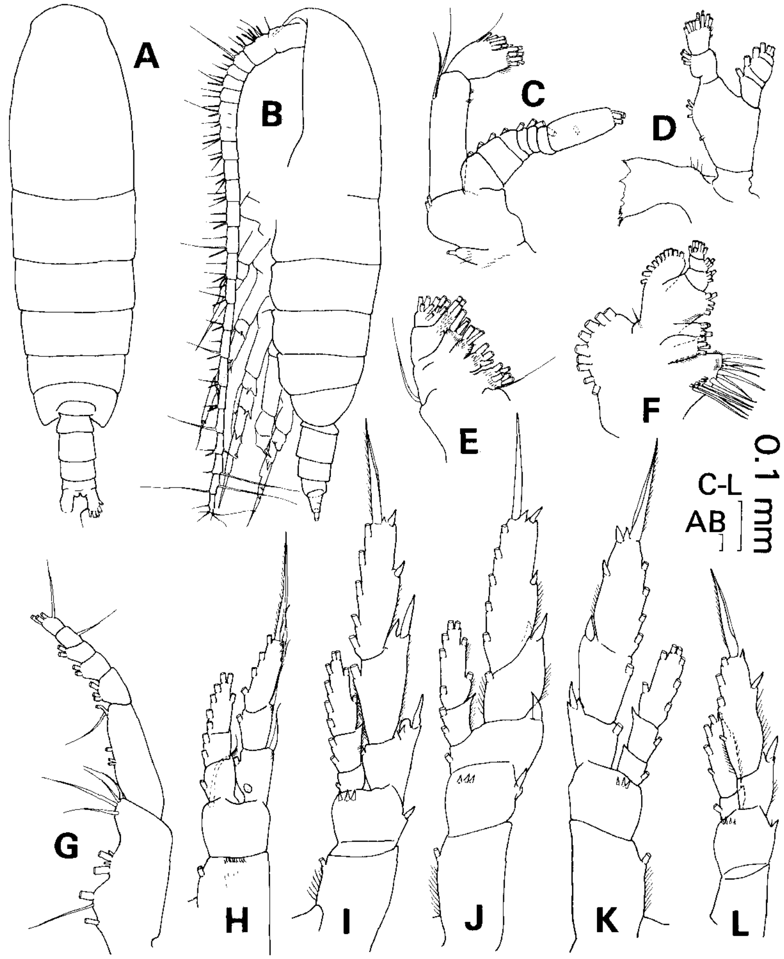


Fig. 11 *Neocalanus tonsus* copepodite V. A, dorsal; B, lateral; C, antenna 2; D, mandible; E, maxilla 1; F, maxilla 2; G, maxilliped; H, leg 1; I, leg 2; J, leg 3; K, leg 4; L, leg 5.

Copepodite I General body shape (Fig. 17A, B) as in *N. tonsus* except length of anal segment about 0.80 times width. Setation of limbs as in *N. tonsus* (Table 4) except maxilliped basipod 2 with four setae (Fig. 17C).

Antenna 1 (Fig. 17B) extends to the posterior border of the caudal rami.

Copepodite II General body shape (Fig. 17D, E) as in *N. tonsus* except length of anal segment approximately equals width. Setation of limbs as in *N. tonsus* (Table 4).

Antenna 1 (Fig. 17E) extends beyond caudal rami by two to three segments.

Swimming leg 2 (Fig. 17F) exopod 1 outer distal extension normal, i.e., not recurved as in *N. tonsus*.

Copepodite III General body shape as in *N. tonsus* (Fig. 18A, B) except that the head in lateral view is rounded and vaulted anteriorly; anal segment length approximately equals width. Setation of limbs as in *N. tonsus* (Table 4).

Antenna 1 (Fig. 18B) extends beyond caudal rami by one segment.

Swimming leg 2 (Fig. 19A) exopod 1 with outer distal extension normal i.e., not recurved as in *N. tonsus*.

Copepodite IV General body shape (Fig. 18C, D) as in *N. tonsus* except that the head in lateral view is rounded and vaulted anteriorly.

