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THE HABITS AND LIFE HISTORY OF *OEDOPARENA GLAUCA* (DIPTERA: DRYOMYZIDAE), A PREDATOR OF BARNACLES[1]

J. F. BURGER, J. R. ANDERSON, AND M. F. KNUDSEN

(JFB) Department of Entomology, University of New Hampshire, Durham, New Hampshire 03824; (JRA, MFK) Department of Entomology and Parasitology, University of California, Berkeley, California 94720.

Abstract.—*Oedoparena glauca* (Coquillett), a common coastal dryomyzid fly occurring from Central California to Alaska in the Nearctic Region, is the first known dipterous predator of intertidal barnacles. Adults occur on or adjacent to barnacle beds and mate there. Eggs are deposited on the operculum of barnacle prey and larvae consume several prey during development. Pupariation occurs in an empty barnacle test. Adults emerge during a morning low tide. The habits of adult flies and the life history of *O. glauca* are discussed; illustrations and a description of the second- and third-instar larva in given, and food habits are compared with related Sciomyzoidea.

In 1966, fly pupae were discovered by M. F. Knudsen and J. F. Burger in empty tests of the intertidal acorn barnacle, *Balanus glandula* Darwin, on the central California coast (Sonoma County). Subsequently, larvae were observed inside the tests of living barnacles. Tests containing puparia were returned to the laboratory and one adult fly emerged within 24 hr. This slate gray and brown fly was identified as *Oedoparena glauca* (Coquillett). Because this was the first record of a dipterous predator of barnacles, we studied its biology and life history. Schlinger (1975: 442–443) briefly summarized *O. glauca* habits.

Oedoparena glauca is a moderately large fly, about 5–9 mm long, inhabiting that part of the intertidal zone colonized by the *Endocladia-Balanus* community. *Endocladia muricata* (Postels and Ruprecht) J. G. Agardh, 1847 is a red alga abundant in the upper tidal zone of California, especially where wave action is moderate. *Balanus glandula* is a rather small barnacle of diverse habits and usually is found in the middle or upper intertidal levels

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on protected and exposed coasts, in relatively stagnant bays and on protected piles (Ricketts et al., 1968). Although these species can exist rather high in the intertidal belt, Glynn (1965) found that at the center of the *Endocladia-Balanus* community, barnacles were submerged 27% of the time during a six month period, or about 45 hr per week. In the present study area, *Balanus* was most abundant in the middle of the association and less abundant at higher and lower levels.

Although much taxonomic work has been done on marine insects, the biology of many species remains poorly known, except in western Europe. Intertidal insects have been little studied on the west coast of North America.

There are only two reports of Diptera associated with barnacles, both from Europe. Rouboud (1903) found dipterous larvae among *Balanus balanoides* Darwin scraped from rocks near The Hague, Netherlands and near le Croisic, France, in Lower Loire Province. He believed them to be a species of *Aphrosylus* (Dolichopodidae). However, since these larvae were not reared, the determination could not be confirmed.

Mercier (1921) described the larvae of *Limnophora aestuum* Villenueve and stated that he frequently found the larvae living within barnacles. He believed the larvae were predaceous and fed on barnacles, but he did not rear larvae to adults.

The taxonomic status of *Oedoparena glauca* is discussed by Mathis and Steyskal (1980) in their revision of the genus *Oedoparena*.

Very little has been published about the habits of flies in the subfamily Dryomyzinae. Hennig (1968) mentioned an 1883 report by Brauer that *Neuroctena* (=*Dryomyza*) *anilis* Fallén larvae lived in fungi and that Portschinsky, in a 1910 report, found them in human excrement. Because these reports are so sketchy and larvae were not reared to adults, their accuracy cannot be verified. Hennig (1968) stated that the adults of *N. anilis* were attracted to the stinkhorn fungus, *Phallus* (=*Ithyphallus*) *impudicus* (L.). Recent unpublished data of B. A. Foote, Kent State University, revealed that *D. anilis* and *Dryomyza simplex* Loew developed on dead animal matter, but not on decaying plant matter (see discussion).

The Study Area

Field studies were conducted at Shell Beach in Sonoma Coast State Park, Sonoma County California (Fig. 1). This area is protected from full wave impact by rock outcroppings forming islands or "chimneys" that dissipate part of the wave energy. This shore type is classified as "protected outer coast" by Ricketts et al. (1968). Two sites were selected for observation within the study area. The first was a rock 2.4 m high and 7.6 m in circumference (Fig. 2). The shoreward side was exposed to sun until early afternoon. The seaward side was sheltered by another large rock next to it and

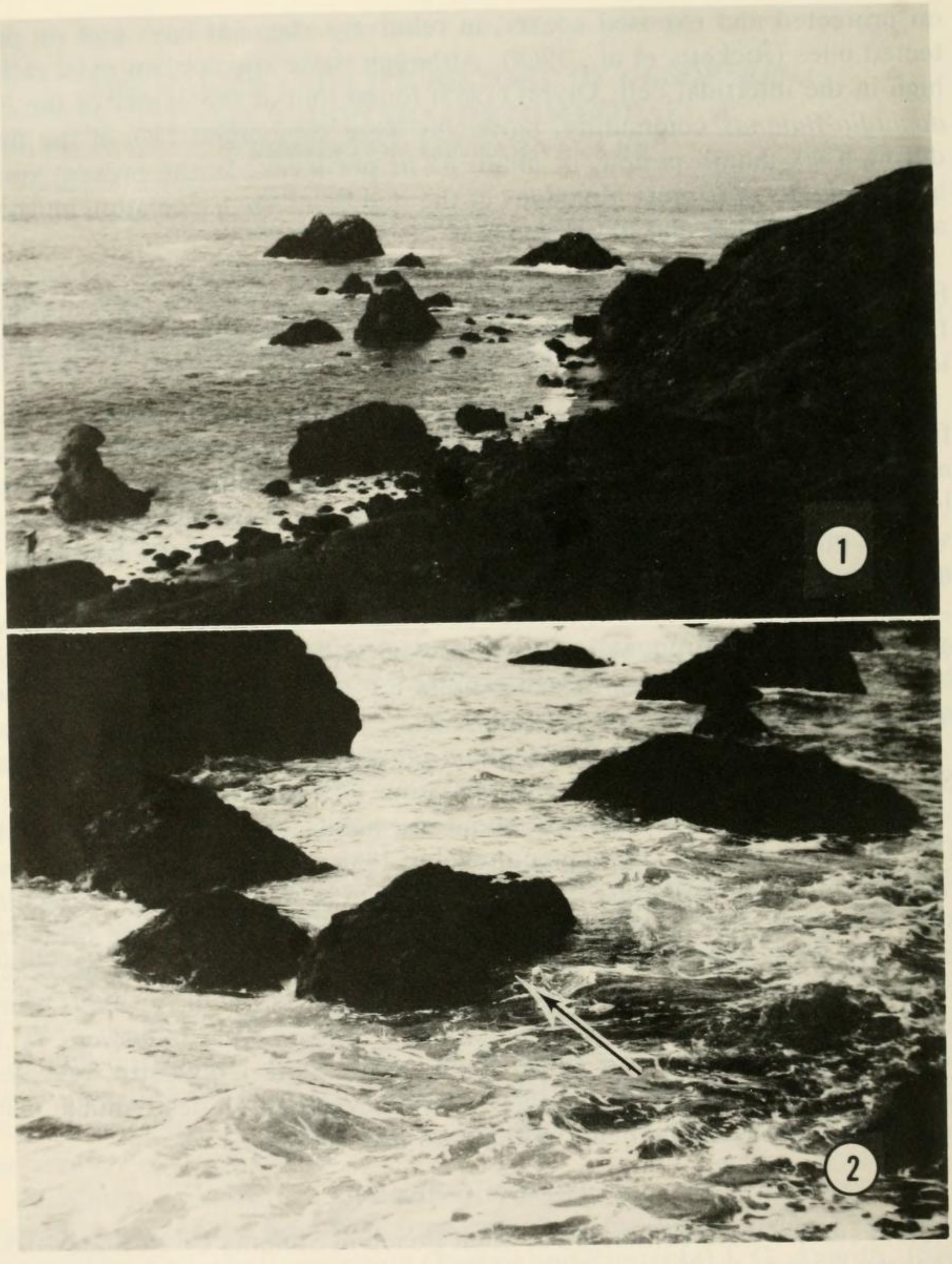


Fig. 1. View of Shell Beach, Sonoma County, California, showing marginal outcroppings of rock. Fig. 2. View of the first study area.

rarely exposed to the sun, remaining moist even on the hottest days. The second site was part of the seaward side of a rock receiving sunlight in the morning and all afternoon. This site also was more directly exposed to wave action. Both sites had many thousands of barnacles available for study.

Materials and Methods

Oedoparena glauca is a reluctant but capable flier and easily disturbed by rapid movement. However, flies were observed by approaching them slowly. Collections were made with an aspirator, since nets were rapidly destroyed by the sharp-edged barnacle beds. Barnacle samples were collected by chipping rock surfaces with a screwdriver and hammer.

Laboratory studies were conducted at the Bodega Bay Marine Laboratory of the University of California. Barnacles were maintained in a wooden aquarium with two glass sides and a plastic top. Sea water (14–17°C) was channelled continuously through the tank at 5 mm depth. This prevented continuous immersion of animals in the tank. Barnacles were placed in finger bowls and immersed in running sea water for several hours each day. Emerging adult flies were held in half-pint and gallon ice cream cartons with nylon screen tops and provided water and sucrose.

Rock chips containing barnacles were placed in finger bowls and immersed in fresh sea water to observe habits of *O. glauca* larvae. Barnacles opened within a few minutes and larvae were observed *in situ* with a dissecting stereoscopic microscope. Some barnacles were reluctant to open but could be stimulated to open by directing a jet of water on the operculum with a serological pipet.

Flies used for ovarian development studies were obtained from field collected pupae. Pupae were obtained by examining the study area for empty barnacle tests. Forceps were used to break some of the plates from the side of the test, revealing fly pupae inside. Pupae could be removed from the test by gentle pressure with forceps. Pupae were placed on damp cotton plugs in 14-dram vials fitted with nylon screen tops. Vials were stored in test tube racks immersed in the aquarium discussed above.

