THE INFLUENCE OF TEMPERATURE ON LARVAL AND JUVENILE GROWTH IN THREE SPECIES OF SOUTHERN CALIFORNIA ABALONES[1]

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ABSTRACT

Larvae of the abalones *Haliotis rufescens*, *H. corrugata*, and *H. fulgens* displayed most rapid growth and best survival at 15°-18°, 18°-21°, and 20°-23°C, respectively. Survival of larvae and postlarvae was poor above these optimal ranges. However, juveniles 3 mo to 1 yr old were tolerant of a broader temperature range. The warm-water species, *H. fulgens*, increased in shell length at an average rate of 88 μ per day at 26°C. Mean shell elongation rates were 77 and 64 μ per day in *H. rufescens* and in *H. corrugata* at their respective optima.

An expanding body of literature exists concerning aspects of the biology and culture of the abalone *Haliotis* (e.g., Sakai, 1962; Oba, 1964; Tamura, 1966; Imai, 1967; Tanaka, 1969; Shibui, 1971a; and McBeth, 1972, which succeeded the pioneering studies of Murayama, 1935, and Ino, 1952). In these studies little attention was directed to problems of larval development, and essentially no information has been obtained on the limitations imposed by temperature on growth and survival of larvae and postlarvae with the single exception of the observations on *H. sorenseni*, reported by Leighton (1972). In 1962, Kan-no and Kikuchi related results of a 3-wk experiment in which juvenile *H. discus hannai* were reared at five different temperatures, but most investigators have merely reported the range of temperature prevailing during observations (e.g., Oba, 1964; Shibui, 1971b).

This paper describes results of experiments in which groups of larvae, postlarvae, and juveniles were reared at a series of temperatures encompassing the natural range to examine the influence of these factors on development and survival. Larvae were obtained from three American west coast species spawned in the laboratory: The red abalone, *H. rufescens*, the pink abalone, *H. corrugata*, and the green abalone, *H. fulgens*.

MATERIAL AND METHODS

Ripe abalone were collected off southern California by diving. In transportation to the laboratory, care was taken to avoid subjecting the animals to desiccation or other physical shock which might have induced premature release of gametes. Adult abalone were allowed a laboratory "conditioning period" of about 2 wk before attempts were made to induce spawning. Water temperature in tanks containing abalone of both sexes was raised approximately 5°-8°C above ambient, following the thermal shock method of Ino (1952) and Oba (1964); a procedure which was only occasionally successful. Most productive spawnings in terms of quantity and viability were those which occurred spontaneously in the laboratory. Natural cues and events associated with "mass spawnings" are not well understood (Owen and Meyer, in press) and were not investigated in this study.

Fertilized eggs were collected as soon as possible after their release. The eggs, which settle rather rapidly, were siphoned or pipetted into freshly filtered seawater (Cuno filter unit,[3] ca. 5 μ) at the same temperature as that of the spawning environment. Repetition of the process several times, each time using freshly filtered seawater, was usually sufficient to wash eggs free of excess sperm and debris. Incubation was carried out at ambient temperatures and larvae treated as described elsewhere (Leighton, 1972).

While some experiments were performed with eggs at early cleavage stages, most observations

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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were initiated with newly hatched trochophore larvae. Trochophores normally hatched from eggs at 15°-18°C within 12 to 18 h. Shortly after hatching, larvae swim to the surface (negative geotaxis) and are easily drawn into a pipette for transfer to experimental containers.

Thermal influence on development and survival of larvae and postlarvae was observed using a temperature gradient apparatus; an aluminum block (30 × 15 × 150 cm) bored to accommodate replicate series of test tubes (25 ml). Cooling coils and heating elements at opposite ends maintained a temperature differential (range: 7°-31°C) with but slight fluctuation (±0.5°C per gradient position) over the course of the average experiment (2-4 wk). The apparatus is similar to that used with *H. sorenseni* larvae (Leighton, 1972) and has been thoroughly described elsewhere (Thomas, Scotten, and Bradshaw, 1963).

In the typical experiment duplicate series of 10 tubes, each tube containing 20 ml of seawater, were placed in the thermal gradient with 50 eggs or larvae. Incubation was carried out in darkness. A foam urethane cover insulated the apparatus. Inspection of the tubes was made daily during the first week and on alternate days thereafter to determine the stage of development attained. As abalone larvae are lecithotrophic, feeding was not necessary until settlement. At that time a mixture of three species of pennate diatoms (*Nitzschia* spp.) was supplied.

Studies on postlarvae were also conducted using the temperature gradient block. Between two and five individuals were placed in each tube. Postlarvae 1-2 mo of age were picked individually from walls of culture containers (Pyrex beakers or polyethylene pails) using a finely bevelled applicator stick. Several drops of the diatom culture were added to each tube twice weekly over the usual 2-wk observation period.

To examine the effect of temperature on the success of juveniles, groups of 8-12 individuals were reared in six 10-liter polyethylene containers maintained at 12°, 15°, 18°, 21°, 24°, and 27°C (±1.0°). Water was continuously aerated and the entire volume exchanged once a week. Food was either a mixture of unicellular and filamentous algae cultured within each container under illumination of a fluorescent lamp or fronds of the brown alga, *Egregia laevigata,* collected in fresh condition every 3-4 days. Growth of juvenile abalones was measured for month-long intervals in these experiments.