Antenna 1 (Fig. 18D) extends beyond caudal rami by two segments. Setation of limbs as in *N. tonsus* (Table 4) except: swimming leg 2 (Fig. 19B) exopod 1 outer distal extension normal (i.e., not recurved as in *N. tonsus*), and basipod 2 of legs 2–5 with posterior surfaces naked.

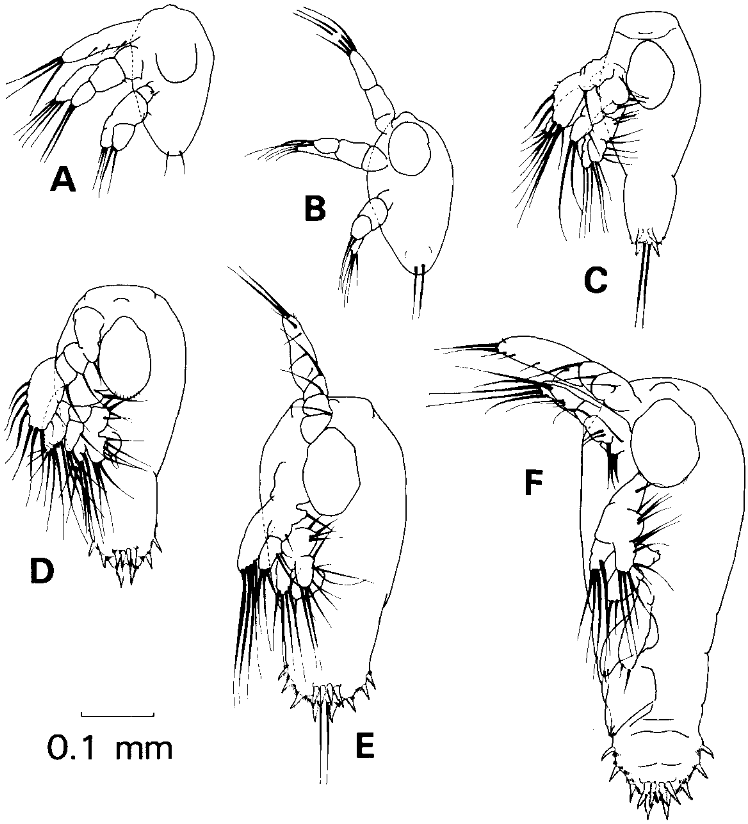


Fig. 12 *Calanoides macrocarinatus* naupliar stages, ventral view. A, nauplius I; B, nauplius II; C, nauplius III; D, nauplius IV; E, nauplius V; F, nauplius VI.

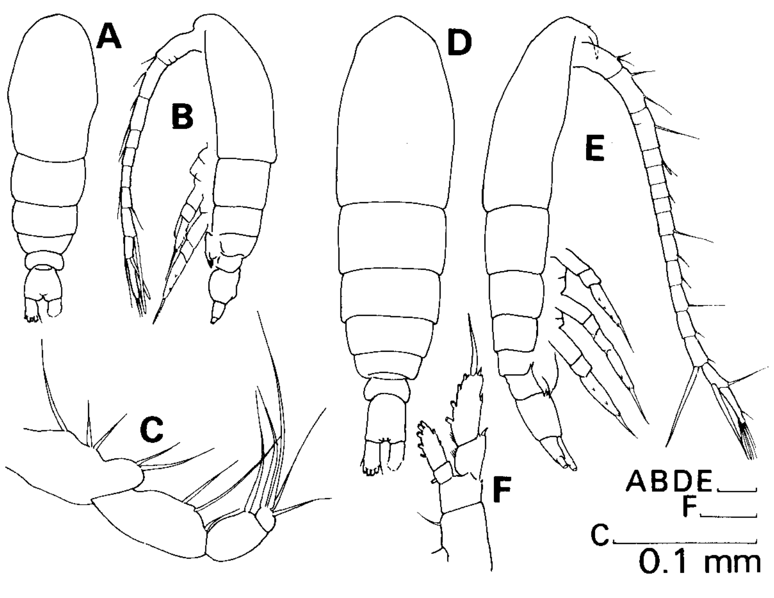


Fig. 13 *Calanoides macrocarinatus*. Copepodite I: A, dorsal; B, lateral; C, maxilliped. Copepodite II: D, dorsal; E, lateral; F, leg 2.