Vials were examined daily to record emergence dates for each fly. After a fly emerged, a cube of sucrose was placed on top of the nylon mesh top. No protein food was provided for any flies, and the only water available was that in the moist pad inside the vial.

At various times after emergence, unmated flies were killed in physiological saline and dissected. The reproductive organs were examined with a stereoscopic and compound microscope to assess egg development in the ovarioles and to determine if male testes contained active sperm. After dissection, reproductive organs were removed to a clear drop of saline for further study. Both wild-caught males and females were dissected to study

the reproductive organs and the digestive system. Some were examined immediately; others were stored for several weeks of −20°C and −50°C.

RESULTS

Adult activity.—Adults of *O. glauca* are conspicuous members of the intertidal zone in central California, especially when they walk across barnacle-encrusted rocks. When disturbed, they fly only a short distance, rarely more than 1 m and again land on barnacle beds. Adult feeding was not observed in the field but the guts of several field-collected adults dissected in the laboratory contained diatoms.

Ovarian development in females.—All reared females dissected had eggs wholly or partially developed. Since all reared females were provided only sucrose and water, this established that *O. glauca* females studied were autogenous in the first gonotrophic cycle. Eggs of nulliparous reared females were fully developed (1.8 mm long) by six days posteclosion.

Based on previous results with other Diptera (e.g. Anderson, 1964; Detinova, 1962), females that had dark, yellow-colored debris present in the ovarian pedicels were judged to be parous. All wild-caught females were judged to be parous when collected. Laboratory-reared females known to be nulliparous had ovarian pedicels with very little or no yellow material in them. No experiments were performed to establish the relationship between amount of yellow-colored follicular debris and degree of parousness.

Mating and oviposition.—Mating activity of *O. glauca* was observed in the field from 16 May to 1 August 1968. Coupled pairs were observed infrequently. Of 127 flies collected during the observation period, 109 (85%) were males; 18 (15%) were females. Individual males did not seem to be actively seeking females but remained stationary until disturbed. If another fly entered the area, a male would try to mount the intruder, regardless of sex or species, but quickly rejected the visitor if not of the opposite sex and not conspecific.

If a female landed on the barnacle bed, a male, if present in the area, would follow her across the bed. Males always followed and mounted females from behind. Coupling was not always successful on the first attempt but usually was accomplished on the second or third attempt. After coupling, the female, with the male above her, continued moving across the barnacle bed.

Adults remained coupled for about 15 min, if undisturbed. After uncoupling, the male remained on the female while she commenced searching behavior, walking across the barnacle bed. When she encountered a suitable barnacle, she passed beyond it, curving her abdomen ventrally while backing into the opercular opening and depositing an egg. The female then moved to another barnacle.

During the oviposition process, the accompanying male repeatedly at-

Fig. 3. Opening of a *Balanus glandula* barnacle with eggs of *Oedoparena glauca* attached. Eggs approximately 1.8 mm long.

tempted coupling. If coupling attempts were successful, searching and oviposition by the female ceased for about 15 min until copulation was completed and oviposition behavior by the female resumed. This sequence would be repeated several times, but, if interrupted, the female would fly away alone. Frequently, single males competed for an occupied female and females often escaped as males fought for her possession.

Copulating pairs were collected in the field and placed in vials containing rock chips covered with barnacles. Flies copulated in the vials but oviposition was not observed directly. After six days, eggs were found on the

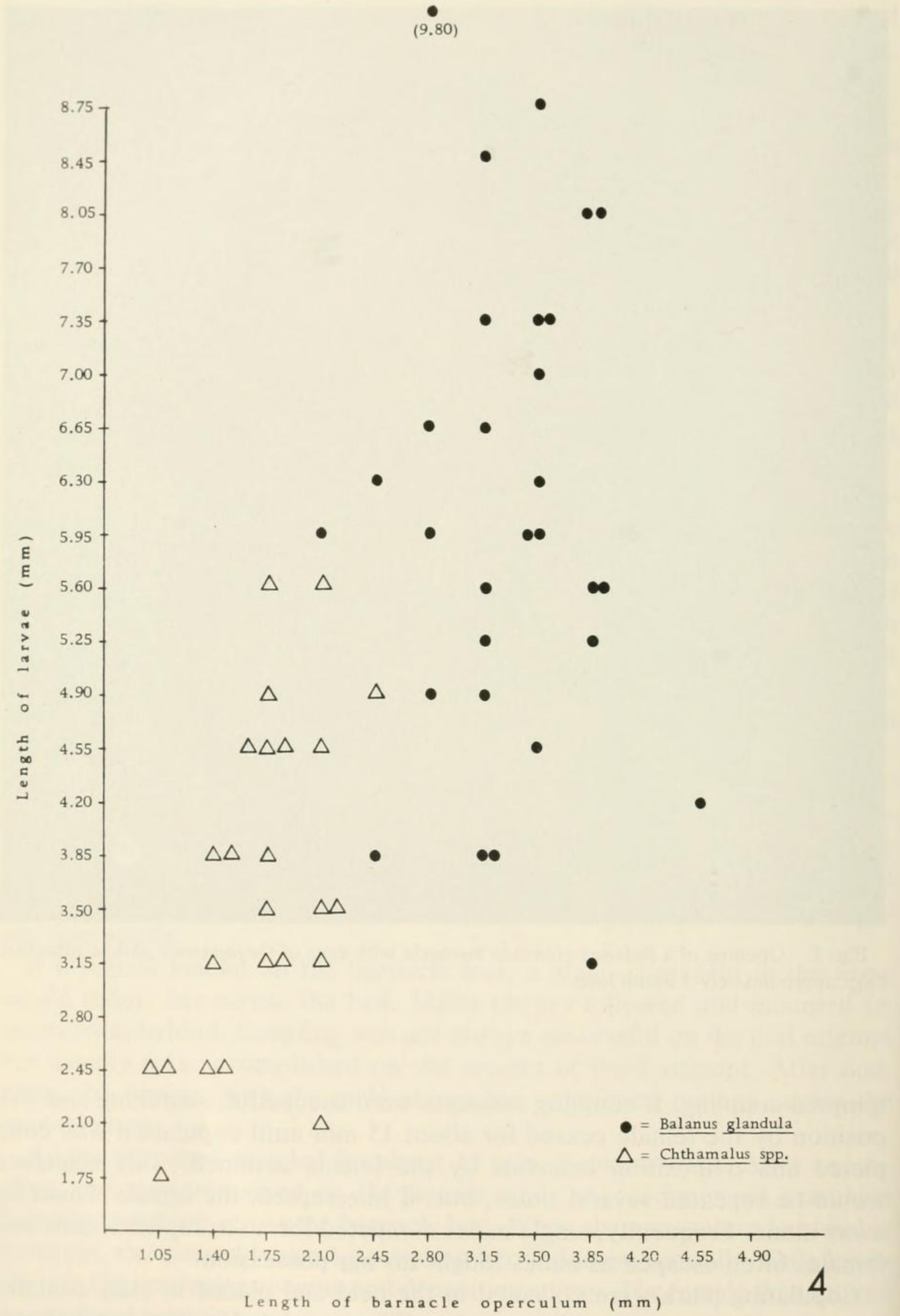


Fig. 4. Correlation between *Oedoparena glauca* larval length and width of prey barnacle opening.

scutes of three *B. glandula* on separate rock chips. Eggs hatched in 48 hr and first-instar larvae invaded the barnacle. Not all ovipositing females were accompanied by males, but males, once stationed on the female, usually remained there during the entire oviposition period.

In the laboratory, *O. glauca* deposited eggs only on *B. glandula,* never on a smaller barnacle, *Chthamalus fissus* Darwin. Eggs usually were placed on the inner surface of the barnacle test or on the turga and scuta (Fig. 3). The eggs bear a pair of flanges extending from each side that may help secure the eggs in the cracks of the barnacle test. They also may be part of the egg's plastron system, for although the surface features of the egg were not examined in this study, we assume the egg has a plastron structure, since it is submerged by sea water during part of the tidal cycle. Hinton (1960) has found that the eggs of most dipterans studied have a plastron structure, allowing them to obtain oxygen during submersion.

Each ovary of the female contains 18 ovarioles, so potentially 36 eggs could be produced per ovarian cycle, however no observed female deposited that many eggs.

Prey selection and entry of larvae.—Although *O. glauca* females preferentially selected *B. glandula* for oviposition in nature, small larvae observed in the laboratory would invade *Chthamalus fissus,* suggesting that first-instar larvae were able to move from *B. glandula* to *C. fissus* or that ovipositing females were more selective in natural habitats. No first-instar larvae were observed outside barnacles in the field.

It is likely that hatching of eggs is related to tidal cycles, probably occurring at any multiple of 12 hr from the time of oviposition. Submerged larvae were unable to survive outside a barnacle because they are buoyant and easily swept away by tidal flow. Eggs hatch during a low tide period and first-instar larvae enter a barnacle before high tide returns. Since barnacles often were not tightly closed, even at low tide, first-instars had no difficulty entering the prey between the opening of the turga and scuta of the operculum.

To determine if there was a correlation between the size of *O. glauca* larvae and their prey, rock chips were maintained in the laboratory and barnacles containing larvae were dissected after measuring the longitudinal opening. The fly larva was then removed and fixed for measurement. Size of the fly larva was highly correlated with barnacle opening size ($P = <0.01$, Fig. 4). *Balanus glandula* openings varied from 2.1 to 4.55 mm and contained *O. glauca* larvae 3.2–9.8 mm long; *Chthamalus fissus* openings were 1.05–2.45 mm wide and contained larvae 1.7–5.6 mm long.

