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FACTORS INFLUENCING THE ABUNDANCE AND DISTRIBUTION OF TWO AQUATIC MOTHS OF THE GENUS *PARARGYRACTIS* (PYRALIDAE)

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ABSTRACT. Two species of aquatic pyralid moths of the genus *Parargyractis* occur sympatrically in parts of northern California. The larvae of both species have similar resource requirements, but have different tolerances to parameters of water quality. Thus, the areas of sympatry reflect locations where tolerances overlap. In such areas, larvae interact with the more aggressive species acquiring suitable shelters for larval web construction and pupation sites. Interactions of this type are density dependent, and related to population levels and the number of suitable shelters on submerged rocks. Principle factors influencing larval populations include water velocity, water temperature, and dissolved oxygen concentrations. *Parargyractis jaliscalis* was more tolerant to lower dissolved oxygen concentrations, reduced water velocity, and higher water temperatures than *P. confusalis*, due to different physiological and behavioral adaptions. Physical parameters of water quality strongly influence the distribution and abundance of both species.

The pyralid genus *Parargyractis* consists of aquatic moths. The eggs, larvae, and pupae of *Parargyractis* live underwater in streams, rivers, and occasionally in lakes. On emergence from the cocoon, the adult floats or swims to the surface of the water and climbs onto debris or protruding rocks, where the wings expand. Moths mate on land, after which the female re-enters the water to oviposit on submerged rocks. The first instar larvae respire cutaneously, while those in the second through fifth instars have gills (Fig. 1). The larvae feed on algae and diatoms under or near silken tents, which are constructed over cracks or crevices on submerged rocks. They pupate in a specially constructed cocoon, which has openings near the periphery to allow circulation of water around an inner cocoon, which contains the



FIGS. 1-2. Parargyractis confusalis 1, mature larva $(3.2\times)$; 2, cocoon $(2\times)$.

pupa (Fig. 2) (Lange, 1956; Tuskes, 1977). Aquatic moths may be common near suitable larval habitat and are a familiar group to aquatic biologists. Munroe (1972) listed 14 species in this genus, which occur north of Mexico.

Two species, *P. jaliscalis* (Schaus) and *P. confusalis* (Walker), were found to occur sympatrically and provided an opportunity to study the mechanisms which allow closely related species to coexist. Both species are widely distributed and are among the few members of the genus that are common as far north as Canada. In California each species has two to three generations per year, and their biology makes them particularly well suited for this type of study. The shelters which larvae construct provide them with territories, which restrict their movements, allowing manipulation of larvae with minimal disturbance, since rocks may be transported in water to the laboratory or other field locations.

METHODS

Physical parameters which might influence the distribution of either species were examined. These included concentrations of nitrate, phosphate, carbon dioxide, dissolved oxygen, and pH, as well as water temperature and velocity. Water velocity was measured with a counter-type pigmy flow meter, which was calibrated at the U.C. Davis Hydraulics Laboratory. All physical parameters were measured at each site approximately 18 times a year.

Field studies were conducted in northern California. Allopatric populations of *P. confusalis* were studied at: Middle Fork of the American River, 8 km S.E. of Auburn, Placer Co., elev. 160 m; and the North Fork of Cache Creek, 11 km N. of Bartlett Springs, Lake Co., elev. 380 m. An allopatric population of *P. jaliscalis* was studied in Putah Creek, 2.6 km S.W. of Davis, Yolo Co., elev. 17 m. Sympatric populations were studied at: Bear Creek, 3.7 km N. of Hwy 20, Colusa

Co., elev. 365 m; and Little Stony Creek, 4.2 km W. of Lodoga, Colusa Co., elev. 365 m.

Behavioral observations in the field were frequently difficult to interpret; therefore, laboratory populations of both species were established. Larvae were collected and placed in 40 to 110 liter aquariums with algae covered rocks. Water was circulated with a bubbling air stone under a plexiglas stand, which directed the rising bubbles at an angle oblique to the surface. Debris on top of the plexiglas stand provided a suitable area on which adults could perch following emergence. A divider, which extended from the bottom to 3 cm above the surface of the water, was used to separate the columns of water moving in opposite directions and improve circulation. A constant current was necessary, because the cocoon is oriented so that water circulates through it.

To examine factors limiting distribution *confusalis* larvae attached to rocks were collected, and the number of larvae per rock was determined. The rocks with larvae were then transported in containers of water to another location in the same stream occupied by only *jaliscalis*. Rocks with larvae of *jaliscalis* attached were treated in a similar manner and transported to a typical *confusalis* habitat. The larvae of each species were left in the habitat of the other species from 1600 to 0900 h. During this time oxygen and carbon dioxide concentrations were monitored at hourly intervals. At the end of approximately 17 h the larvae were removed and transported in well oxygenated water to the laboratory, where mortality was determined. Larvae showing no sign of activity after two hours were considered dead.