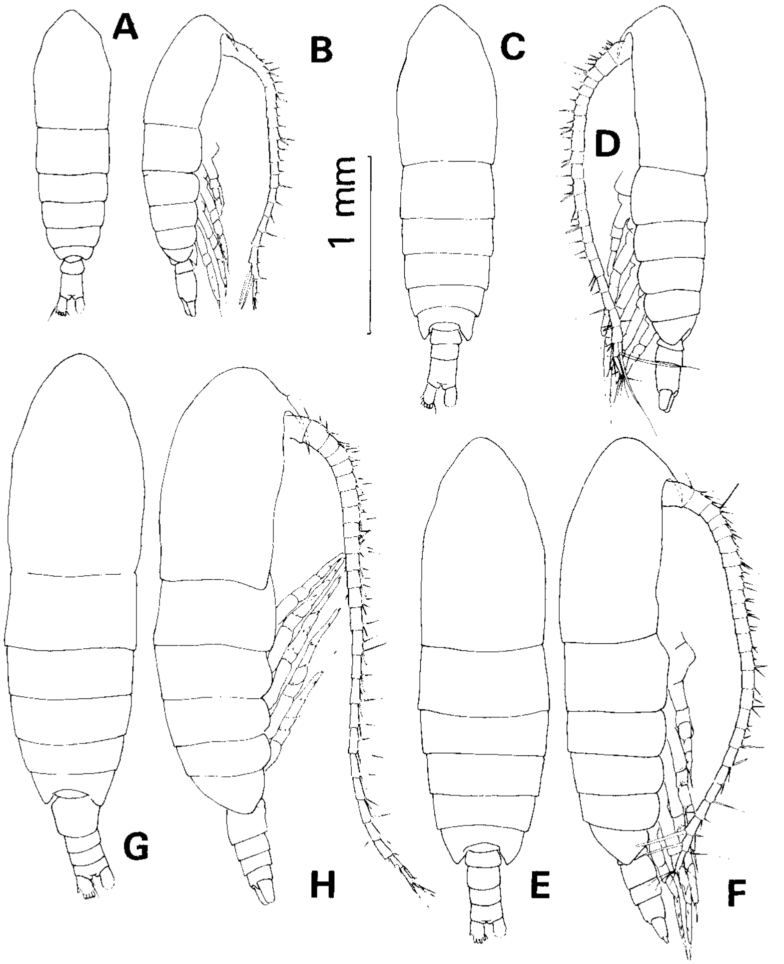


Fig. 14 *Calanoides macrocarinatus* whole animal. Copepodite III: A, dorsal; B, lateral. Copepodite IV: C, dorsal; D, lateral. Copepodite V: E, dorsal; F, lateral. Adult female: G, dorsal; H, lateral.

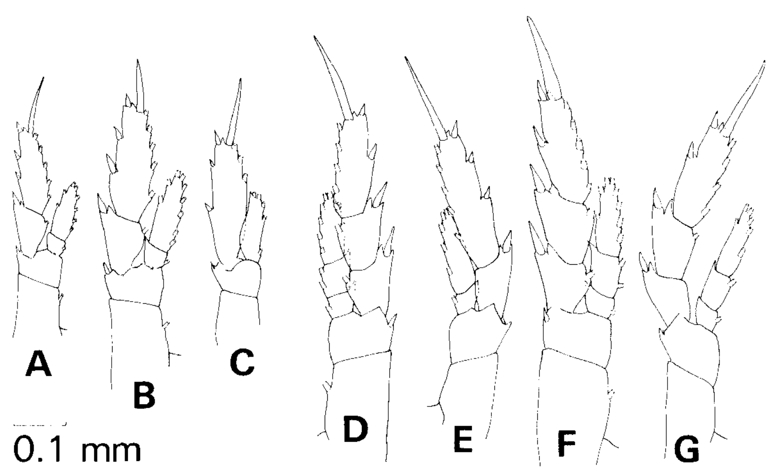


Fig. 15 *Calanoides macrocarinatus* swimming legs. Copepodite III: A, leg 2. Copepodite IV: B, leg 2; C, leg 5. Copepodite V: D, leg 2; E, leg 5. Adult female: F, leg 2; G, leg 5.

