JOURNAL OF CRUSTACEAN BIOLOGY, 9(2): 242–256, 1989

COMPARISON OF LARVAL AND ADULT STAGES OF *CHTHAMALUS DALLI* AND *CHTHAMALUS FISSUS* (CIRRIPEDIA: THORACICA)

Kristina M. Miller, Sally M. Blower, Dennis Hedgecock, and Jonathan Roughgarden

ABSTRACT

Adult and larval forms of *Chthamalus dalli* and *Chthamalus fissus* are compared and distinguishing characteristics described. Adult forms of these species differ in malate dehydrogenase enzyme allozymes, in the setae of the second cirrus, and in shell characteristics. Larval forms are morphologically identical, although larvae cultured from adults collected at Monterey Bay differ in size at naupliar stages I–III and at the cyprid stage.

Chthamalus dalli Pilsbry is a common northern barnacle inhabiting the high intertidal zone from Alaska to San Diego and northern Japan. *Chthamalus fissus* Darwin, a close relative of *C. dalli,* is a southern barnacle inhabiting the high intertidal zone from San Francisco to Baja California. In the region between San Francisco and San Luis Obispo, these species are abundant and can be found in combined densities reaching 70,000 per m^2 in the same high intertidal band on the shore (cf. Newman and Abbott, 1980).

The community structure of barnacle populations has been studied extensively in the past twenty-five years. Early studies focused on the roles of competition and predation on adult barnacles in structuring benthic communities (Connell, 1961a, b; Southward, 1976). Recent work has explored the role of settlement in benthic communities (Gains and Roughgarden, 1985; Roughgarden *et al.,* 1985). Current studies are examining factors that determine the settlement rate such as currents and predation in the plankton (Roughgarden *et al.,* 1987; Roughgarden *et al.,* 1988). Such work requires identification of barnacle larvae in mixed-species plankton samples. The present study was conducted to examine the morphological differences between the larvae of *C. fissus,* not previously described, and *C. dalli,* previously described from Russian material by Korn and Osyannikova (1979). Electrophoretic and morphological characters together with distinguishing shell features are presented. We found that adult *C. dalli* and *C. fissus* can be separated by the MDH allozymes, by the setae of the second cirrus (W.A. Newman, personal communication), and by a combination of external features. The larvae of these species appear to be morphologically identical.

MATERIALS AND METHODS

Mass Culturing Techniques.—Ripe eggs were obtained from freshly collected adult barnacles and placed in 1 μm-filtered sea water. Newly hatched larvae were collected by pipetting them from areas of maximum light intensity created by a point light source. The larvae were then placed in a 4-l glass jar at a density of one larva per 2 ml sea water. The jars, each of which contained fresh 1 μm-filtered sea water at 33.5 ppt salinity, were kept at either 13° or 18°C and mildly aerated with filtered air from a ⅓ hp oil-free pump. The larvae were fed the Tahitian strain of *Isochrysis galbana* at a density of 1×10^5 cells per ml.

The water in the jars was changed on alternate days by pouring the contents through 100-μm filters, washing the larvae in the filters (continually immersed in water) with 1 μm-filtered sea water, placing the larvae in small bowls, and pipetting active larvae into beakers with fresh 1 μm-filtered sea water. Subsamples of these larvae were preserved for later use in 3% Formalin. Larvae that were inactive at the bottom of the bowls were presumed unhealthy or dead. Such larvae were usually alive but not feeding and were more prone to bacterial infection than the active larvae. To minimize the risk of bacterial contamination, the unhealthy larvae were discarded.

Larvae of *Chthamalus* are particularly prone to becoming caught on debris due to their fine setulation and small size. Therefore, to rear these larvae successfully, all particulate contaminates coming from the air or filter bags were removed regularly and the alga was monitored carefully for evidence of clumping.

Analysis of Larvae.—Formalin-preserved larvae were examined under a compound microscope with a combined phase contrast/Nomarski attachment. Size was determined with an ocular micrometer. Total length was measured from the frontal margin to the tip of the dorsal thoracic spine. Cephalic shield length was measured from its frontal margin to its posterior border,

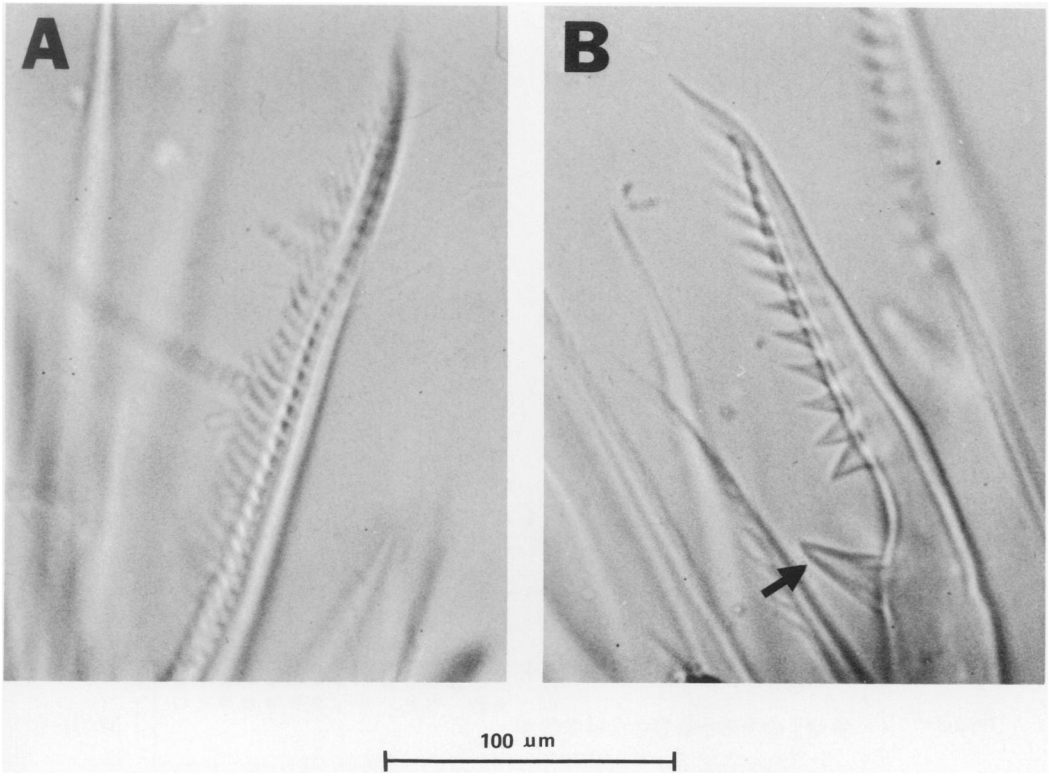

Fig. 1. Photographs of the characteristic setae of the second cirrus of adult *Chthamalus dalli* and *C. fissus*. Setae of *C. dalli* (A) are finely bipectinate, while setae of *C. fissus* (B) are coarsely bipectinate and have a pair of basal guards (see arrow).

and its width measured behind the frontolateral horns. In addition, drawings were made with a camera lucida attachment. At least 50 larvae of each species at each stage were examined for the drawings.

Adult Descriptions.—Adult *C. dalli* and *C. fissus* were collected from the field to examine and to photograph the characteristic differences in the second cirrus, a feature noted by W. A. Newman (personal communication). In addition, shell features that might be used to separate the species in the field were quantified.

Electrophoresis.—Adult barnacles, *Chthamalus* spp., were collected, dissected, and identified to species by the second cirrus characteristic. Sixty barnacles of each species (the sample of *C. fissus* included all three opercular morphs) were then placed in individual wells in a plastic tray and covered with a few drops of 0.5M Tris-HCL buffer, pH 7.1. Each barnacle was homogenized within the well with a glass pestle and the barnacle extract was absorbed with a filter-paper wick. Horizontal starch-gel electrophoresis and enzyme-staining were carried out on the samples as described by Hedgecock (1979). The samples were then stained for malate dehydrogenase enzyme.