Laboratory studies were conducted to determine the effects of oxygen stress. Larvae of both species were collected and maintained separately under similar conditions for 24 h before the tests to determine if any larvae had been injured. One liter flasks were filled with water collected from a stream inhabited by both species. The desired O_2 level was attained by bubbling N_2 through the water. The O_2 concentration was monitored with an IBC differential oxygen analyzer. For each test, five larvae of each species were placed in a 1 liter flask at 22°C and the top sealed with a double layer of Parafilm. After 8 h the seals were removed and the oxygen concentration measured again. The larvae were then placed in Petri dishes containing well oxygenated water (11 ppm). At 10 min intervals, immobile larvae were touched with a probe and considered dead if no movement was noted during a period of 2 h.

Overwintering habits were studied at Bear Creek from late October

to April. Rocks, which were naturally fused in a conglomerate to the stream bed, were selected for similar texture, orientation to current, and larval distribution. During each sampling period larvae were removed from $1/_6$ of the surface area of each rock, and returned to the laboratory, where they were sorted to species and instar. The density on each rock was determined, and the average density of each species was calculated. The total area sampled varied ± 44.5 cm²; therefore, samples were standardized by multiplying density by the typical sample size of 1090 cm².

RESULTS

Changes in the larval densities of both species were correlated with water temperature and velocity. During the winter months at water temperatures of 1.7 to 11°C, larvae were active but slow to develop. The peak in *confusalis* larval populations occurred during late spring when water temperatures were above 12°C but below 25°C. An aquatic fungus, which is parasitic, was associated with this species when the water temperature rose above 21°C. The density of *jaliscalis* increased when water temperatures were above 17°C and continued to do so throughout the summer. Larvae of *jaliscalis* appeared resistant to fungal attack at all temperatures observed in the field.

Though some larvae occurred in still water, densities of both species were highest in flowing water. Peak densities of *jaliscalis* larvae occurred in velocities ranging from 0.2 to 1.1 m/sec, with a maximum of 1.7 m/sec. Larvae of *confusalis* were most abundant in velocities from 0.3 to 1.4 m/sec, with some occurring in velocities as high as 2.6 m/sec.

Fig. 3 shows a typical O_2 -CO₂ profile for two different habitats in the same creek but separated by 5.1 km. Diurnal O_2 concentrations were sufficiently high to support both species, but at night O_2 concentrations were too low for *confusalis* in areas of abundant algal growth, due to dark phase respiration. In habitat A there was from 120 to 190 times more algae (dry weight) than in habitat B. During the summer oxygen concentrations in habitat A frequently declined to 2 ppm at night. The lowest O_2 concentration recorded for habitat B was 6.8 ppm. Habitat A represented a normally allopatric population of *jaliscalis*, while B was an area occupied by *confusalis*. Only 2.0% of the 181 *jaliscalis* larvae transported to the *confusalis* habitat died (this may have been handling injury), while *confusalis* larvae moved to the *jaliscalis* habitat incurred 34.5% and 27.7% mortality (n = 96, 108). Levels of NO₃ and PO₄ were very low and did not appear to be influencing either species.

The overwintering study indicated that during a 6 month period



FIG. 3. Aquatic oxygen, carbon dioxide profile of Bear Creek, Lake Co., Calif. Habitat A represents an area inhabited by only *P. jaliscalis*. Habitat B is an area dominated by *P. confusalis*.

(October to April) the larval density of *confusalis* decreased by 25.5%. During this same period, the decrease in the *jaliscalis* population was 71% (Table 1). No samples could be taken during February, due to high water.

In the laboratory *jaliscalis* larvae were more aggressive than those of *confusalis* and moved across the rock surface, frequently attempting to enter the webs of *confusalis*. In approximately 16% of such encounters, the larvae of *confusalis* were displaced. Second or third instar larvae of *jaliscalis* were found within the cocoons of *confusalis*, and it was observed that many of these pupa usually failed to hatch. Occasionally the pupa was found to be damaged by the intruding

TABLE 1. Changes in larval density during overwintering, Bear Creek.

| | P. confusalis | | | | | | P. jaliscalis | | | | | | | |
|-------------|------------------------|----|----|----|-------|-------|------------------|------------------------|----|----|----|-------|-------|------------------|
| | No. collected & instar | | | | | | D | No. collected & instar | | | | | D | |
| Date | 2 | 3 | 4 | 5 | Total | % Δ | /cm ² | 2 | 3 | 4 | 5 | Total | % Δ | /cm ² |
| October 30 | 8 | 42 | 38 | 29 | 117 | _ | .113 | 3 | 23 | 20 | 48 | 94 | | .090 |
| December 31 | 0 | 12 | 41 | 48 | 101 | -18.0 | .093 | 0 | 0 | 22 | 50 | 72 | -25.5 | .067 |
| January 31 | 0 | 0 | 24 | 72 | 96 | -5.5 | .088 | 0 | 0 | 2 | 31 | 33 | -54.5 | .030 |
| March 30 | 0 | 0 | 0 | 98 | 98 | +1.0 | .087 | 0 | 0 | 0 | 26 | 26 | -21.0 | .024 |
| April 30 | 0 | 0 | 0 | 92 | 92 | -3.5 | .084 | 0 | 0 | 0 | 21 | 21 | -20.5 | .019 |

 $\% \Delta = \%$ change in density from previous month.