Copepodite V General body shape (Fig. 18E, F) as in *N. tonsus*.

Antenna 1 (Fig. 18F) does not extend beyond the caudal rami.

Setation of limbs as in *N. tonsus* (Table 4) except: swimming leg 2 (Fig. 19D) exopod 1 outer distal extension normal (i.e., not recurved as in *N. tonsus*), basipod 2 of legs 2–5 with posterior surfaces naked, and swimming leg 5, basipod 1 with inner edge teeth (Fig. 19E).

Adult General body shape (Fig. 18G, H) as in *N. tonsus* except that the genital segment is less bulbous in dorsal view. The description conforms to that for the species (Brodsky 1959).

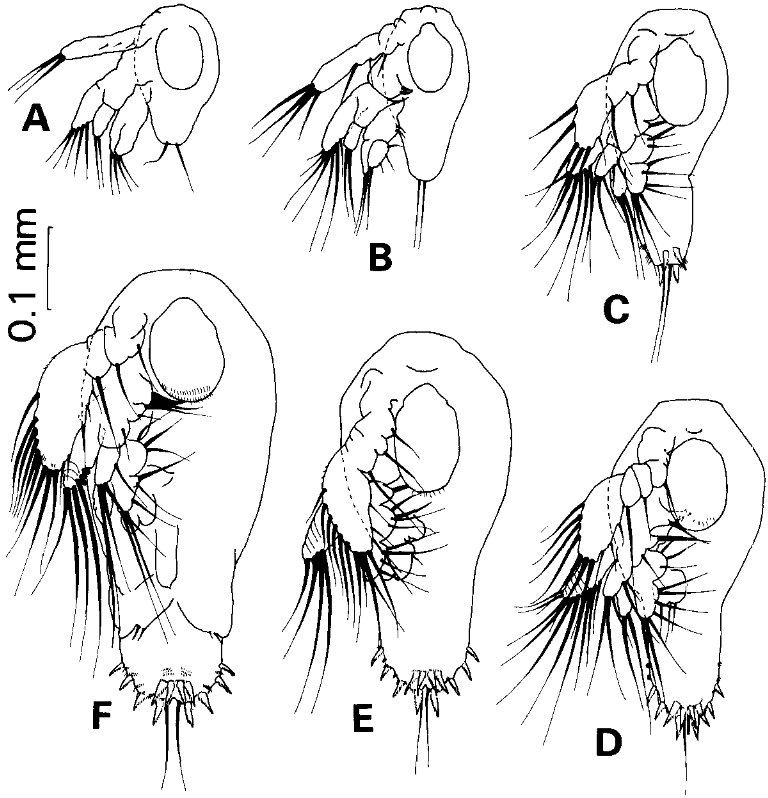


Fig. 16 *Calanus australis* naupliar stages, ventral view. A, nauplius I; B, nauplius II; C, nauplius III; D, nauplius IV; E, nauplius V; F, nauplius VI.