RESULTS

Adult Descriptions

Under microscopic observation (400×), the setae on the second cirri of *Chthamalus dalli* appear finely bipectinate (Fig. 1A), while the setae of *C. fissus* are coarsely bipectinate and have a pair of basal guards (Fig. 1B). Using this setal characteristic to separate the species initially, electrophoresis showed that *C. fissus* and *C. dalli* can be clearly distinguished on the basis of their malate dehydrogenase (MDH) enzymes (Fig. 2A). *Chthamalus* has two loci encoding malate dehydrogenase (*Mdh-1* and *Mdh-2*, see Figs. 2A, B); both enzymes are dimers, so that the single-banded phenotypes represent homozygotes and triple-banded phenotypes represent heterozygotes. Although both *Mdh-1* and *Mdh-2* are highly polymorphic loci, the two species have different alleles (further work with larger samples has led to the identification of at least six alleles at each locus (Blower and Hedgecock, unpublished observations)). The difference in the alleles is particularly clear for the *Mdh-1* locus (Fig. 2A), and served to confirm the species classification using the setae on the second cirri.

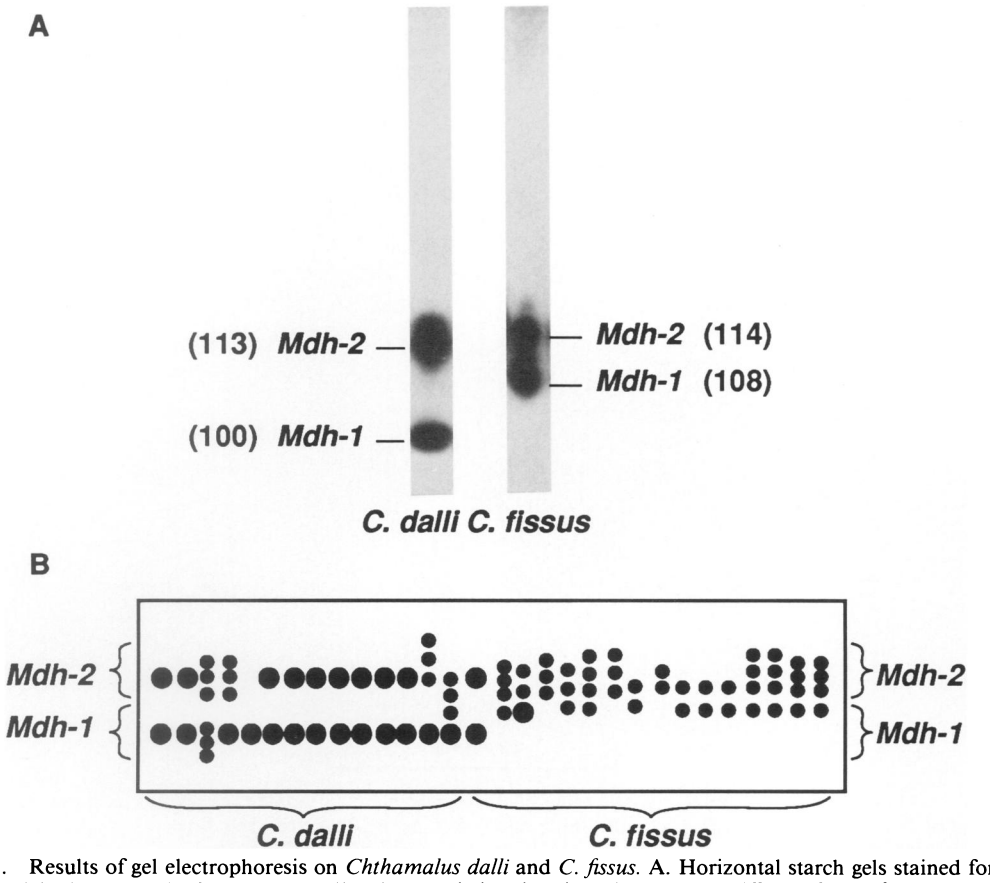

Fig. 2. Results of gel electrophoresis on *Chthamalus dalli* and *C. fissus*. A. Horizontal starch gels stained for malate dehydrogenase (MDH) enzyme. The characteristic migration distances are different for *C. fissus* and *C. dalli* and hence this assay can be used for species identification. The single bands at both the *Mdh-1* and *Mdh-2* loci of both species indicates homozygosity. B. A drawing of a horizontal starch gel stained for malate dehydrogenase (MDH) enzyme. Both species are extremely polymorphic at both loci (*Mdh-1* and *Mdh-2*). Both heterozygotes (3 bands) and homozygotes (1 band) at each locus are shown.

External characters allow an approximate distinction of *C. dalli* from *C. fissus* to be made in the field. We have found that the two species can be identified in the field with approximately 90% accuracy, measured against the setal characteristics, using a combination of shell features including shape of orifice, color at the base, and relative degree of corrugation of the shell (see Table 1 and Fig. 3). The orifice of *C. dalli* is always broad and oval (Fig. 3A, B), while that of *C. fissus* varies from slitlike, overhanging, or oval (Pilsbry, 1916; Fig. 3C–E). Therefore, individuals with slitlike or overhanging orifices can be immediately classified as *C. fissus*. Moreover, individuals with oval orifices that have smooth shells with even, light brown coloration are *C. dalli* (Fig. 3A, B); those with corrugated shells and a dark brown band at the base are *C. fissus* (Fig. 3C–E). However, we found that 12% of adult *Chthamalus* spp. with oval orifices possessed a mixture of these characteristics (19/156 of *C. dalli* and *C. fissus* combined; Table 1). In *C. dalli,* 4% of the adults had brown bases and 2% possessed corrugated shells. Alternatively, of adults of *C. fissus,* 6% had even coloration and 31% had relatively smooth shells (individuals with slit or overhanging orifices showed slightly less variability). In the case of mixed characteristics, the second cirrus should be examined before a definite identification can be made.

Larval Descriptions

In the laboratory, *C. dalli* and *C. fissus* developed at approximately the same rate

when reared at 18°C (Fig. 4) and both species took 17–18 days for the first cyprids to appear. They spent an average of 3–4 days at each of the six naupliar stages, excluding the first which lasted less than a day. At the lower temperature (13°C), however, the developmental time to cyprid for *C. dalli* was extended by about five days (to 22–23 days), while *C. fissus* ceased to develop past the third stage.

The nauplii of *C. dalli* and *C. fissus* have the same morphological features of other species so far described in the genus *Chthamalus* (*C. malayensis* Pilsbry (see Karande and Thomas, 1976); *C. fragilis* Darwin (see Lang, 1979); *C. stellatus* Poli (see Bassindale, 1936; Daniel, 1958)), and in a species of *Euraphia* (*E. aestuarii* Stubbings, originally classified in the genus *Chthamalus*; see Sandison, 1967). In addition, the present descriptions of *C. dalli* and *C. fissus* are similar to Korn and Osyannikova's (1979) description of larvae of *C. dalli* with the exception of four setae and slight differences in general shape. The shape of the larvae described in the present paper differs from that described by Korn and Osyannikova (1979) in that the cephalic shield in naupliar stages I–V is slightly less rounded, the anterior portion of the labrum is rounded, and the anterior and posterior ends of the cyprid carapace are less pointed.

In general, the convex dorsal shield of nauplii of *Chthamalus* is round, with the width nearly equaling the length. When the cephalic shield differentiates from the trunk in stages IV–VI, it has no paired posterior spines as often found in other genera. The labrum of nauplii of *Chthamalus* is unilobate and the sequence of spine formation in successive stages is similar in all species thus far described. The successive formation of spines on the thorax is also similar in all species of *Chthamalus* described. The decreasing ratio of the dorsal thoracic spine to the trunk is similar in species of *Chthamalus* and *Euraphia* (Sandison, 1967). Furthermore, nauplii of *Chthamalus* generally have highly setulose appendages, often with many plumose or feathery setae. Sandison (1967) cited the presence of "hispid" setae as unique to the family Chthamalidae. However, these setae have since been found by Lewis (1975) on the naupliar appendages of *Pollicipes polymerus* Sowerby, a pedunculate barnacle considered to be close to the stem of the sessile barnacles (Darwin, 1854).

Table 1. External features of adult *Chthamalus dalli* and *C. fissus*. Percentages and sample numbers (*N*) are shown. For each character type, the total number of individuals examined is equal to the sum of the *N*'s. Color and rugosity characters were scored only on individuals with oval orifices. Color indicates the color of the basal region of the shell, while rugosity indicates the roughness of the base of the shell. The symbol O-H stands for overhanging.