FIG. 4. Recovery and mortality rates of *P. jaliscalis* and *confusalis* last instar larvae which were subjected to varying degrees of oxygen stress.

larva, but the usual cause of pupal death was believed to be suffocation resulting from the larva disrupting the circulation of water around the pupa. No *jaliscalis* larvae were observed entering a conspecific's web. Unlike *jaliscalis* larvae, those of *confusalis* were not observed to displace or attempt to enter another individual's web.

The number of gills per larva in the second through fifth instar of both species differs significantly (P < 0.05) (Table 2). The gills of both species are about the same size, but the larvae of *jaliscalis* had from 24 to 43% more gills than *confusalis* of the same instar. Larvae of *jaliscalis* exhibited a greater tolerance to lower O₂ concentrations than *confusalis*, as they recovered faster with lower mortality than *confusalis* under similar oxygen stressed conditions (Fig. 4).

DISCUSSION

Field and laboratory observations indicate that both *P. confusalis* and *P. jaliscalis* can, and do, exist sympatrically. *Parargyractis jaliscalis* is the predominant species in the Central Valley of California, while *confusalis* is more abundant above the valley floor in both the Coast Range and the Sierra Nevada. A number of factors influence the distribution of *confusalis*.

Behavioral observations suggest the larvae of *jaliscalis* are more active and aggressive and may enter the cocoons of *confusalis* through

| Instar | P. jalise | calis | P. confu | | |
|--------|-----------------------|-------|-----------------------|------|-------|
| | Average # of gills | S.D. | Average # of gills | S.D. | t |
| 2 | 47.35 | 3.65 | 39.70 | 2.85 | 14.82 |
| 3 | 136.70 | 7.38 | 76.70 | 3.56 | 19.38 |
| 4 | 174.14 | 5.10 | 123.24 | 6.62 | 18.41 |
| 5 | 208.00 | 6.18 | 160.84 | 7.10 | 13.82 |

TABLE 2. Comparison of gill number per larval instar between *P. jaliscalis* and *P. confusalis*.

S.D. = Standard Deviation.

Sample size equals 40 individuals per instar/species.

openings around the cocoon's periphery (Fig. 2). This intrusion usually resulted in the death of the pupa. Such interactions are density dependent phenomena, and occur primarily when the number of suitable locations for web or cocoon construction is low in relation to larval density.

In areas which undergo nocturnal oxygen stress, morphological and physiological adaptations to this stress influence the distribution of larvae. In each larval stage that utilizes gills, *jaliscalis* has from 24 to 42% more gills than confusalis (Table 2), and thus, has a correspondingly greater gill surface area for respiration. In addition to differential mortality at O₂ concentrations below 5 ppm (Fig. 4), the larvae of *jaliscalis* remained active longer and recovered faster than confusalis under identical O₂ stress. In areas of sympatry confusalis was infrequently observed where the dissolved oxygen concentration is below 7.2 ppm. However, in allopatric areas confusalis was found to occur where the oxygen concentration frequently reached a minimum of 5.25 ppm. Laboratory experiments also indicated that confusalis can exist at O_2 levels 1.5 to 2.0 ppm less than that observed in areas of sympatry. It appears that *jaliscalis* is better adapted to warmer. less well oxygenated water, and this, combined with its aggressive nature, allows it to out-compete confusalis when the O2 concentration is below 7.0 to 7.5 ppm.

Physical factors and a reduced competitive advantage limit the distribution of *jaliscalis*. Although *jaliscalis* larvae are abundant in the fall, samples in sympatric areas indicate a substantial decrease in larval density throughout the winter. It was found that 30 to 60% of the *jaliscalis* larvae are dislodged from rocks following the first substantial rain of the season. The mortality is related to maximum water velocities, with higher mortality occurring in swift portions of the stream, especially where water velocity exceeds 1.2 m/sec. A survey of larval distribution along a water velocity gradient during the summer indicated that *confusalis* larvae occurred in velocities as high as 2.6 m/sec, while the maximum for *jaliscalis* was 1.7 m/sec. As water velocity increases the active behavior of *jaliscalis* larvae becomes a disadvantage; for when they leave the shelter of their silken webs, they are swept away by the current.

Of the two, *jaliscalis* larvae are more active and adapted morphologically and physiologically to slower, warmer, less well oxygenated water. *Parargyractis confusalis*, on the other hand, is better adapted to colder, fast flowing, well oxygenated water. Though each species utilizes similar resources, each has a refuge, or a portion of its niche which is non-overlapping with that of its potential competitor. During the course of the year, the ability of the larvae to withstand various combinations of physical factors influences the abundance and distribution of each species. These factors play an important role in the outcome of density dependent larval competition between these two aquatic moths.

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