Smaller larvae were found in both *B. glandula* and *C. fissus* and in a wider size range of barnacles than were longer larvae, implying that as a larva grew, it required progressively larger prey. Since *B. glandula* is larger at

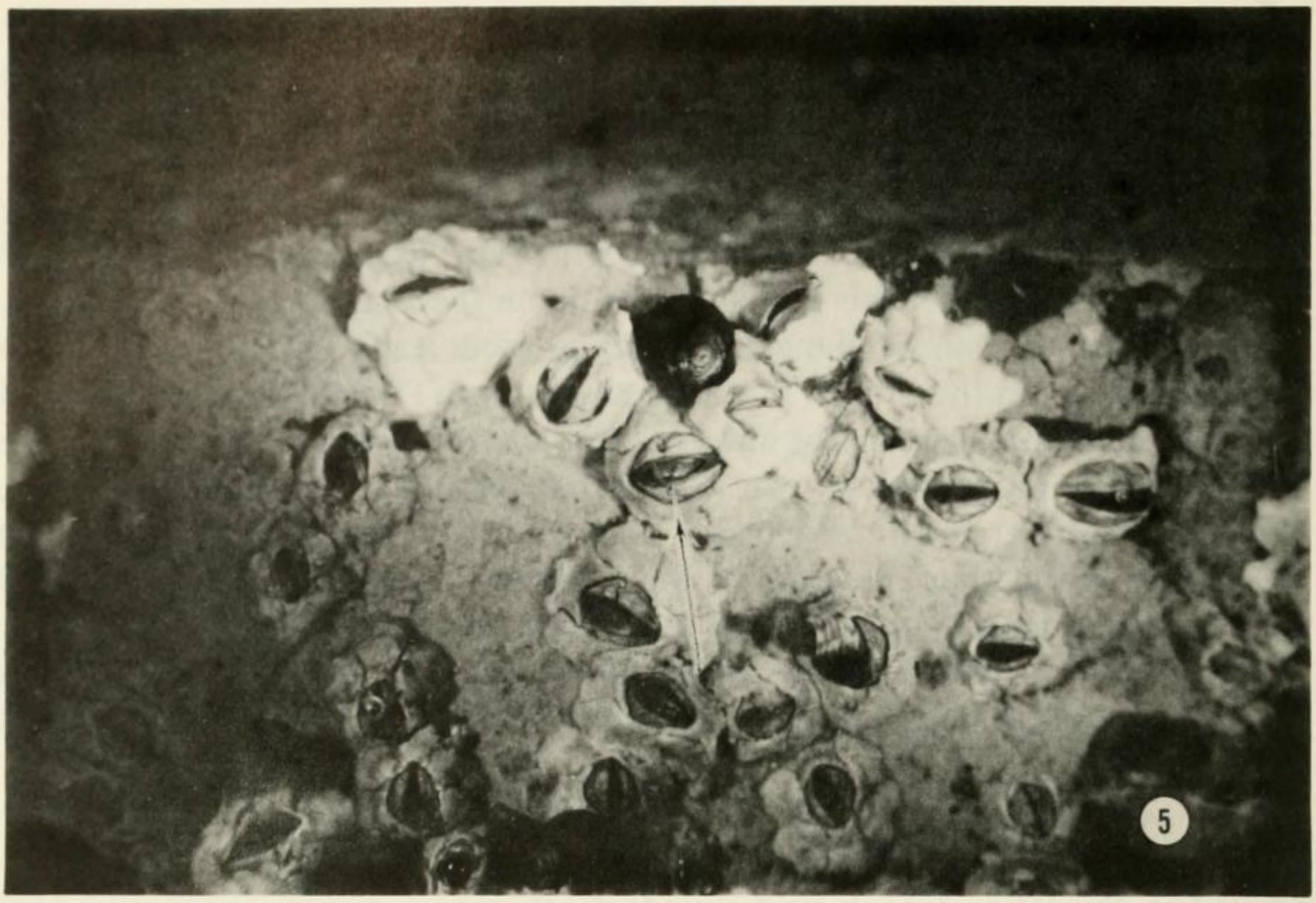


Fig. 5. Third-instar larva of *Oedoparena glauca* protruding from a barnacle prey.

maturity than *C. fissus*, larger larvae usually occurred in *B. glandula*, preferentially selecting them for invasion.

Larvae were observed searching for new prey in laboratory aquaria. A larva moved slowly until it encountered a barnacle operculum; then the mouthparts were moved rapidly in a hoeing motion. If the larva encountered a small opening in the prey's operculum, the mouthparts were lodged in the opening to anchor the larva to the operculum. Once anchored, larvae remained inactive for up to 24 hr. In the field, larvae probably complete entry when the tide returns. In the laboratory, barnacles opened as soon as immersed in sea water, allowing *O. glauca* larvae to complete entry. Larvae not securely anchored to the barnacle were easily washed off by immersion in sea water. In the laboratory, all larvae had entered a prey within 24 hr.

In nature, third-instar larvae often were observed wandering over the barnacle beds. Except for newly-hatched larvae, no first- or second-instar larvae were observed outside a barnacle prey. Many wandering larvae were observed executing the same searching behavior discussed above, securing themselves to a barnacle operculum with the mouthhooks. Possibly the greater food requirements of larger larvae forces them to seek fresh prey more frequently. Usually, only one larva was present per barnacle; only rarely were two larvae present in a single prey.

Recently hatched larvae could not be reared to the pupal stage in the laboratory because barnacles could not be kept alive for the extended periods necessary for larval development. Larval development is slow, requiring several months, possibly because of the relatively low temperature in the surrounding environment.

Distribution of *O. glauca* larvae in barnacle beds.—A vertical transect was made through one of the study sites to determine if larvae were equally distributed throughout the barnacle beds. Three sites were sampled, one each in the upper, middle, and lower portions of the barnacle bed. All barnacles in a 5 cm^2 area at each site were examined. Larval density was greater in the lower and middle portions of the bed, but since smaller barnacles were concentrated in the upper portions of the bed, larval density probably is related to barnacle size rather than other factors.

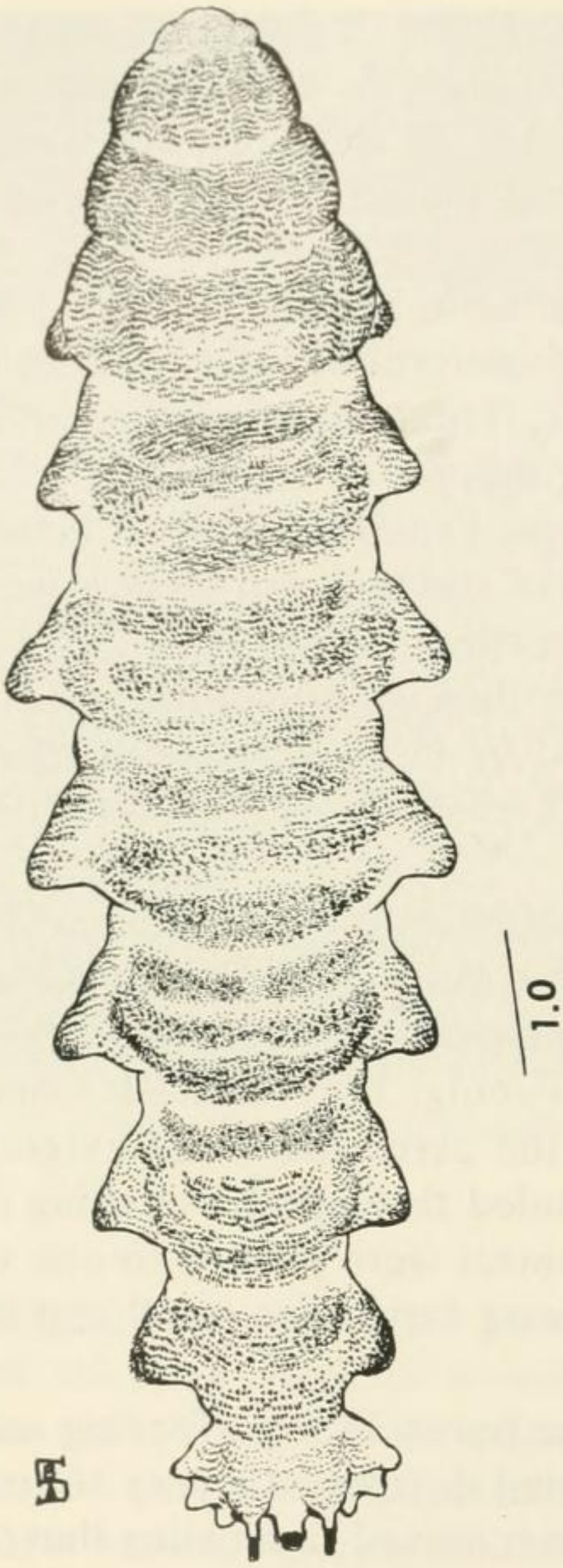
Oedoparena glauca larvae were found in 11.0–12.5% of barnacles examined in the middle and lower portions of the bed, but only in 5.0% of those in the upper bed.

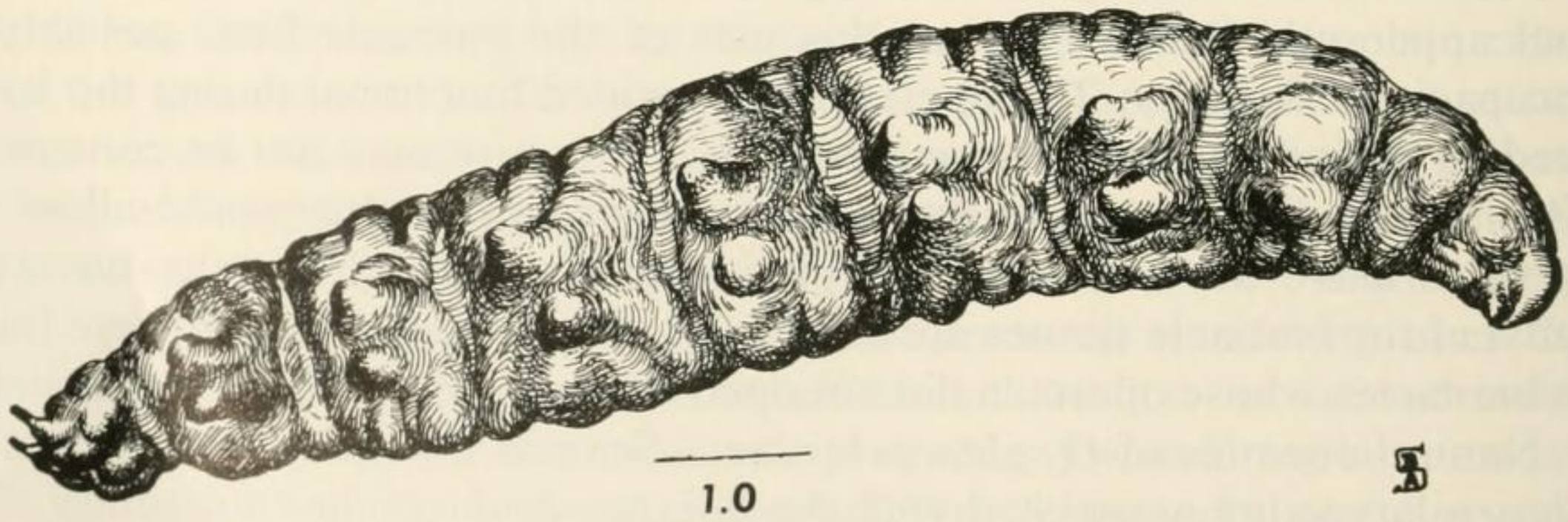
Effects of *O. glauca* on their prey.—Observations were made on the effects of *O. glauca* larvae on individual barnacles. When barnacles were submerged in laboratory aquaria, they opened the turga and scuta rapidly, extended the cerrci and commenced sweeping. Prey barnacles opened as rapidly as non-infested individuals, but the cerrci were not extended and the posterior spiracles of the larva protruded through the opening (Fig. 5), preventing extension of the cerrci. The cerrci were pushed to one side and remained immobile, even when the infesting larva was small and the prey quite large.