Character	Percentage			
	C. dalli	*N*	*C. fissus*	*N*
Orifice				
Oval	100	122	29	36
Slit	0	0	61	76
O-H	0	0	10	12
Color				
Even	96	116	6	2
Brown	4	6	94	34
Rugosity				
Smooth	98	119	31	11
Corrugated	2	3	69	25

All of these characteristics can be used in making distinctions between nauplii of *Chthamalus* and nauplii of other species, but by far the easiest distinction is their small relative size at all stages. With this distinction alone, a separation can be made between most larvae of *Chthamalus* and those of other barnacle species thus far described on the California Coast, with the exception of *Pollicipes polymerus* (see Discussion).

In this study, no morphological differences were found between the larvae of *C. dalli* and *C. fissus*. The only possible distinguishing characteristic (at least in the vicinity of Monterey Bay) is the size of the two species at same stages, although size should be used as a character with caution (Barnes, 1953). At 18°C, *Chthamalus dalli* starts out in the first stage as the larger of the two species at 248 ± 4 μm in length and 138 ± 3 μm in width (Table 2). *Chthamalus fissus* is only slightly smaller at 206 ± 3 μm × 124 ± 5 μm. These size differences continue to diverge through the third stage, after which the larvae of both species become indistinguishable in size. However, at the cyprid stage, the larvae of *C. fissus* are slightly larger than those of *C. dalli* (493 ± 3 μm × 246 ± 3 μm versus 448 ± 10 μm × 229 ± 5 μm; Table 2). Sizes of larvae grown at 13°C are similar (Table 2).

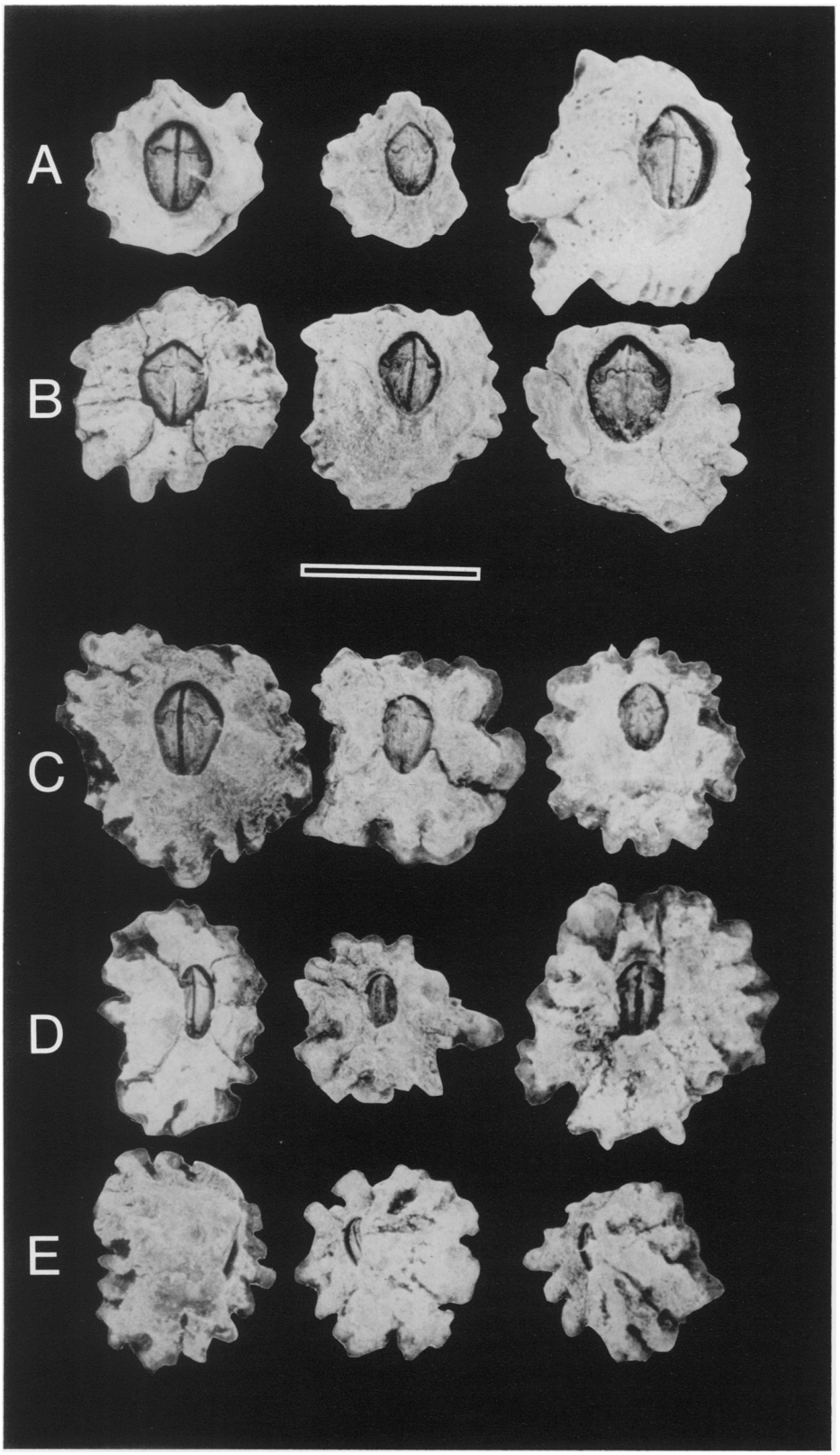

Fig. 3. Photographs showing a range of external shell features of *Chthamalus dalli* (rows A, B) and *C. fissus* (rows C–E). An oval orificial opening, smooth shell, and even coloration at the base of the shell are features of