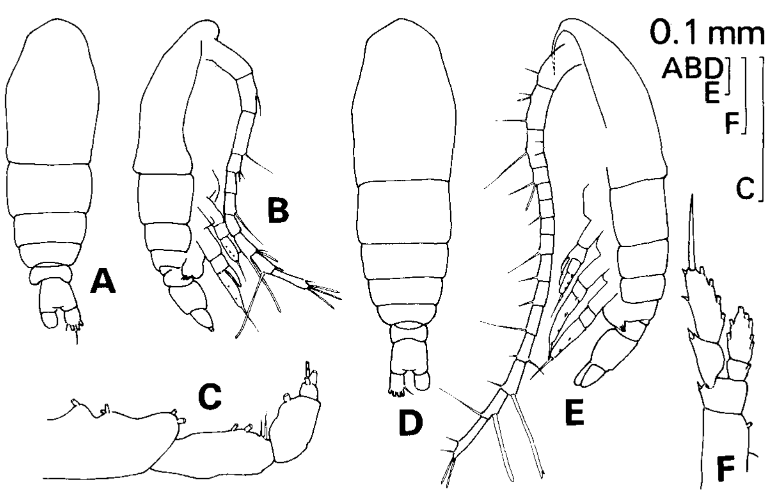


Fig. 17 *Calanus australis*. Copepodite I: A, dorsal; B, lateral; C, maxilliped. Copepodite II: D, dorsal; E, lateral, F, leg 2.

Fig. 18 *Calanus australis* whole animal; Copepodite III: A, dorsal; B, lateral: Copepodite IV: C, dorsal; D, lateral. Copepodite V: E, dorsal; F, lateral. Adult female: G, dorsal; H, lateral.

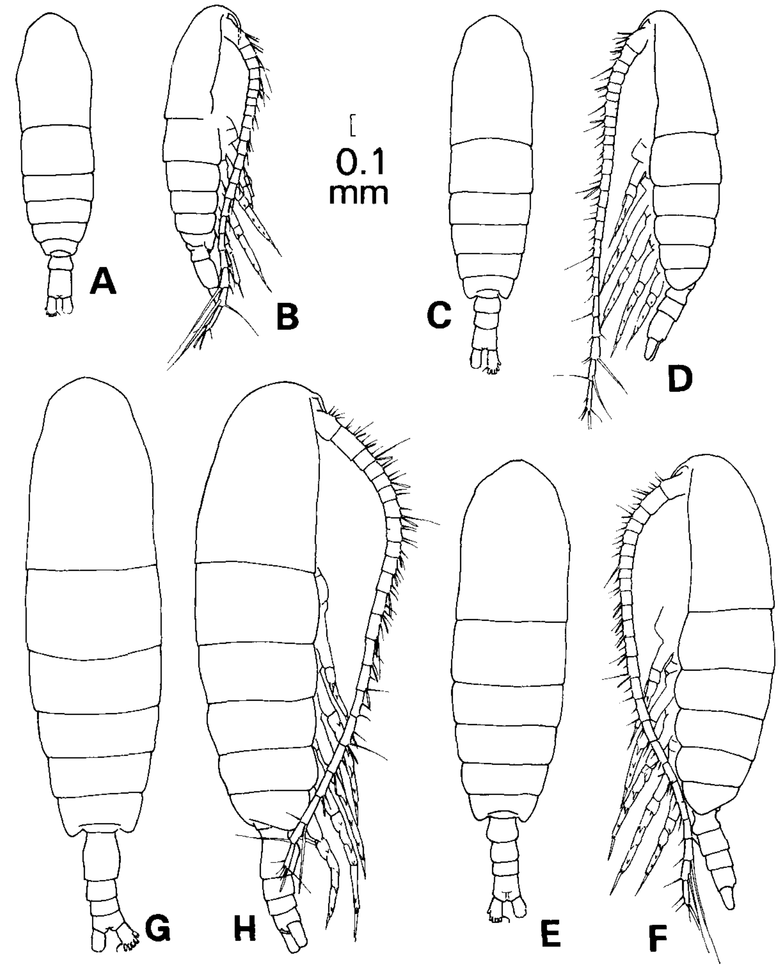
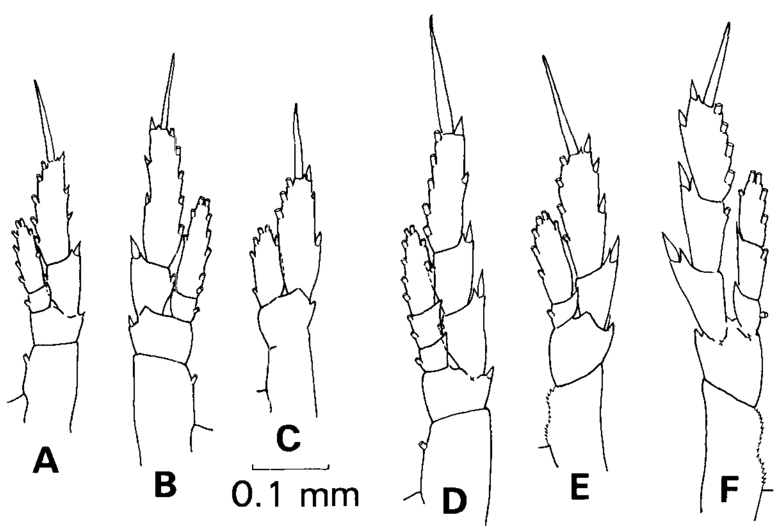