Occlusion of the opening prevented the barnacle from feeding and probably contributed to weakening and eventual death of the prey. Cerrci were unable to function even when larvae were removed, indicating that *O. glauca* may sever the nerve connectives or muscles operating the cerrci.

Tissues of the basal portion of a prey barnacle were extensively damaged and apparently larvae feed on this part of the barnacle first, possibly to incapacitate the prey. The operculum remained functional during the larval feeding period and muscles operating this structure may not be consumed. This would allow periodic flushing of the prey and also would allow the larva to leave the host after completion of feeding. Ultimately, however, most of the barnacle tissues are consumed. Occasionally, larvae were found in barnacles whose opercula did not open when immersed in fresh sea water.

Natural enemies of *O. glauca* larvae.—Several potential predators of *O. glauca* larvae are associated with the *Balanus-Endocladia* community. Presumably larvae are protected from predators while in the barnacle and were attacked only when moving from one prey to another. Once, a staphylinid beetle was observed feeding on an *O. glauca* larva, and sluggish larvae may be vulnerable to such active predators. Pupae, however, usually are wedged





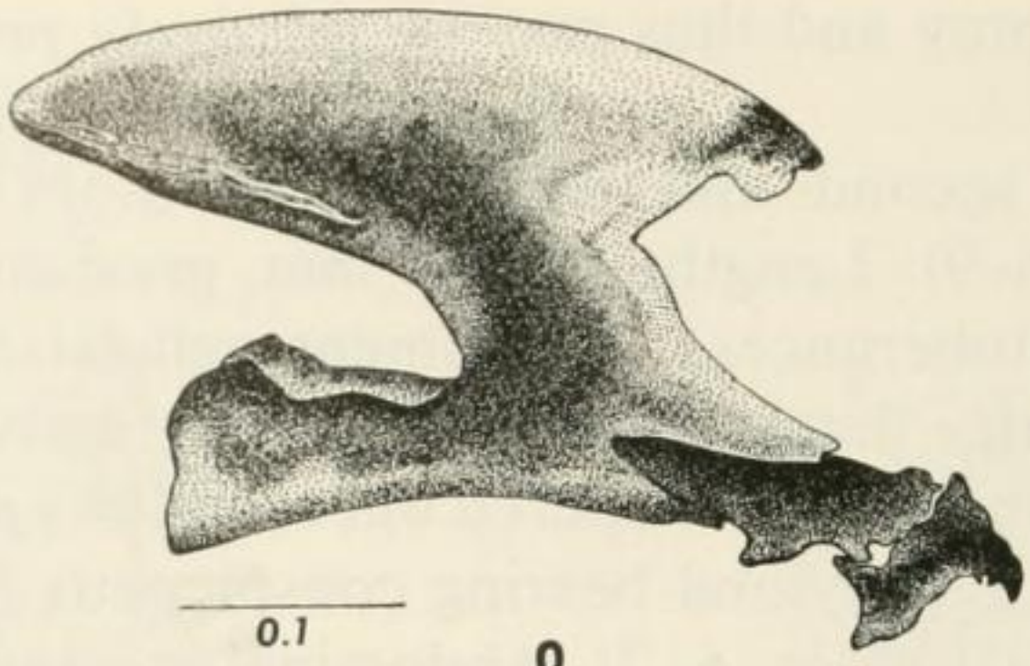
Figs. 6–7. *Oedoparena glauca*, second-instar larva. 6, Dorsal view with enlargement of spinules. 7, lateral view.

in the tests of their prey and thus may be relatively protected from predation.

Description of the second- and third-instar larva of *O. glauca*.—*Second-Instar Larva* (Figs. 6–9): Length: 4.5–6.0 mm, greatest width 1.4 mm (not including lateral protuberances). Integument yellowish white, semi-transparent. Body elongate, flattened dorsoventrally, narrower anteriorly and posteriorly (Fig. 6); anterior end tapered but rounded apically; posterior end broadly rounded posteriorly and bearing conspicuous fleshy protuberances laterally and posteriorly (Figs. 6, 7). Abdominal segments bearing 2 pairs of large, pointed fleshy protuberances laterally and ventrolaterally, the lateral pair about twice as large as ventrolateral ones (Fig. 7), very small on 1st abdominal segment, largest on 3rd through 5th abdominal segments. Segment I with minute spinule ridges present only on posterior ½ of segment. Paired anterior spiracles (Fig. 8) light brown, distinctly bilobed, with 7 papillae on each lobe, projecting from anterolateral margin of segment II. Segments II and III uniformly covered with spinule ridges, individual spinules rounded on dorsal surface, elongate and acutely pointed on ventral surface (Fig. 6); spinule ridges on segments IV to X in 3 transverse rows dorsally, interrupted by 2 intersegmental furrows; lateral and ventrolateral protuberances and ventral surfaces of these segments uniformly covered with spinule ridges, configuration similar to that on segments II and III. Segment XI bearing 3 pairs of large, rounded fleshy tubercles laterally and 1 pair of pointed tubercles posteriorly between posterior spiracles; anal lobes large, rounded. Posterior spiracles elongate, borne on fleshy protuberances posteriorly, separated by 2–3 × length of spiracular tube; spiracular tube black, about twice as long as broad.

Cephalopharyngeal skeleton (Fig. 9) brownish to black, 0.4 mm long. Indentation index 55. Dorsal cornua 1.6 times length of ventral cornua, dorsal cornua lighter anteriorly and along dorsal margin; dorsal cornua with very narrow dorsal window. Dorsal bridge moderately developed, with a few lightly pigmented areas present below. Accessory rods rather broad, acutely pointed dorsoapically. Mouthhooks stout and broad, with a very short broadly rounded hook apically and 2 small accessory teeth along the ventral margin; posterior margin extended ventrally into a long rod articulating with the ventral surface of the hypostomal sclerite. Hypostomal sclerite long and slender, blunt anteriorly, gradually narrowed to a point posteriorly where it articulates with the pharyngeal sclerite.

Third-instar larva (Figs. 10–12): Length: 6.0–9.8 mm, greatest width 1.8 mm (not including lateral protuberances). Integument yellowish white, with dark brown pubescence present dorsally and laterally on segments II–IV and dorsally on segments V–X (Fig. 10), pubescence uniformly covering posterior ⅓ of segments V–X, present medianly and laterally between the intersegmental furrows and laterally only on the anterior ⅓ of segments V–



Figs. 8–9. *Oedoparena glauca*, second-instar larva. 8, Cephalopharyngeal skeleton, lateral view. 9, Anterior spiracle.

X. Lateral abdominal protuberances about ⅓ longer than ventrolateral pair. Spinule ridges conspicuous on segment I dorsally and ventrally and all of segments I–IV and IX–XI, less distinct on segments V–VIII and obscured by brown pubescence. Paired anterior spiracles (Fig. 11) not noticeably bilobed as in the second-instar larva, bearing 14 distinct papillae. Posterior spiracular tubes separated by a distance about equal to their length.

Cephalopharyngeal skeleton (Fig. 12) black, 0.5 mm long. Dorsal cornua 1.8× length of ventral cornua. Mouthhooks with 1 accessory tooth along the ventral margin. Otherwise third-instar larva similar to that of the second-instar.

Known larvae of *Dryomyza* differ from *Oedoparena* in lacking lateral fleshy protuberances; mouthhooks more slender; integumental spinules more slender and elongate, less densely packed and not distributed in well-defined rows dorsally; anal segment with more widely spaced lateral protuberances; and spiracles not borne on elongate spiracular tubes.

Pupation and adult emergence.—Mature *O. glauca* larvae commenced prepupation activity by wandering over the barnacle bed adjacent to its last prey. Larvae probed each barnacle encountered with their mouthparts. Living barnacles were rejected, but empty tests were examined for a longer time. When a favorable site was found, the larva entered the test.