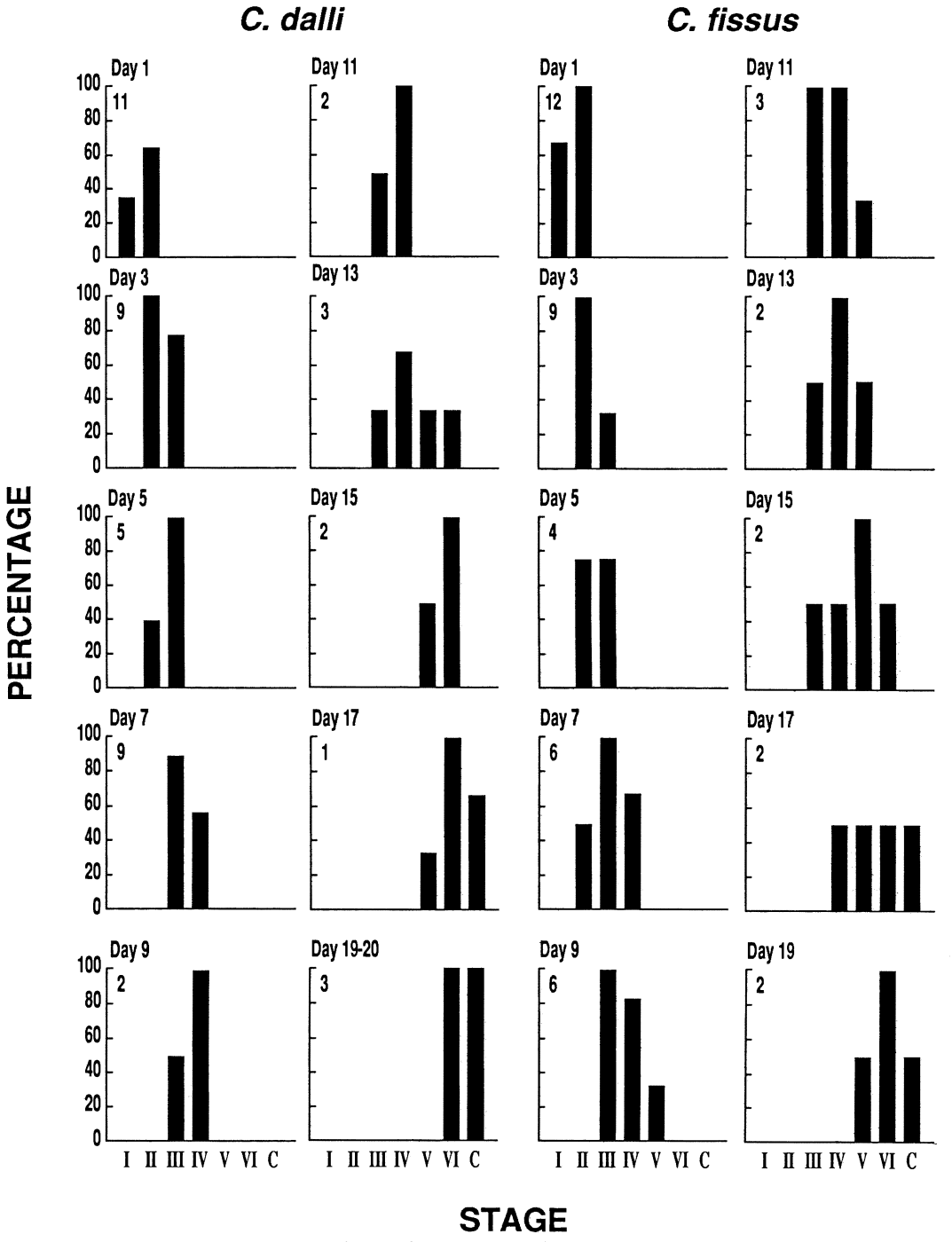

Fig. 4. Developmental timetable for *Chthamalus dalli* and *C. fissus*. Histograms indicate the percentage of jars with stages present on the indicated day. Since jars often contain more than one stage on a given day, these percentages do not add up to 100, nor do they give the actual proportion of stages present for a given day. They indicate only the presence of a given stage on a given day. Numbers in the upper left corner (under day) indicate the number of jars examined.

←

C. dalli (A, B). Alternatively, *C. fissus* is characterized by corrugation of the shell, a dark brown band at the base of the shell, and variability in the shape of the orifice including oval (C), slit (D), and overhanging (E) forms. Scale bar equals 2 mm.

Table 2. Sizes of larvae of *Chthamalus dalli* and *C. fissus* grown at 18° and 13°C. Total length was measured from the frontal margin to the tip of the dorsal thoracic spine. Cephalic shield length was measured from the frontal margin to the posterior border of the cephalic shield. Width was measured as the maximum cephalic shield width. Means are given, with standard errors in parentheses.

		Chthamalus dalli				*Chthamalus fissus*			
Stage	Tempera-ture	Total length	Width	Carapace length	*N*	Total length	Width	Carapace length	*N*
I	18°C	248 (4)	138 (3)	—	22	206 (3)	124 (5)	—	22
II	18°C	309 (3)	175 (3)	—	13	271 (3)	156 (7)	—	5
	13°C	318 (2)	191 (2)	—	35	264 (2)	162 (2)	—	31
III	18°C	361 (5)	219 (6)	—	7	305 (2)	193 (3)	—	13
	13°C	353 (3)	209 (2)	—	16	309 (3)	194 (3)	—	16
IV	18°C	383 (2)	257 (3)	285 (3)	20	346 (7)	248 (3)	270 (4)	26
	13°C	379 (3)	250 (3)	293 (2)	15	—	—	—	—
V	18°C	414 (3)	303 (3)	348 (3)	24	416 (5)	316 (6)	348 (4)	20
	13°C	421 (7)	307 (4)	357 (5)	5	—	—	—	—
VI	18°C	470 (10)	354 (8)	404 (8)	14	465 (7)	380 (4)	423 (4)	27
C	18°C	448 (10)	229 (5)	—	7	493 (3)	246 (3)	—	14

Since the larvae of *C. dalli* and *C. fissus* are similar in all other aspects except size, their morphological features will be described together throughout the remainder of this paper. The ventral views of the larvae are illustrated in Fig. 5, while lateral views of the posterior portion of the body are presented in Fig. 6. In addition, drawings of

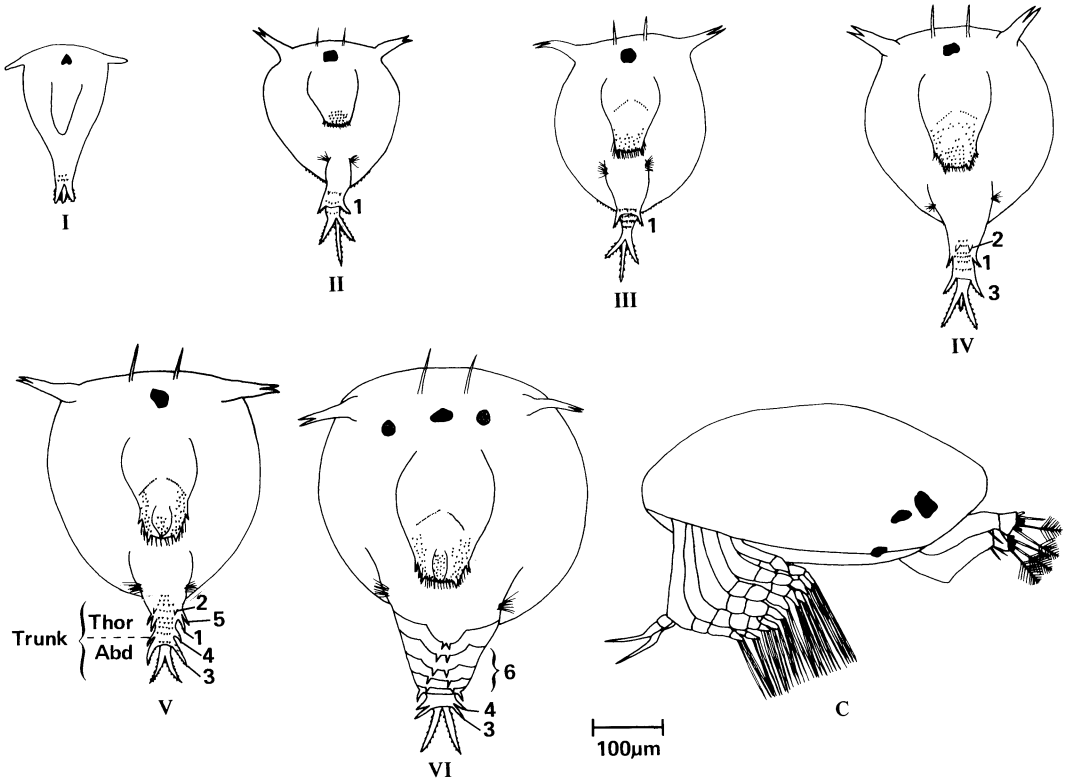

Fig. 5. Body forms of larvae of *Chthamalus dalli* and *C. fissus*. The six naupliar stages, indicated by Roman numerals, are drawn from their ventral aspect, while the cyprid stage, indicated by "C," is a lateral view. The spines on the thorax are labeled, in order of appearance, with Arabic numerals. The abbreviations Thor and Abd labeled on stage V stand for Thorax and Abdomen, respectively.

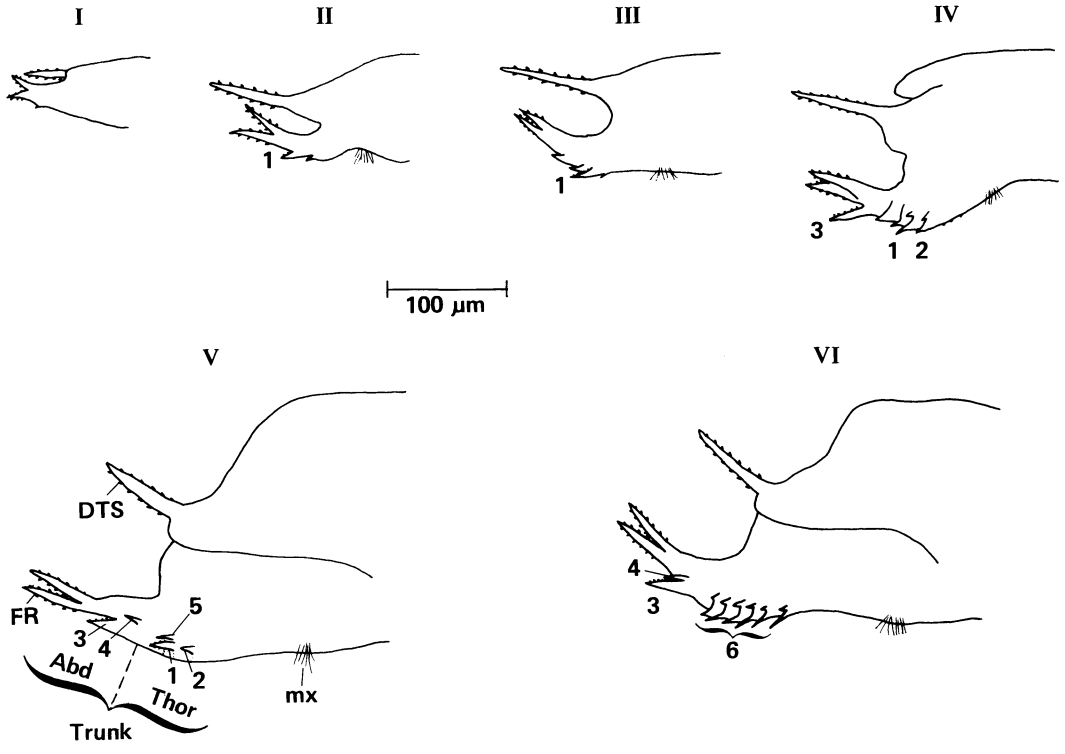

Fig. 6. Lateral view of the posterior portion of the body of the six naupliar stages of *Chthamalus dalli* and *C. fissus*. Spines on the trunk are labeled in order of appearance with Arabic numerals. Naupliar stages are indicated with Roman numerals. Abbreviations include: Abd = Abdomen, Thor = Thorax, DTS = Dorsal Thoracic Spine, FR = Furcal Rami, and mx = Maxillae.