Fig. 19 *Calanus australis* swimming legs. Copepodite III: A, leg 2. Copepodite IV: B, leg 2; C, leg 5. Copepodite V: D, leg 2; E, leg 5. Adult female: F, leg 5.



DISCUSSION

The development times of *N. tonsus, C. macrocarinatus*, and *C. australis* to copepodite I are comparable to those reported for other members of the Calanidae (Mullin & Brooks 1970; Paffenhöfer 1970; Hirche 1980; Thompson 1982; Landry 1983). Development times for *N. tonsus* and *C. australis* to reach copepodite V are among the longer times reported for calanid species at 15 °C. Replication of these experiments under carefully controlled food concentrations and a range of temperatures would now be useful.

Comparison of prosome lengths of copepods cultivated in the laboratory with those collected *in situ* reveals that laboratory specimens were consistently smaller (Table 5). This is probably a function of the lower ambient temperatures in subantarctic and Southland Current waters off the Otago Peninsula (Jillett 1969) than the experimental temperature (15 °C) as copepod body size often is a negative function of temperature (e.g., Deevey 1960). However, with *C. australis*, Deevey (1966) showed that annual changes in the length of females in the field were related to the phytoplankton cycle. Selection of the experimental temperature and food regime was guided by time constraints rather than any effort to reproduce natural conditions. Consequently, identification of field specimens beyond the egg stage should be based upon meristic characters and body proportions rather than absolute size.

In uniform laboratory conditions the size of *N. tonsus* stages changed from being the smallest of the three species in early development, to the largest after copepodite III (Fig. 1). This pattern is consistent with the suggestion that larger copepod species show a higher growth increment in their later developmental stages than smaller copepods (McLaren & Corkett 1984; Longhurst 1986). Because development times to the copepodite V were comparable for *N. tonsus* and *C. australis* (see Table 1), *N. tonsus* had not only a larger increment of tissue but also a higher rate of growth than *C. australis* during the late copepodite stages.

The nauplii of the Calanidae may be separated from other nauplii which have bilaterally symmetrical caudal armature, by the series of minute spines present, from nauplius III onwards, on the dorsoproximal border of the last segment of antenna 1.

The previously cited differences between calanid nauplii (e.g., Björnberg 1972; Hirche 1980) appear not to hold for the New Zealand species. The developmental stages of *N. tonsus* can be identified with certainty from other co-occurring calanids from nauplius IV onwards (Table 6). Nauplii IV–VI of *N. tonsus* can be distinguished stage by stage from *C. macrocarinatus* and *C. australis* by the non-overlapping cluster formed when their maximum body width is plotted against the ratio of maximum body width to the width of the posterior body at the level of the anterior caudal hooks (Fig. 4). *Calanoides macrocarinatus* and *C. australis* cannot be practically separated from each other as they overlap both in body width and the ratio of body width to width at the anterior caudal spines. Thus *Calanus australis* and *C. macrocarinatus* can be identified with certainty only in the copepodite stages; the first copepodite stages are the least easily distinguished under low magnification. If *C. macrocarinatus* were known to be absent then *N. tonsus* and *C. australis* nauplii could be separated on size and body proportions. *Calanoides macrocarinatus* eggs can be separated easily from the eggs of the other two species (Table 6) but its naupliar stages overlap in size with both *N. tonsus* and *C. australis* and the body proportions of naupliar stages IV-VI overlap with those of *C. australis.*

Table 5 Prosome lengths of copepods (μm) raised in the laboratory at 15 °C from eggs compared with field specimens collected concurrently (M.D.O. unpubl. data).