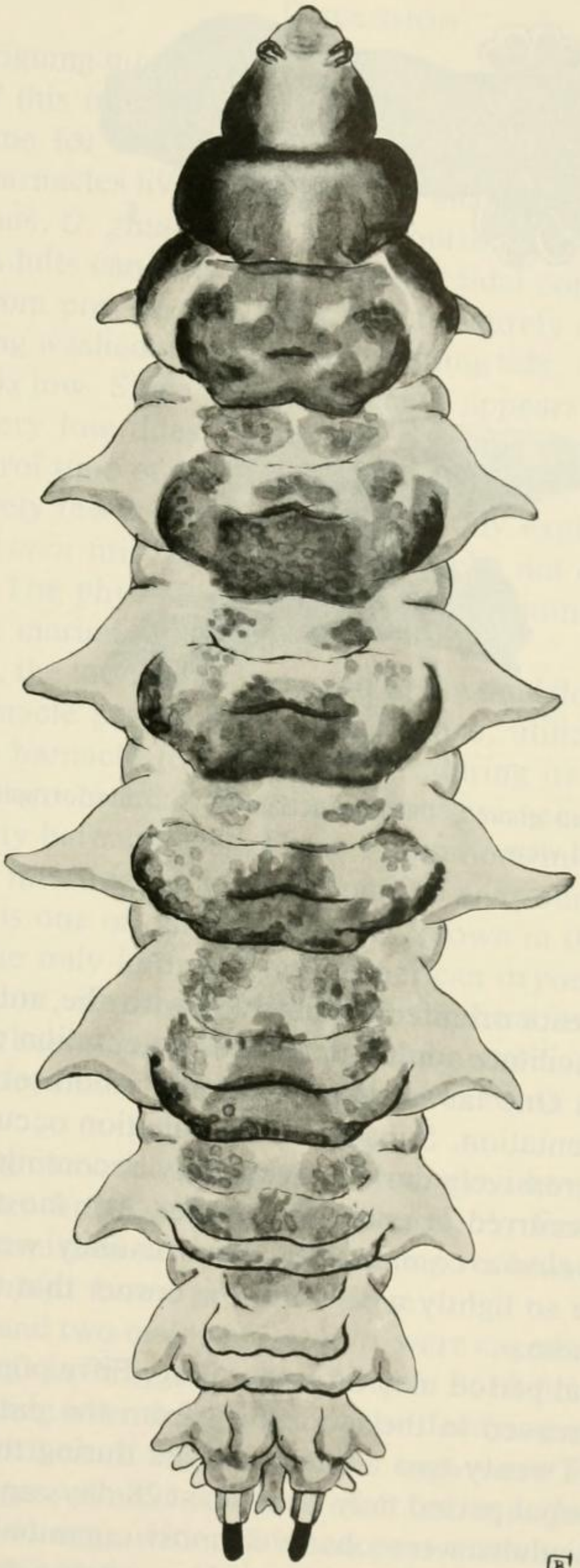
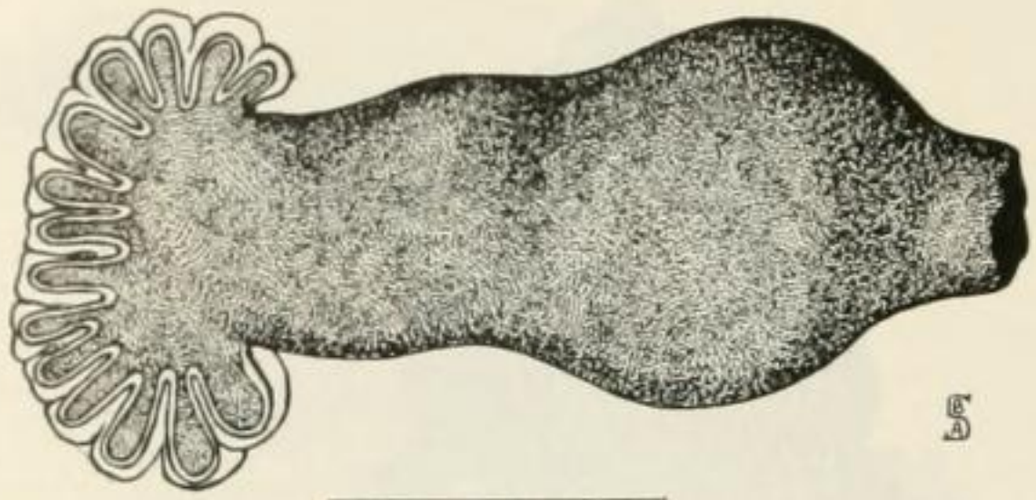


Fig. 10. *Oedoparena glauca*, third-instar larva, dorsal view.



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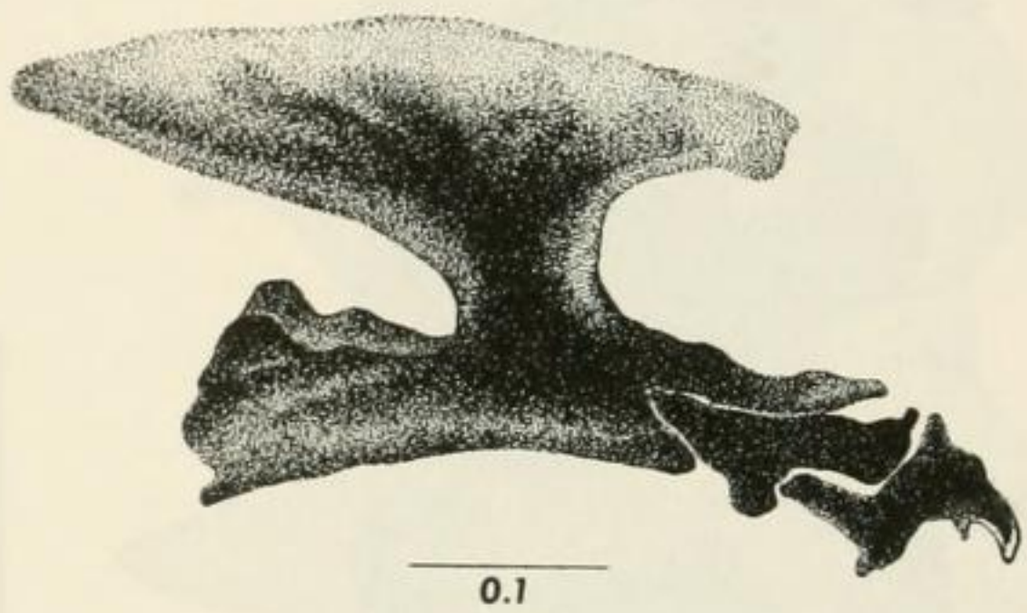

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Figs. 11–12. *Oedoparena glauca*, third-instar larva. 11, Anterior spiracle. 12, Cephalopharyngeal skeleton, lateral view.

Larvae in empty tests oriented themselves with the anterior end facing out, presumably to facilitate adult emergence. Orientation prior to pupation is a lengthy process. One larva observed in the laboratory required three days to complete orientation. Subsequently, pupation occurs and the larval cuticle becomes progressively darker, eventually becoming dark red-brown.

Pupae always occurred in empty barnacle tests, most commonly high in the *Balanus-Endocladia* community. Pupae usually were in the bottom of the tests and were so tightly wedged into a corner that the test had to be broken to remove them.

Length of the pupal period may be rather long. Fifty pupae from the Shell Beach site were observed in the laboratory from the date of collection (2 July) until 30 July. Twenty-two adults emerged during this 28 day period, indicating that the pupal period may be at least 28 days and possibly longer.

Recently eclosed adults were observed most commonly in the morning and adult activity was especially high on days when tides were very low. Newly emerged adults usually rested on barnacles and spread their wings during the hardening process. Teneral flies were always much lighter colored than older ones and thus easily observed.

Discussion

Several intriguing questions remain to be answered about the biology and life history of this interesting fly. There are many rather unique problems to be overcome for the fly to successfully exploit the intertidal barnacle niche. Since barnacles live in a constantly changing environment, with daily tidal fluctuations, *O. glauca* must synchronize its activities to coincide with tidal cycles. Adults can only oviposit when tidal conditions permit. Larvae can migrate from prey to prey only when securely anchored to a barnacle to prevent being washed away by the returning tide. Adults can emerge only when the tide is low. Since adult emergence appears to be synchronized on mornings of very low tides, there may be some physiological rhythm operating to control time of emergence.

Since relatively few insects have successfully exploited the marine environment, *O. glauca* utilizes an ecological niche not occupied by any other known insect. The physiology of the larvae presumably is adapted to the demands of the marine environment.

Behaviorally, the larvae have adapted to the tidal flow by anchoring themselves to a barnacle prey during submergence, utilizing the effect of submersion on the barnacle to enter the host during its normal feeding time. Pupae are resistant to tidal flow since they are securely anchored to the base of the empty barnacle test. These adaptations indicate strong selection for living in the intertidal zone of the marine environment.

Since *glauca* is one of only two species known in the genus *Oedoparena* and these are the only known North American dryomyzids with a strictly coastal distribution, we suggest that their food habits are unique. Related flies whose food habits are known, i.e. Helcomyzinae, other Dryomyzidae, Coelopidae etc. feed in wrack beds on beaches or on decaying animal matter.

Habits of North American species of *Dryomyza* have not been published and apparently are little-studied, however, B. A. Foote, Kent State University, kindly furnished unpublished rearing records for *Dryomyza anilis* Fallén and *D. simplex* Loew presented here.

Three females and two males of *D. anilis* were caged with fresh hamburger meat (ground beef) in May 1973. On June 6, 8–10 first- and second-instar larvae were crawling over the surface of the decaying meat. Eggs also were present on the surface of the meat. The eggs were white and possessed broad lateral flanges, similar to those of *O. glauca*. In September 1973, a female deposited 41 eggs within 5 hr on peat moss near fresh hamburger. Eggs hatched in 36–48 hr and the first larval stadium lasted about 24 hr. After four days, most larvae were in the third instar and two each were transferred to dead earthworms, dead crane flies (*Tipula trivittata*), dead polygyrid snails, a dead milkweed caterpillar, a dead *Arion* slug, rotting

agaric mushroom and rotting grass. Larvae appeared to feed on everything except the grass. Pupation occurred on all the above substances except grass and adults emerged over 14–30 days following pupation. Additional observations on larvae of *D. anilis* revealed that they failed to survive to maturity on decaying pumpkin flesh, decaying lettuce, and cow mature.

In September 1974, three apparently gravid females of *D. simplex* were collected with four males and placed in jars containing fresh hamburger and rotting caps of gill mushrooms. Within two days, four newly-molted third-instar larvae were found on hamburger. One larva formed a puparium but eventually died.

The above observations do not support earlier records of *D. anilis* living or developing in fungi or excrement. It seems most likely that larvae of *Dryomyza* species are scavengers on dead, decaying animal matter. Since both *D. anilis* and *D. simplex* larvae developed on hamburger meat, other species in *Dryomyza* may have similar habits. Egglishaw (1960) found that larvae of *Helcomyza ustulata* Curtis in the Helcomyzinae fed in wrack beds with other flies, especially Coelopidae.

Sciomyzidae are restricted to preying on the Phylum Mollusca, although feeding habits of a few species are similar to *O. glauca*. It is possible that the feeding habits of *O. glauca* evolved independently within the Sciomyzoidea. Regardless of the origin, the unique habits of *O. glauca* dramatically illustrate the striking ecological diversity within the order Diptera so thoroughly documented by Oldroyd (1964).