the antennules (Fig. 7), the antennae (Fig. 8), and the mandibles (Fig. 9) are referred to in the following descriptions. A presentation of the setation formulae (following Newman, 1965) is given in Table 3.

Stage I larvae are wineglass-shaped with horns 30 μm long (Fig. 5). The dorsal thoracic spine and trunk are approximately equal in length at 24 μm. The labrum is smooth and rounded at the distal margin, the setae on the appendages are all simple, and no frontal filaments are apparent at this stage. The exopodite of the antenna has only five simple setae (Fig. 8), while that of the mandible shows four (Fig. 9). The antennule setation formula is 00042110 (Fig. 7, Table 3).

Stage II nauplii appear sometime during the first day after the hatching of stage I nauplii. The characteristic feature of stage II is the seven to nine spines 8.5 μm long on the lower margin of the pubescent labrum (Fig. 5). At this stage, the broad and somewhat rounded cephalic shield has a fine row of five to seven spinules on its lower margin. The dorsal thoracic spine becomes longer than the trunk, giving these a ratio of 1.2:1. There is one pair of spines 17 μm long with spinules on the lower margin as well as three rows of fine spinules on the thorax (Fig. 5). The dorsal thoracic spine and furcal rami are covered with small spines from this stage forward. In addition, many of the setae of the appendages develop fine setules, giving them a plumose or feathery appearance in this and subsequent stages (Figs. 7–9). The exopodite of the antenna receives two more setae, but the antennule still has no preaxial setae at this stage.

Stage III larvae appear around the third day and are characterized by a loss of three to five spines on the pubescent labrum, leaving two spines 11 μm long on the posterolateral margin (Fig. 5). It should be noted that, in some instances, the larvae of *C. fissus* retain a fine row of spines 2 μm long between the paired 11-μm spines. The nauplii in stage III are otherwise similar to those

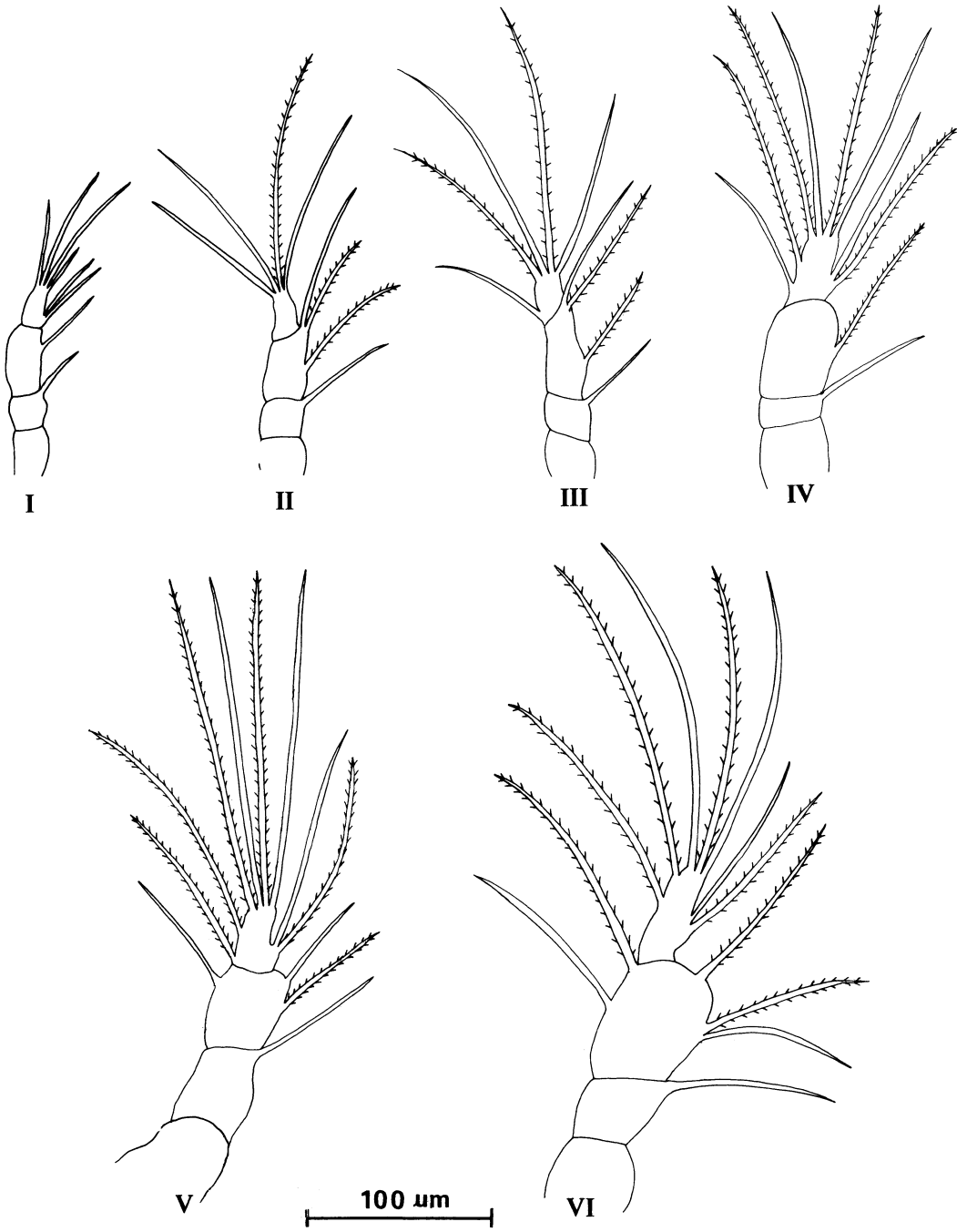

Fig. 7. Antennules of the nauplii of *Chthamalus dalli* and *C. fissus*. Naupliar stages are indicated by Roman numerals.

in stage II in that the cephalic shield has yet to differentiate from the body, there are still five pairs of spines 17 µm long with spinules on the lower margin as well as three rows of fine spinules on the thorax (Fig. 5). The dorsal thoracic spine and furcal rami are covered with small spines from this stage forward. The exopodite of the antenna re-