Species	Developmental stage	Laboratory Mean	Laboratory *N*	Laboratory Range	Field Mean	Field *N*	Field Range
Calanus australis	copepodite V	1726	14	1414–2004	2419	20	2291–2568
	female	2087	14	1778–2311	2469	20	2370–2607
Neocalanus tonsus	copepodite V	2427	3	2272–2581	2802	38	2632–3017
	female	–	–	–	3050	120	2632–3483
Calanoides macrocarinatus	copepodite V	2311	12	1810–2728	2950	24	2844–3042
	female	2563	2	2550–2576	3121	3	3042–3239

Table 6 Distinguishing characteristics of developmental stages of three calanid species. N, nauplius; C, copepodite; y, ratio anterior body width to posterior body width; x, anterior body width (µm); A, antenna; B, basipod; Mxp, maxilliped; P, leg; Re, exopod; Ri, endopod.

Stage	Character	*Neocalanus tonsus*	*Calanoides macrocarinatus*	*Calanus australis*
Egg	Shape	Spherical	Spherical surrounded by transparent region with slightly wrinkled surface 68 ± 30 µm thick	Spherical
	Pigment	None	Refractile yellow-orange droplets usually visible within egg	None
NIV	$y =$	$0.015x + 0.157$	–	$0.0066x + 1.053$
NV	$y =$	$0.0102x + 0.378$	$0.0093x - 0.071$	$0.0077x + 0.334$
NVI	$y =$	$0.0057x + 1.078$	$0.0061x + 0.425$	–
CI	Anal segment length:width	1	≈ 0.75	≈ 0.80
	A1 length	Extends beyond caudal rami by 1 segment	Shorter than caudal rami	Extends to posterior border of caudal rami
	Mxp B2 setae	3	3	4
CII	Anal segment length:width	1.33	1	1
	A1 length	Extends beyond caudal rami by 2 segments	Extends to posterior border of caudal rami	Extends beyond caudal rami by 2–3 segments
	Outer distal extension Re 1 of P2	Recurved	Normal	Normal
CIII	Head, lateral view	Flattened	Pointed	Rounded, vaulted
	Anal segment length:width	1.25	1	1
	A1 length	Extends beyond caudal rami by 3 segments	Extends to posterior border of caudal rami	Extends beyond caudal rami by 1 segment
	Outer distal extension Re 1 of P2	Recurved	Normal	Normal
CIV	Head, lateral view	Flattened	Pointed	Rounded, vaulted
	Last prosome segment, lateral view	Rounded	Angular	Rounded
	Length (µm)	1989–2436	1785–2665	1435–1815
	A1 length	Extends beyond caudal rami by 2 segments	Does not extend to posterior border of anal segment	Extends beyond caudal rami by 2 segments
	Outer distal extension Re 1 of P2	Recurved	Normal	Normal
	B2, P2–5 posterior surface	Spinous	Naked	Naked
	P5 Ri setae	6	5	6
CV	Head, lateral view	Rounded	Pointed	Rounded
	Last prosome segment, lateral view	Rounded	Angular	Rounded
	Length (µm)	2859–3055	2168–3188	1836–2469
	A1 length	Extends to caudal rami	Does not extend to anal segment	Extends to caudal rami
	Outer distal extension Re 1 of P2	Recurved	Normal	Normal
	B2, P2–5 posterior surface	Spinous	Naked	Naked
	P5 Ri setae	6	5	6
	P5 B1 inner border	Naked	Naked	Toothed

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