It is possible that Sciomyzoidea in other parts of the world have exploited niches similar to *O. glauca,* but since the role of insects in intertidal ecosystems is still poorly studied in most parts of the world, no other dipterous barnacle predators have been discovered to date.

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The authors wish to express their appreciation to B. A. Foote, Kent State University, for providing unpublished biological data and specimens for *Dryomyza anilis* and *D. simplex*; H. J. Teskey, Biosystematics Research Institute, Ottawa, for providing larvae of *O. glauca* for study; and to B. A. Foote, Lloyd Knutson, IIBIII, USDA, and A. C. Borror and L. G. Harris, Department of Zoology, University of New Hampshire for their comments and suggestions. The data presented in this paper were adapted from a thesis for the Master of Science degree by Mark F. Knudsen at the University of California, Berkeley. We also express thanks to Barbara Sniffen for her work on the illustrations of *O. glauca* larvae.

Literature Cited

Anderson, J. R. 1964. Methods for distinguishing nulliparous from parous flies and for estimating the ages of *Fannia canicularis* and some other cyclorrhaphous Diptera. Ann. Entomol. Soc. Am. 57: 226–236.

Detinova, T. S. 1962. Age-grouping methods in Diptera of medical importance, with special reference to some vectors of malaria. W.H.O. Monogr. Ser. No. 47, 216 pp.

Egglishaw, H. J. 1960. The life history of *Helcomyza ustulata* Curt. (Dipt., Dryomyzidae). Entomol. Mon. Mag. 1960: 39–42.

Glynn, P. W. 1965. Community composition, structure and interrelationships in the marine intertidal *Endocladia muricata–Balanus glandula* association in Monterey Bay, California. Beaufortia 12: 1–198.

Hennig, W. 1968. Die Larvenformen der Dipteren. 3. Teil. Akademie Verlag, Berlin. 628 pp.

Hinton, H. E. 1960. The chorionic plastron and its role in the eggs of the Muscinae (Diptera). Q. J. Microsc. Sci. 101: 313–332.

Mathis, W. N. and G. C. Steyskal. 1980. A revision of the genus *Oedoparena* Curran (Diptera: Dryomyzidae: Dryomyzinae). Proc. Entomol. Soc. Wash. 82: 349–359.

Mercier, L. 1921. La larve de *Limnophora aestuum* Villen., Diptere marin. Compt. Rend. Acad. Sci. Paris 173: 1410–1413.

Oldroyd, H. 1964. The natural history of flies. W. W. Norton and Co., New York. 324 pp.

Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. 1968. Between Pacific Tides. 4th Ed. Stanford Univ. Press, Stanford. 614 pp.

Rouboud, M. 1903. Sur les larves marines de Dolichopodes attribuées au genre *Aphrosylus* (Walker). Bul. Mas. Nat. 9: 338–340.

Schlinger, E. I. 1975. Diptera, pp. 436–446. *In* Smith, R. I. and J. T. Carlton, eds., Light's manual: Intertidal invertebrates of the central California coast. Third ed., Univ. Calif. Press, Berkeley. 716 pp.

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THE HABITS AND LIFE HISTORY OF OEDOP ARENA GLAUCA (DIPTERA: DRYOMYZIDAE), A PREDATOR OF BARNACLES'

J. F. Burger, J. R. Anderson, and M. F. Knudsen

(JFB) Department of Entomology, University of New Hampshire, Durham, New Hampshire 03824; (JRA, MFK) Department of Entomology and Parasitology, University of California, Berkeley, California 94720.

Abstract. — Oedoparena f^lauca (Coquillett), a common coastal dryomyzid fly occurring from Central California to Alaska in the Nearctic Region, is the first known dipterous predator of intertidal barnacles. Adults occur on or adjacent to barnacle beds and mate there. Eggs are deposited on the operculum of barnacle prey and larvae consume several prey during development. Pupariation occurs in an empty barnacle test. Adults emerge during a morning low tide. The habits of adult flies and the life history of O. glaiica are discussed; illustrations and a description of the second- and third-instar larva in given, and food habits are compared with related Sciomyzoidea.

In 1966, fly pupae were discovered by M. F. Knudsen and J. F. Burger in empty tests of the intertidal acorn barnacle, Balaniis gkindiila Darwin, on the central California coast (Sonoma County). Subsequently, larvae were observed inside the tests of living barnacles. Tests containing puparia were returned to the laboratory and one adult fly emerged within 24 hr. This slate

gray and brown fly was identified as Oedoparena glaucu (Coquillett). Because this was the first record of a dipterous predator of barnacles, we studied its biology and life history. Schlinger (1975: 442-443) briefly summarized O. glauca habits.

Oedoparena glauca is a moderately large fly, about 5-9 mm long, inhabiting that part of the intertidal zone colonized by the Endocladia-Balanus community. Endocladia muricata (Postels and Ruprecht) J. G. Agardh, 1847 is a red alga abundant in the upper tidal zone of California, especially where wave action is moderate. Balanus glandula is a rather small barnacle of diverse habits and usually is found in the middle or upper intertidal levels

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on protected and exposed coasts, in relatively stagnant bays and on protected piles (Ricketts et al., 1968). Although these species can exist rather high in the intertidal belt, Glynn (1965) found that at the center of the Endocladia-Balanus community, barnacles were submerged 27% of the time during a six month period, or about 45 hr per week. In the present study area, Balanus was most abundant in the middle of the association and less abundant at higher and lower levels.

Although much taxonomic work has been done on marine insects, the biology of many species remains poorly known, except in western Europe. Intertidal insects have been little studied on the west coast of North America.

There are only two reports of Diptera associated with barnacles, both from Europe. Rouboud (1903) found dipterous larvae among Balanus halanoides Darwin scraped from rocks near The Hague, Netherlands and near le Croisic, France, in Lower Loire Province. He believed them to be a species of Aphrosylus (Dolichopodidae). However, since these larvae were not reared, the determination could not be confirmed.

Mercier (1921) described the larvae of Limnophora aestimm Villenueve and stated that he frequently found the larvae living within barnacles. He believed the larvae were predaceous and fed on barnacles, but he did not rear larvae to adults.

The taxonomic status of Oedoparena glauca is discussed by Mathis and Steyskal (1980) in their revision of the genus Oedoparena.

Very little has been published about the habits of flies in the subfamily Dryomyzinae. Hennig (1968) mentioned an 1883 report by Brauer that Neiiroctena i=D/yomyza) anilis Fallen larvae lived in fungi and that Portschin sky, in a 1910 report, found them in human excrement. Because these reports are so sketchy and larvae were not reared to adults, their accuracy cannot be verified. Hennig (1968) stated that the adults of N. anilis were attracted to the stinkhorn fungus. Phallus (=Itliyphallus) impudicus (L.). Recent unpublished data of B. A. Foote, Kent State University, revealed that D. anilis and Dryomyza simplex Loew developed on dead animal mat-

ter, but not on decaying plant matter (see discussion).

The Study Area

Field studies were conducted at Shell Beach in Sonoma Coast State Park, Sonoma County California (Fig. 1). This area is protected from full wave impact by rock outcroppings forming islands or "chimneys"' that dissipate part of the wave energy. This shore type is classified as "protected outer coast" by Ricketts et al. (1968). Two sites were selected for observation within the study area. The first was a rock 2.4 m high and 7.6 m in circumference (Fig. 2). The shoreward side was exposed to sun until early afternoon. The seaward side was sheltered by another large rock next to it and

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Fig. I. View of Shell Beach, Sonoma County, California, showing marginal outcroppings of rock. Fig. 2. View of the first study area.

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rarely exposed to the sun, remaining moist even on the hottest days. The second site was part of the seaward side of a rock receiving sunHght in the morning and all afternoon. This site also was more directly exposed to wave action. Both sites had many thousands of barnacles available for study.

Materials and Methods

Oedoparena glauca is a reluctant but capable flier and easily disturbed by rapid movement. However, flies were observed by approaching them slowly. Collections were made with an aspirator, since nets were rapidly destroyed by the sharp-edged barnacle beds. Barnacle samples were collected by chipping rock surfaces with a screwdriver and hammer.

Laboratory studies were conducted at the Bodega Bay Marine Laboratory of the University of California. Barnacles were maintained in a wooden aquarium with two glass sides and a plastic top. Sea water (14-17°C) was channelled continuously through the tank at 5 mm depth. This prevented continuous immersion of animals in the tank. Barnacles were placed in finger bowls and immersed in running sea water for several hours each day. Emerging adult flies were held in half-pint and gallon ice cream cartons with nylon screen tops and provided water and sucrose.

Rock chips containing barnacles were placed in finger bowls and immersed in fresh sea water to observe habits of O. glauca larvae. Barnacles opened within a few minutes and larvae were observed in situ with a dissecting stereoscopic microscope. Some barnacles were reluctant to open

but could be stimulated to open by directing a jet of water on the operculum with a serological pipet.

Flies used for ovarian development studies were obtained from field collected pupae. Pupae were obtained by examining the study area for empty barnacle tests. Forceps were used to break some of the plates from the side of the test, revealing fly pupae inside. Pupae could be removed from the test by gentle pressure with forceps. F^ipae were placed on damp cotton plugs in 14-dram vials fitted with nylon screen tops. Vials were stored in test tube racks immersed in the aquarium discussed above.

Vials were examined daily to record emergence dates for each fly. After a fly emerged, a cube of sucrose was placed on top of the nylon mesh top. No protein food was provided for any flies, and the only water available was that in the moist pad inside the vial.

At various times after emergence, unmated flies were killed in physiological saline and dissected. The reproductive organs were examined with a stereoscopic and compound microscope to assess egg development in the ovarioles and to determine if male testes contained active sperm. After dissection, reproductive organs were removed to a clear drop of saline for further study. Both wild-caught males and females were dissected to study

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the reproductive organs and the digestive system. Some were examined immediately; others were stored for several weeks of -20°C and -50°C.

Results

Adult activity. — Adults of O. ghiuca are conspicuous members of the intertidal zone in central California, especially when they walk across barnacle-encrusted rocks. When disturbed, they fly only a short distance, rarely more than 1 m and again land on barnacle beds. Adult feeding was not observed .n the field but the guts of several field-collected adults dissected in the laboratory contained diatoms.