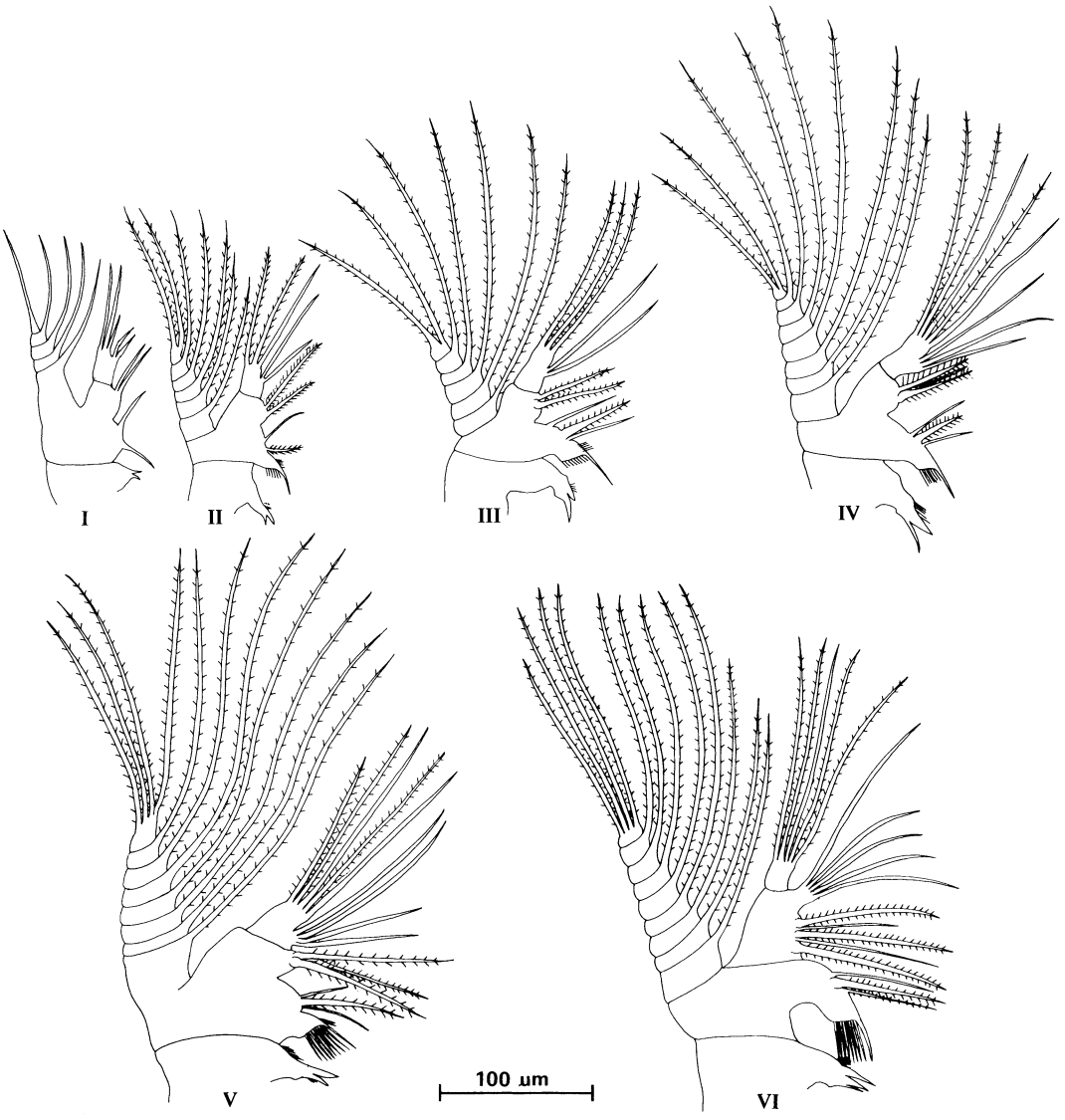

Fig. 8. Antennae of the nauplii of *Chthamalus dalli* and *C. fissus*. Naupliar stages are indicated by Roman numerals.

ceives two more setae, but the antennule still has no preaxial setae at this stage.

Stage IV individuals appear on the seventh day (Fig. 4). In stage IV, the cephalic shield further differentiates from the body, becoming more shieldlike with a smooth lower margin. The dorsal thoracic spine is approximately equal in length to the trunk (90 µm each). The characteristic feature of this stage is the appearance of two more pairs of trunk spines (one thoracic, one abdominal) with lower margin spinules (Figs. 5, 6). The abdominal spines 32 µm long, the third pair, located directly above the furcal rami (46 µm), are the most prominent of the three pairs of trunk spines, while the second pair of spines 10 µm long, located anterior to the first and more towards the center of the thorax, are less visible. In addition, the thorax possesses six rows of fine spinules and appears more segmented. From this stage forward, the highly pubescent labrum possesses two pairs of spines, the first on the lower margin, the second on the lat-

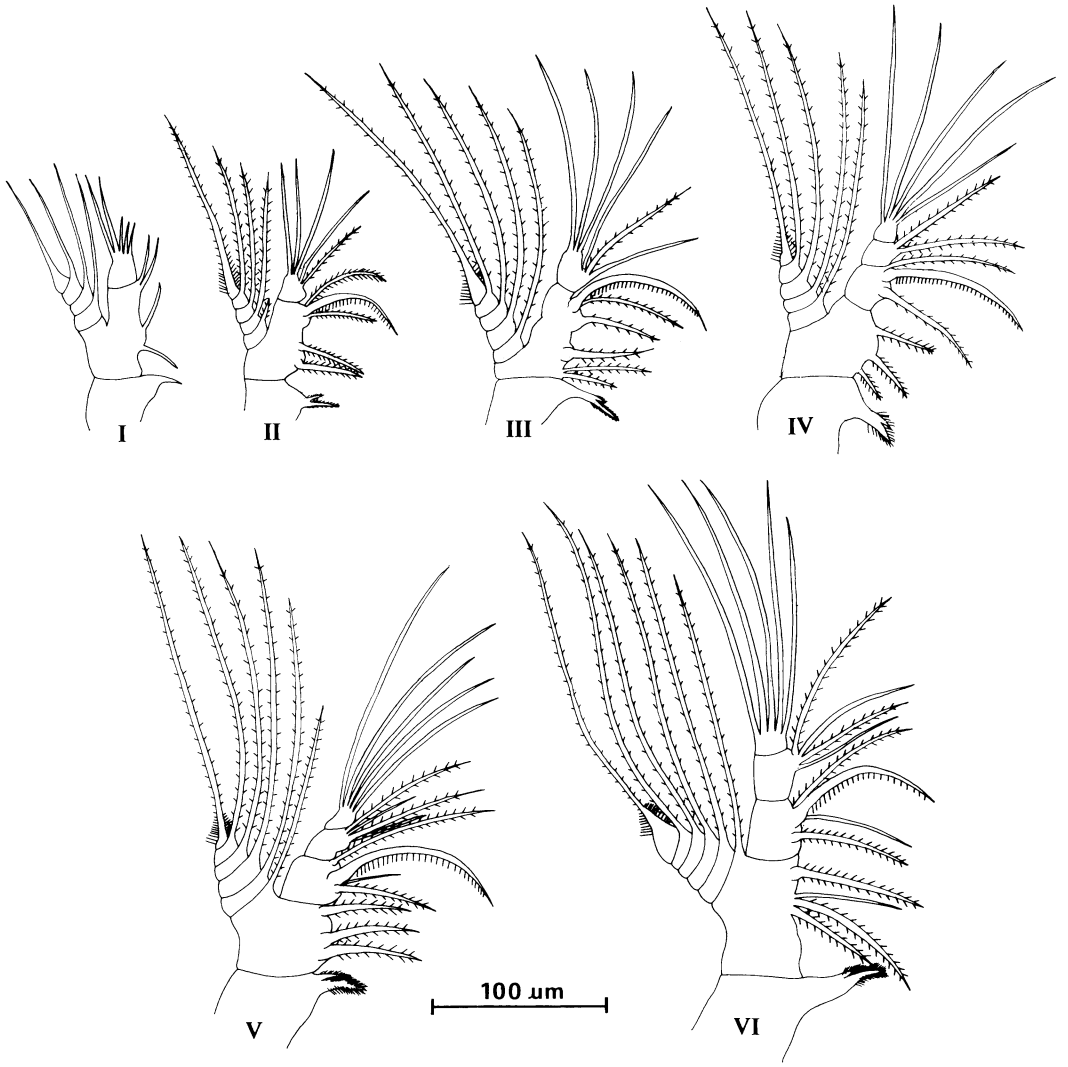

Fig. 9. Mandibles of the nauplii of *Chthamalus dalli* and *C. fissus*. Naupliar stages are indicated by Roman numerals.

eral margin. The exopodite of the antenna of stage IV individuals has nine setae, while the endopodite of both the antenna and the mandible receive two to three new setae (Figs. 8, 9). The antennule bears two preaxial setae (Fig. 7).