Ovarian development in females. — All reared females dissected had eggs wholly or partially developed. Since all reared females were provided only sucrose and water, this established that O. glauca females studied were autogenous in the first gonotrophic cycle. Eggs of nulliparous reared females were fully developed (1.8 mm long) by six days posteclosion.

Based on previous results with other Diptera (e.g. Anderson, 1964; Detinova, 1962), females that had dark, yellow-colored debris present in the ovarian pedicels were judged to be parous. All wild-caught females were judged to be parous when collected. Laboratory-reared females known to be nulliparous had ovarian pedicels with very little or no yellow material in them. No experiments were performed to establish the relationship between amount of yellow-colored follicular debris and degree of parousness.

Mating and oviposition. — Mating activity of O. glauca was observed in the field from 16 May to 1 August 1968. Coupled pairs were observed infrequently. Of 127 flies collected during the observation period, 109 (85%)

were males; 18 (15%) were females. Individual males did not seem to be actively seeking females but remained stationary until disturbed. If another fly entered the area, a male would try to mount the ititruder, regardless of sex or species, but quickly rejected the visitor if not of the opposite sex and not conspecific.

If a female landed on the barnacle bed, a male, if present in the area, would follow her across the bed. Males always followed and mounted females from behind. Coupling was not always successful on the first attempt but usually was accomplished on the second or third attempt. After coupling, the female, with the male above her, continued moving across the barnacle bed.

Adults remained coupled for about 15 min, if undisturbed. After uncoupling, the male remained on the female while she commenced searching behavior, walking across the barnacle bed. When she encountered a suitable barnacle, she passed beyond it, curving her abdomen ventrally while backing into the opercular opening and depositing an egg. The female then moved to another barnacle.

During the oviposition process, the accompanying male repeatedly at-

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Fig. 3. Opening of a Balanus glanduUi barnacle with eggs oi Oedoparenu i^louca attached. Eggs approximately 1.8 mm long.

tempted coupling. If coupling attempts were successful, searching and oviposition by the female ceased for about 15 min until copulation was completed and oviposition behavior by the female resumed. This sequence would be repeated several times, but, if interrupted, the female would fly away alone. Frequently, single males competed for an occupied female and females often escaped as males fought for her possession.

Copulating pairs were collected in the field and placed in vials containing rock chips covered with barnacles. Flies copulated in the vials but oviposition was not observed directly. After six days, eggs were found on the

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Length of barnacle operculum (mm)

Fig. 4. Correlation between Oedoparena glauca larval length and width of prey barnacle opening.

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scutes of three B. glandula on separate rock chips. Eggs hatched in 48 hr and first-instar larvae invaded the barnacle. Not all ovipositing females were accompanied by males, but males, once stationed on the female, usually remained there during the entire oviposition period.

In the laboratory, O. glauca deposited eggs only on B. glandula, never on a smaller barnacle, Chthamolus fissus Darwin. Eggs usually were placed on the inner surface of the barnacle test or on the turga and scuta (Fig. 3). The eggs bear a pair of flanges extending from each side that may help secure the eggs in the cracks of the barnacle test. They also may be part of the egg's plastron system, for although the surface features of the egg were not examined in this study, we assume the egg has a plastron structure, since it is submerged by sea water during part of the tidal cycle. Hinton (1960) has found that the eggs of most dipterans studied have a plastron structure, allowing them to obtain oxygen during submersion.

Each ovary of the female contains 18 ovarioles, so potentially 36 eggs

could be produced per ovarian cycle, however no observed female deposited that many eggs.

Prey selection and entry of larvae. — Although O. glauca females preferentially selected B. glandula for oviposition in nature, small larvae observed in the laboratory would invade Chthamalus fissus, suggesting that first-instar larvae were able to move from B. glandula to C. fissus or that ovipositing females were more selective in natural habitats. No first-instar larvae were observed outside barnacles in the field.

It is likely that hatching of eggs is related to tidal cycles, probably occurring at any multiple of 12 hr from the time of oviposition. Submerged larvae were unable to survive outside a barnacle because they are buoyant and easily swept away by tidal flow. Eggs hatch during a low tide period and first-instar larvae enter a barnacle before high tide returns. Since barnacles often were not tightly closed, even at low tide, first-instars had no difficulty entering the prey between the opening of the turga and scuta of the operculum.

To determine if there was a correlation between the size of O. glauca larvae and their prey, rock chips were maintained in the laboratory and barnacles containing larvae were dissected after measuring the longitudinal opening. The fly larva was then removed and fixed for measurement. Size of the fly larva was highly correlated with barnacle opening size ($P = <0.01$, Fig. 4). Balanus glandula openings varied from 2.1 to 4.55 mm and contained O. glauca larvae 3.2-9.8 mm long; Chthamalus fissus openings were 1.05-2.45 mm wide and contained larvae 1.7-5.6 mm long.

Smaller larvae were found in both B. glandula and C. fissus and in a wider size range of barnacles than were longer larvae, implying that as a larva grew, it required progressively larger prey. Since B. glandula is larger at

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Fig. 5. Third-instar larva of Oedoparena glaucci protruding from a barnacle prey.

maturity than C. fissus, larger larvae usually occurred in B. glandida, preferentially selecting them for invasion.

Larvae were observed searching for new prey in laboratory aquaria. A larva moved slowly until it encountered a barnacle operculum; then the mouthparts were moved rapidly in a hoeing motion. If the larva encountered a small opening in the prey's operculum, the mouthparts were lodged in the opening to anchor the larva to the operculum. Once anchored, larvae remained inactive for up to 24 hr. In the field, larvae probably complete entry when the tide returns. In the laboratory, barnacles opened as soon as immersed in sea water, allowing O. glauca larvae to complete entry. Larvae not securely anchored to the barnacle were easily washed off by immersion in sea water. In the laboratory, all larvae had entered a prey within 24 hr.

In nature, third-instar larvae often were observed wandering over the

barnacle beds. Except for newly-hatched larvae, no first- or second-instar larvae were observed outside a barnacle prey. Many wandering larvae were observed executing the same searching behavior discussed above, securing themselves to a barnacle operculum with the mouthhooks. Possibly the greater food requirements of larger larvae forces them to seek fresh prey more frequently. Usually, only one larva was present per barnacle; only rarely were two larvae present in a single prey.

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Recently hatched larvae could not be reared to the pupal stage in the laboratory because barnacles could not be kept alive for the extended periods necessary for larval development. Larval development is slow, requiring several months, possibly because of the relatively low temperature in the surrounding environment.

Distribution of O. i^lauca larvae in barnacle beds. — A vertical transect was made through one of the study sites to determine if larvae were equally distributed throughout the barnacle beds. Three sites were sampled, one each in the upper, middle, and lower portions of the barnacle bed. All barnacles in a 5 cm^ area at each site were examined. Larval density was greater in the lower and middle portions of the bed, but since smaller barnacles were concentrated in the upper portions of the bed, larval density probably is related to barnacle size rather than other factors.

Oedoparena glauca larvae were found in 11.0-12.5% of barnacles examined in the middle and lower portions of the bed, but only in 5.09f of those in the upper bed.

Effects of O. glauca on their prey. — Observations were made on the effects of O. glauca larvae on individual barnacles. When barnacles were submerged in laboratory aquaria, they opened the turga and scuta rapidly, extended the cerrci and commenced sweeping. Prey barnacles opened as rapidly as non-infested individuals, but the cerrci were not extended and the posterior spiracles of the larva protruded through the opening (Fig. 5), preventing extension of the cerrci. The cerrci were pushed to one side and remained immobile, even when the infesting larva was small and the prey quite large.

Occlusion of the opening prevented the barnacle from feeding and probably contributed to weakening and eventual death of the prey. Cerrci were unable to function even when larvae were removed, indicating that O. glauca may sever the nerve connectives or muscles operating the cerrci.

Tissues of the basal portion of a prey barnacle were extensively damaged and apparently larvae feed on this part of the barnacle first, possibly to incapacitate the prey. The operculum remained functional during the larval feeding period and muscles operating this structure may not be consumed. This would allow periodic flushing of the prey and also would allow the larva to leave the host after completion of feeding. Ultimately, however, most of the barnacle tissues are consumed. Occasionally, larvae were found in barnacles whose opercula did not open when immersed in fresh sea water.

Natural enemies of O. glauca larvae. — Several potential predators of O.

glauca larvae are associated with the Balanus-Endocladia community. Presumably larvae are protected from predators while in the barnacle and were attacked only when moving from one prey to another. Once, a staphylinid beetle was observed feeding on an O. glauca larva, and sluggish larvae may be vulnerable to such active predators. Pupae, however, usually are wedged

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Figs. 6-7. Oedoparena gUiuca, second-instar larva. 6, Dorsal view with enlargement of spinules. 7, lateral view.

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in the tests of their prey and thus may be relatively protected from predation.

Description of the second- and third-instar larva of O. glauca. — Second-Instar Larva (Figs. 6-9): Length: 4.5-6.0 mm, greatest width 1.4 mm (not including lateral protuberances). Integument yellowish white, semi-transparent. Body elongate, flattened dorsoventrally, narrower anteriorly and posteriorly (Fig. 6); anterior end tapered but rounded apically; posterior end broadly rounded posteriorly and bearing conspicuous fleshy protuberances laterally and posteriorly (Figs. 6, 7). Abdominal segments bearing 2 pairs of large, pointed fleshy protuberances laterally and ventrolaterally, the lateral pair about twice as large as ventrolateral ones (Fig. 7), very small on 1st abdominal segment, largest on 3rd through 5th abdominal segments. Segment I with minute spinule ridges present only on posterior Vi of segment. Paired anterior spiracles (Fig. 8) light brown, distinctly bilobed, with 7 papillae on each lobe, projecting from anterolateral margin of segment II. Segments II and III uniformly covered with spinule ridges, individual spinules rounded on dorsal surface, elongate and acutely pointed on ventral surface (Fig. 6); spinule ridges on segments IV to X in 3 transverse rows dorsally, interrupted by 2 intersegmental furrows; lateral and ventrolateral protuberances and ventral surfaces of these segments uniformly covered with spinule ridges, configuration similar to that on segments II and III. Segment XI bearing 3 pairs of large, rounded fleshy tubercles laterally and 1 pair of pointed tubercles posteriorly between posterior spiracles; anal lobes large, rounded. Posterior spiracles elongate, borne on fleshy protuberances posteriorly, separated by 2-3 x length of spiracular tube; spiracular tube black, about twice as long as broad.