Stage V individuals appear between days nine (*C. fissus*) to thirteen (*C. dalli*; Fig. 4). The trunk in stage V is much more prominent and segmented than in previous stages. The abdominal portion bears a fourth pair of 14-µm spines located between the first and third pair (Fig. 5). In addition, a fifth pair of trunk spines, on the thoracic portion, is visible next to the first (Fig. 6). The cephalic shield becomes much rounder in appearance and the dorsal thoracic spine is slightly shorter than the trunk with a ratio of 0.7: 1. The exopodite of the antenna has 11 setae in this stage, while that of the mandible bears six setae (previously 5). In addition, the endopodites of both the mandible and the antenna receive more simple setae and there is a third preaxial seta on the antennule (Figs. 7–9).

Stage VI larvae appear on days 13 and 15 (Fig. 4). The trunk in this stage bulges and protrudes forward, and is clearly segmented with six new paired spines spread out in a V-shaped pattern on the ventral surface of

the thorax (Figs. 5, 6). These are the precursors of the six pairs of swimming limbs of the cyprid larva, which in turn become the cirri of the adult. All other spines except the third and fourth are lost. Late stage VI nauplii possess paired compound lateral eyes alongside the unpaired median eye present in all stages. The cephalic shield is broad and even rounder than in previous stages and the horns, which become harder to distinguish, are directed sideways. The exopodite of the antenna of stage VI individuals bears 12 setae and the antennule gains one postaxial seta (Figs. 7, 8).

The cyprid larvae appear on days 17 and 18 (Fig. 4). The cyprids retain both the median and lateral eyes (Fig. 5). The dorsal curvature of the carapace is greater than the ventral curvature, and the posterior margin is broad and evenly curved, while the anterior margin is pointed.

Discussion

Chthamalidae are a taxonomically difficult group with many species being recognized, and while most tend to be allopatric or allotopic, species of *Chthamalus* are frequently sympatric over part of their range (Southward, 1976; Hedgecock, 1979; Dando *et al.*, 1979; Dando and Southward, 1980, 1981; Achituv and Mizrahi, 1987). The genus *Chthamalus* apparently underwent a rapid radiation in the late Cenozoic (Stanley and Newman, 1980), and often the only reliable characteristics separating species are found internally, by dissecting reproductive or feeding structures. An example is the morphologically different setae of the second cirri of *C. dalli* and *C. fissus* (W. A. Newman, personal communication). Using the MDH allozyme analysis, the cirral characteristic separating the species was validated with total reliability. Moreover, the specimens for this study were collected at the same site (Hopkins Marine Station), which indicates that the species differences between *C. dalli* and *C. fissus* are observed at sites where both are sympatric. However, when species identifications must be made on live animals in the field, a combination of external characteristics must be employed. The shape of the orifice of *Chthamalus fissus,* for example, can be slitlike (originally classified as *C. microtretus* Cornwall, 1937), overhanging, or oval. The pro-

Table 3. Setation formula for *Chthamalus dalli* and *C. fissus*. Setal designations follow Newman (1965): S = simple, P = plumose, F = feathery, C = comblike, G = gnathobase; and Sandison (1967): H = hispid, Exop = exopodite, Endop = endopodite.

Stage	Antennule	Antenna		Mandible	
		Exop	Endop	Exop	Endop
1	SSSS:SS :S :S	S:4S	SSS:2S:SS :SS :G	S:3S	3S:SS :SS :SS :G
2	SSPS:SP :P :S	2P:5P	PPS:2S:FF :SFH :G	P:4P	3S:SP :PCP :PP :G
3	S:PSPS:SP :P :S	2P:5P	PPP:2S:FF :SFSH:G	P:4P	3S:SPS :PCP :PPP :G
4	S:P:PSPS:SP :P :S	2P:7P	PPSPS:3S:FSF :SFSH:G	P:4P	5S:PP :PCP :PPP :G
5	S:P:P:PSPS:SP:S:P :S	4P:7P	PPSPS:4S:FFF :SFSH:G	P:5P	5S:PSPS:PCSP:PPP :G
6	S:P:P:PSPS:SP:P:PS:S	4P:8P	PPSPP:5S:FSFSF:SFPH:G	P:5P	5S:PSPS:PCSP:PSPP:G

portions of these three morphs can be spatially variable in the field, and possibly related to environmental conditions. For example, Lively (1986) found that the overhanging (bent) form of *Chthamalus anisopoma* Pilsbry was an environmentally induced developmental response elicited by the presence of a carnivorous gastropod. He further demonstrated that the overhanging form of this barnacle was more resistent to predatory attack by these snails. A similar situation could be happening in the case of *C. fissus*. Alternatively, the orifice of *Chthamalus dalli* is always oval (Pilsbry, 1916; Newman and Abbott, 1980). Therefore, with the orifice characteristic alone, many, but not all *C. fissus* can be identified. For those individuals with an oval orifice, the presence of a dark brown band at the base of the shell and a high degree of corrugation of the shell are good indicators for *C. fissus*. However, since these shell features are measured relative to *C. dalli,* and there can be variability among individuals, up to 10% of *Chthamalus* spp. cannot be positively identified using even all three of these external characteristics.

Chthamalus dalli and *C. fissus* are even more similar in their larval forms. No morphological differences were detected in the larvae of the two species (except in about 5% of the stage II nauplii where the spines on the labrum differed). However, slight size divergence between the two species in naupliar stages I–III and in the cyprid larvae was apparent. In this study, the nauplii of *C. dalli* were larger than those of *C. fissus* in the first three stages, but due to a faster growth rate at 18°C (in size, not stage), *C. fissus* surpassed *C. dalli* in size at the cyprid stage. In addition, both species developed (in stage) at similar rates at 18°C, a temperature within the range both species experience. However, *C. dalli* developed more slowly at a temperature of 13°C and the more southern barnacle, *C. fissus,* did not develop at this colder temperature. The inability of larvae of *C. fissus* to grow at temperatures of 13°C or less could be a factor affecting the northernmost limit of their distribution.

Barnes (1953) found that there was variation in cyprid size within a single species and subsequently argued that size is not a valid characteristic with which to separate species in the plankton. Crisp (1959) also found variations in egg sizes and showed a decrease in egg size from north to south along both coasts of the North Atlantic. Patel and Crisp (1960) examined differences in egg size due to temperature and showed that egg size was larger at lower temperatures (hence, in the north) possibly due to slower development rates. The findings in this study support the notion of slower development rates at lower temperatures and similar development rates of southern and northern barnacle larvae grown at the same temperature (within their temperature tolerance range). However, no intraspecific differences in size were shown for nauplii grown at low (13°C) or high (18°C) temperatures. In addition, the sizes of *C. dalli* measured in this study coincided with those measured by Korn and Ovsyannikova (1979) in the sea of Japan. However, since sizes of larvae of *C. fissus* and *C. dalli* were measured on a limited number of laboratory-reared broods collected in Monterey Bay, and differences in size have not been substantiated by planktonic comparisons, the size criterion for separating the species should be used with caution.

The known larvae of other sessile barnacles on the central coast of California (north of Point Conception), namely *Balanus glandula* Darwin, *B. crenatus* Bruguière, *B. nubilus* Darwin, and *Semibalanus cariosus* Pallas, are 100–200 μm greater in length than *C. dalli* and *C. fissus* (Herz, 1933; Barnes and Barnes, 1959; Standing, 1981; Branscomb and Vedder, 1982; Brown and Roughgarden, 1985). They also differ in having paired dorsal spines on the cephalic shield in stages IV–VI, a trilobate labrum, lack of hispid and feathery setae, and a narrower shape of their cephalic shield. *Tetraclita,* represented by *T. squamosa rubescens* Darwin on the central California coast, follows a similar pattern (Barnes and Achituv, 1981).

A more difficult distinction is found between chthamalids and lepadids when comparing *C. fissus* and *C. dalli* to *Pollicipes polymerus* (noted by Lewis, 1975). The nauplii of these barnacles do not differ markedly in size (although *P. polymerus* is closer to the size of *C. dalli* in stages I–III than *C. fissus*) and are similar in their lack of paired posterior spines on their cephalic shield, presence of a unilobate labrum, and pres-

ence of hispid and feathery setae. In addition, the setation of their appendages is remarkably similar. Even the increasing ratio of the trunk to dorsal thoracic spines with stage is similar. The only noticeable differences between these species are the patterns of spine formation on the labrum and the overall goblet shape of *P. polymerus*.

The similarity between larvae of pollicipoids and chthamaloids accords with the similarity of the adult stage. As early as 1854, Darwin noted resemblances between the shell of chthamaloid and the capitulum of pollicipoid adults and hypothesized a transitional link. Other similarities exist between these families, such as a thick and bullate labrum and the use of the first and second cirri for cleaning and transferring food to the mouth. These similarities support the phylogenetic hypothesis that the Chthamalidae descended from a pollicipoid lepadomorph, possibly with an intermediate brachylepadomorphan-like ancestor, and that it is morphologically as well as stratigraphically older than the Balanidae (Zullo, 1963; Newman and Ross, 1976; Newman, 1987).

In conclusion, this study has confirmed that *C. dalli* and *C. fissus* are two distinct species. The adults can be separated electrophoretically, by malate dehydrogenase enzyme allozymes, and morphologically by the setae on the second cirri and by certain shell features. The larvae, however, could not be separated morphologically, but the size differences in naupliar stages I–III and the cyprid stage may be useful in making distinctions in the vicinity of Monterey Bay. Further work is now in progress using immunological assays to separate these species in the plankton.

Acknowledgements

We gratefully acknowledge the photographic skill of C. Patton, discussions and technical assistance by S. Gaines, B. Miller, G. Ruiz, R. Saunders, and F. Sly. In addition, we thank Granite Canyon Laboratory for supplying algal cultures. Support was provided by the Division of Ecological Research, Department of Energy (Contract EV10108).

Literature Cited

Achituv, Y., and L. Mizrahi. 1987. Allozyme differences between tidal levels in *Tetraclita squamosa* Pilsbry from the Red Sea.—Journal of Experimental Marine Biology and Ecology 108: 181–189.

Barnes, H. 1953. Size variations in the cyprids of some common barnacles.—Journal of the Marine Biological Association of the United Kingdom 32: 297–304.

———, and M. Barnes. 1959. The naupliar stages of *Balanus nubilus* Darwin.—Canadian Journal of Zoology 37: 15–23.

Barnes, M. and Y. Achituv. 1981. The nauplius stages of the cirripede *Tetraclita squamosa rufotincta* Pilsbry.—Journal of Experimental Marine Biology and Ecology 54: 149–165.

Bassindale, R. 1936. The developmental stages of three English barnacles, *Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli), and *Verruca stroemia* (O. F. Müller).—Proceedings of the Zoological Society of London 106: 57–74.

Branscomb, E. S., and K. Vedder. 1982. A description of the naupliar stages of the barnacles *Balanus glandula* Darwin, *Balanus cariosus* Pallas, and *Balanus crenatus* Bruguière (Cirripedia, Thoracica).—Crustaceana 42: 83–95.

Brown, S. K., and J. Roughgarden. 1985. Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia: Thoracica).—Journal of Crustacean Biology 5: 574–590.

Connell, J. H. 1961a. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*.—Ecological Monographs 31: 61–104.

———. 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*.—Ecology 42: 710–723.

Cornwall, I. E. 1937. A new species of barnacle from the coast of California.—Annals and Magazine of Natural History, series 10, 20: 232–235.

Crisp, D. J. 1959. The rate of development of *Balanus balanoides* (L.) embryos in vitro.—Journal of Animal Ecology 28: 119–132.

Dando, P. R., and A. J. Southward. 1980. A new species of *Chthamalus* (Crustacea:Cirripedia) characterized by enzyme electrophoresis and shell morphology : with a revision of other species of *Chthamalus* from the western shores of the Atlantic Ocean.—Journal of the Marine Biological Association of the United Kingdom 60: 787–831.

———, and ———. 1981. Existence of "Atlantic" and "Mediterranean" forms of *Chthamalus montagui* (Crustacea: Cirripedia) in the western Mediterranean.—Marine Biology Letters 2: 239–248.

———, ———, and D. J. Crisp. 1979. Enzyme variation in *Chthamalus montagui* (Crustacea: Cirripedia): evidence for the presence of *C. montagui* in the Adriatic.—Journal of the Marine Biological Association of the United Kingdom 59: 307–320.

Daniel, A. 1958. The development and metamorphosis of three species of sessile barnacles.—Journal of the Madras University 28,B: 23–47.

Darwin, C. 1854. A monograph on the sub-class Cirripedia with figures of all the species. The Balanidae, Verrucidae, etc.—Ray Society, London. Pp. 1–684.

Gaines, S. D., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone.—Proceedings of the National Academy of Science 82: 3707–3111.

Hedgecock, D. 1979. Biochemical genetic variation

and evidence of speciation in *Chthamalus* barnacles of the tropical eastern Pacific Ocean.—Marine Biology 54: 207–214.

Herz, L. E. 1933. The morphology of the later stages of *Balanus crenatus* Bruguière.—Biological Bulletin 64: 432–442.

Karande, A. A., and M. K. Thomas. 1976. The larvae of the inter-tidal barnacle *Chthamalus malayensis* Pilsbry.—Proceedings of the Indian Academy of Science 83B: 210–219.

Korn, O. M., and I. I. Ovsyannikova. 1979. Larval development of the barnacle *Chthamalus dalli*.—Soviet Journal of Marine Biology 5: 423–430.

Lang, W. H. 1979. Larval development of shallow water barnacles of the Carolinas (Cirripedia: Thoracica) with keys to naupliar stages.—National Oceanographic and Atmospheric Administration, Technical Report National Marine Fisheries Service Circular 421: 1–23.

Lewis, C. A. 1975. Development of the gooseneck barnacle *Pollicipes polymerus* (Cirripedia: Lepadomorpha): fertilization through settlement.—Marine Biology 32: 141–153.

Lively, C. M. 1986. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*.—Evolution 40: 232–242.

Newman, W. A. 1965. Prospectus on larval cirriped setation formulae.—Crustaceana 9: 51–56.

———. 1987. Evolution of cirripedes and their major groups. —*In:* A. J. Southward, ed., Barnacle biology. Pp. 3–42. A. A. Balkema, Rotterdam.

———, and D. P. Abbott. 1980. Cirripedia: the barnacles.—*In:* R. H. Morris, D. P. Abbott, and E. C. Haderlie, text contributors, Intertidal invertebrates of California. Pp. 504–535. Stanford University Press, Stanford, California.

———, and A. Ross. 1976. Revision of the balanomorph barnacles; including a catalogue of the species.—Memoirs of the San Diego Society of Natural History 9: 1–108.

Patel, B., and D. J. Crisp. 1960. The influence of temperature on the breeding and the molting activities of some warm-water species of operculate barnacles.—Journal of the Marine Biological Association of the United Kingdom 39: 667–680.

Pilsbry, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species.—Bulletin of the United States National Museum 93: 1–366.

Roughgarden, J., S. D. Gaines, and S. W. Pacala. 1987. Supply side ecology: the role of physical transport processes.—*In:* P. Giller and J. Gee, eds., Organization of communities: past and present. Pp. 459–486. Proceedings of the British Ecology Society Symposium, Aberystwyth, Wales.

———, ———, and H. Possingham. 1988. Recruitment dynamics in complex life cycles.—Science 241: 1460–1466.

———, Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment.—Ecology 66: 54–67.

Sandison, E. E. 1967. The naupliar stages of *Balanus pallidus stutsburi* Darwin and *Chthamalus aestuarii* Stubbings (Cirripedia Thoracica).—Crustaceana 13: 161–174.

Southward, A. J. 1976. On the taxonomic status and distribution of *Chthamalus stellatus* (Cirripedia) in the north-east Atlantic region: with a key to the common intertidal barnacles of Britain.—Journal of the Marine Biological Association of the United Kingdom 56: 1007–1028.

Standing, J. D. 1981. Common inshore barnacle cyprids of the Oregonian faunal province (Crustacea: Cirripedia).—Proceedings of the Biological Society of Washington 93: 1184–1203.

Stanley, S. M., and W. A. Newman. 1980. Competitive exclusion in evolutionary time: the case of the acorn barnacles.—Paleobiology 6: 173–183.

Zullo, V. A. 1963. A classification and phylogeny of the Chthamalidae (Cirripedia: Thoracica).—Proceedings of the XVI International Congress of Zoology, Washington, D.C. 1: 190.

RECEIVED: 19 April 1988.
ACCEPTED: 19 November 1988.

Addresses: (KMM and JR) Hopkins Marine Station, Stanford University, Pacific Grove, California 93950; (SMB) Parasite Epidemiology Research Group, Department of Pure and Applied Biology, Imperial College, University of London, London SW7 2BB, England; (DH) University of California, Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, California, 94923.