Cephalopharyngeal skeleton (Fig. 9) brownish to black, 0.4 mm long.

Indentation index 55. Dorsal cornua 1.6 times length of ventral cornua, dorsal cornua lighter anteriorly and along dorsal margin; dorsal cornua with very narrow dorsal window. Dorsal bridge moderately developed, with a few lightly pigmented areas present below. Accessory rods rather broad, acutely pointed dorsoapically. Mouthhooks stout and broad, with a very short broadly rounded hook apically and 2 small accessory teeth along the ventral margin; posterior margin extended ventrally into a long rod articulating with the ventral surface of the hypostomal sclerite. Hypostomal sclerite long and slender, blunt anteriorly, gradually narrowed to a point posteriorly where it articulates with the pharyngeal sclerite.

Third-instar larva (Figs. 10-12): Length: 6.0-9.8 mm, greatest width 1.8 mm (not including lateral protuberances). Integument yellowish white, with dark brown pubescence present dorsally and laterally on segments II-IV and dorsally on segments V-X (Fig. 10), pubescence uniformly covering posterior '/6 of segments V-X, present medianly and laterally between the intersegmental furrows and laterally only on the anterior '/3 of segments V-

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Figs. 8-9. Oedoparena glauca, second-instar larva. 8, Cephalopharyngeal skeleton, lateral view. 9, Anterior spiracle.

X. Lateral abdominal protuberances about V2, longer than ventrolateral pair. Spinule ridges conspicuous on segment I dorsally and ventrally and all of segments I-IV and IX-XI, less distinct on segments V-VIII and obscured by brown pubescence. Paired anterior spiracles (Fig. 11) not noticeably bilobed as in the second-instar larva, bearing 14 distinct papillae. Posterior spiracular tubes separated by a distance about equal to their length.

Cephalopharyngeal skeleton (Fig. 12) black, 0.5 mm long. Dorsal cornua 1.8x length of ventral cornua. Mouthhooks with 1 accessory tooth along the ventral margin. Otherwise third-instar larva similar to that of the second-instar.

Known larvae of Dryomyza differ from Oedoparena in lacking lateral fleshy protuberances; mouthhooks more slender; integumental spinules more slender and elongate, less densely packed and not distributed in well-defined rows dorsally; anal segment with more widely spaced lateral protuberances; and spiracles not borne on elongate spiracular tubes.

Pupation and adult emergence. — Mature O. i^lauca larvae commenced prepupation activity by wandering over the barnacle bed adjacent to its last prey. Larvae probed each barnacle encountered with their mouthparts. Living barnacles were rejected, but empty tests were examined for a longer time. When a favorable site was found, the larva entered the test.

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Fig. 10. Oedoparena f;luuca, third-instar larva, dorsal

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Figs. 11-12. Oedoparena glauca, third-instar larva. 11, Anterior spiracle. 12, Cephalo-pharyngeal skeleton, lateral view.

Larvae in empty tests oriented themselves with the anterior end facing out, presumably to facilitate adult emergence. Orientation prior to pupation is a lengthy process. One larva observed in the laboratory required three days to complete orientation. Subsequently, pupation occurs and the larval cuticle becomes progressively darker, eventually becoming dark red-brown. Pupae always occurred in empty barnacle tests, most commonly high in the Balanus-Endocladia community. Pupae usually were in the bottom of the tests and were so tightly wedged into a corner that the test had to be broken to remove them.

Length of the pupal period may be rather long. Fifty pupae from the Shell Beach site were observed in the laboratory from the date of collection (2

July) until 30 July. Twenty-two adults emerged during this 28 day period, indicating that the pupal period may be at least 28 days and possibly longer.

Recently eclosed adults were observed most commonly in the morning and adult activity was especially high on days when tides were very low. Newly emerged adults usually rested on barnacles and spread their wings during the hardening process. Teneral flies were always much lighter colored than older ones and thus easily observed.

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Discussion

Several intriguing questions remain to be answered about the biology and life history of this interesting fly. There are many rather unique problems to be overcome for the fly to successfully exploit the intertidal barnacle niche. Since barnacles live in a constantly changing environment, with daily tidal fluctuations, O. glaiica must synchronize its activities to coincide with tidal cycles. Adults can only oviposit when tidal conditions permit. Larvae can migrate from prey to prey only when securely anchored to a barnacle to prevent being washed away by the returning tide. Adults can emerge only when the tide is low. Since adult emergence appears to be synchronized on mornings of very low tides, there may be some physiological rhythm operating to control time of emergence.

Since relatively few insects have successfully exploited the marine environment, O. glaiica utilizes an ecological niche not occupied by any other known insect. The physiology of the larvae presumably is adapted to the demands of the marine environment.

Behaviorally, the larvae have adapted to the tidal flow by anchoring themselves to a barnacle prey during submergence, utilizing the effect of submersion on the barnacle to enter the host during its normal feeding time. Pupae are resistant to tidal flow since they are securely anchored to the base of the empty barnacle test. These adaptations indicate strong selection for living in the intertidal zone of the marine environment.

Since glauca is one of only two species known in the genus Oedoparena and these are the only known North American dryomyzids with a strictly coastal distribution, we suggest that their food habits are unique. Related flies whose food habits are known, i.e. Helcomyzinae, other Dryomyzidae, Coelopidae etc. feed in wrack beds on beaches or on decaying animal matter.

Habits of North American species of Dry omyza have not been published and apparently are little-studied, however, B. A. Foote, Kent State University, kindly furnished unpublished rearing records for Dryomyza anilis Fallen and D. simplex Loew presented here.

Three females and two males of D. anilis were caged with fresh hamburger meat (ground beef) in May 1973. On June 6, 8-10 first- and second-instar larvae were crawling over the surface of the decaying meat. Eggs also were present on the surface of the meat. The eggs were white and possessed broad lateral flanges, similar to those of O. glauca. In September 1973, a

female deposited 41 eggs within 5 hr on peat moss near fresh hamburger. Eggs hatched in 36-48 hr and the first larval stadium lasted about 24 hr. After four days, most larvae were in the third instar and two each were transferred to dead earthworms, dead crane flies (Tipula trivittata), dead polygyrid snails, a dead milkweed caterpillar, a dead Arion slug, rotting

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agaric mushroom and rotting grass. Larvae appeared to feed on everything except the grass. Pupation occurred on all the above substances except grass and adults emerged over 14-30 days following pupation. Additional observations on larvae of D. anilis revealed that they failed to survive to maturity on decaying pumpkin flesh, decaying lettuce, and cow mature.

In September 1974, three apparently gravid females of D. simplex were collected with four males and placed in jars containing fresh hamburger and rotting caps of gill mushrooms. Within two days, four newly-molted third-instar larvae were found on hamburger. One larva formed a puparium but eventually died.

The above observations do not support earlier records of D. anilis living or developing in fungi or excrement. It seems most likely that larvae of Dryomyza species are scavengers on dead, decaying animal matter. Since both D. anilis and D. simplex larvae developed on hamburger meat, other species in Dryomyza may have similar habits. Egglishaw (1960) found that

larvae of Helcomyza ustulata Curtis in the Helcomyzinae fed in wrack beds with other flies, especially Coelopidae.

Sciomyzidae are restricted to preying on the Phylum Mollusca, although feeding habits of a few species are similar to O. glaiica. It is possible that the feeding habits of O. glauca evolved independently within the Sciomyzoidea. Regardless of the origin, the unique habits of O. glauca dramatically illustrate the striking ecological diversity within the order Diptera so thoroughly documented by Oldroyd (1964).

It is possible that Sciomyzoidea in other parts of the world have exploited niches similar to O. glauca, but since the role of insects in intertidal ecosystems is still poorly studied in most parts of the world, no other dipterous barnacle predators have been discovered to date.

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Literature Cited

Anderson, J. R. 1964. Methods for distinguishing nulliparous from parous flies and for estimating the ages of Fannia caniciilaris and some other cyclorrhaphous Diptera. Ann. Entomol. Soc. Am. 57: 226-236.

[Begin Page: Page 377]

Detinova, T. S. 1962. Age-grouping methods in Diptera of medical importance, with special reference to some vectors of malaria. W.H.O. Monogr. Ser. No. 47, 216 pp.

Egglishaw, H. J. 1960. The life history of Helcomyza ustuUita Curt. (Dipt., Dryomyzidae). Entomoi. Mon. Mag. 1960: 39-42.

Glynn, P. W. 1965. Community composition, structure and interrelationships in the marine intertidal Endocladia intiricatci-BaUinus glandula association in Monterey Bay, California. Beaufortia 12: 1-198.

Hennig, W. 1968. Die Larvenformen der Dipteren. 3. Teil. Akademie Verlag, Berlin. 628 pp.

Hinton, H. E. 1960. The chorionic plastron and its role in the eggs of the Muscinae (Diptera). Q. J. Microsc. Sci. 101: 313-332.

Mathis, W. N. and G. C. Steyskal. 1980. A revision of the genus Oedoparena Curran (Diptera: Dryomyzidae: Dryomyzinae). Proc. Entomoi. Soc. Wash. 82: 349-359.

Mercier, L. 1921. La larve de Limnophora aestiium Villen., Diptere marin. Compt. Rend. Acad. Sci. Paris 173: 1410-1413.

Oldroyd, H. 1964. The natural history of flies. W. W. Norton and Co., New York. 324 pp.

Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. 1968. Between Pacific Tides. 4th Ed. Stanford Univ. Press, Stanford. 614 pp.

Rouboud, M. 1903. Sur les larves marines de Dolichopodes attribuees au genre Aphrosxhis (Walker). Bui. Mas. Nat. 9: 338-340.

Schlinger, E. L 1975. Diptera, pp. 436-446. In Smith, R. I. and J. T. Carlton, eds.. Light's manual: Intertidal invertebrates of the central California coast. Third ed., Univ. Calif. Press, Berkeley. 716 pp.