Progeny of each spawning were maintained in the laboratory for over 1 yr providing comparative information on juvenile growth rate in aquaria. Diatoms and minute filamentous algae served as food during their first few months. Older juveniles were provided larger algae, *Egregia laevigata, Eisenia arborea, Macrocystis pyrifera,* and *Laminaria farlowii.*

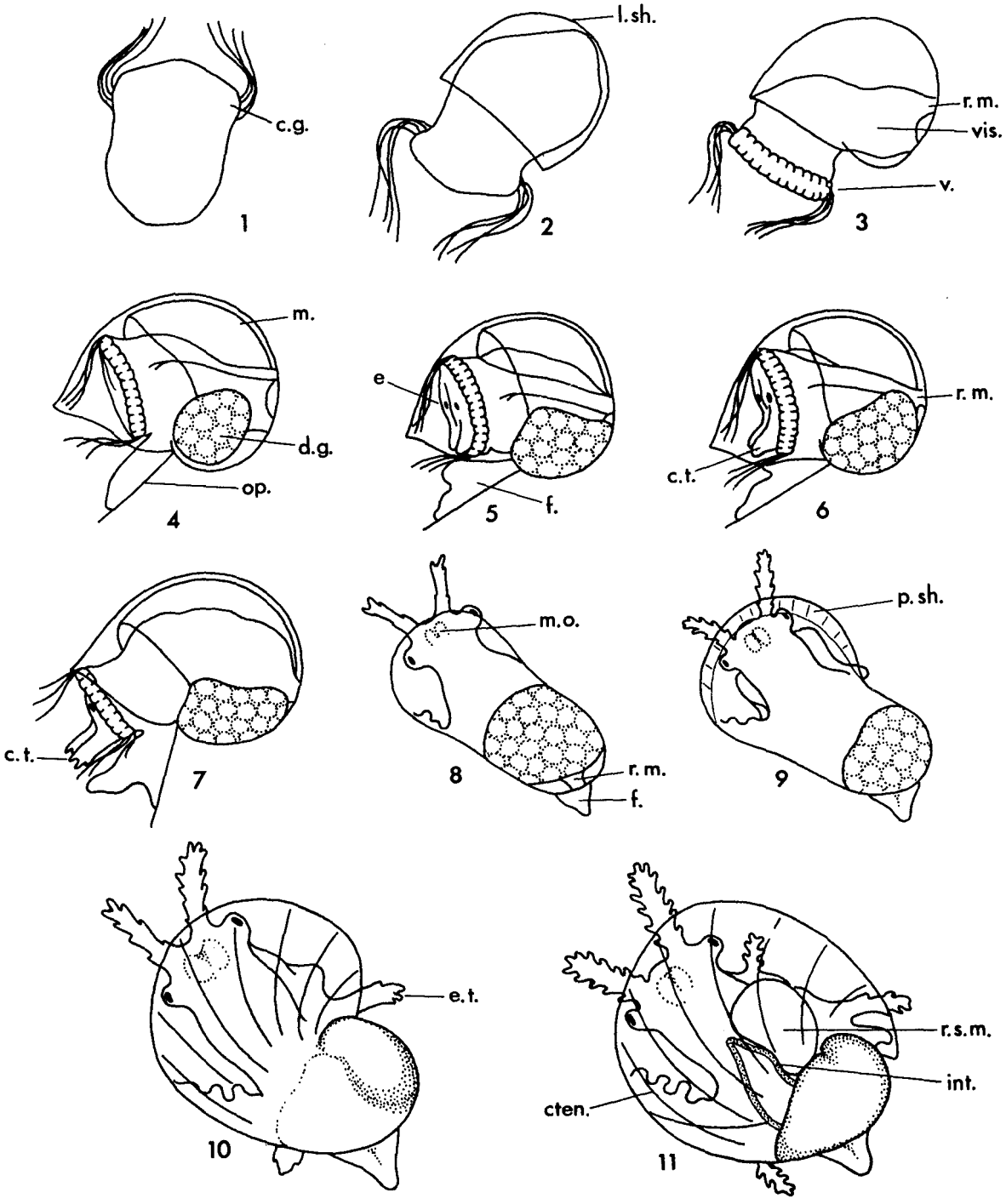
DEVELOPMENTAL FEATURES OF LARVAE, POSTLARVAE, AND JUVENILES

While morphogenesis is gradual and does not progress in a stepwise manner, various stages of larval and postlarval development are recognizable. Development rate was measured in terms of the time required for larvae to first gain features distinctive to each stage. Eleven such stages are passed from trochophore larva to circular-shelled postlarva (Figure 1). Settlement (the crawling stage) marks the end of larval life. Postlarval development then begins with the deposition of peristomial shell and persists to formation of the first respiratory pore ("notch stage," Leighton, 1972) at an age of 1-3 mo. Thenceforth to first sexual maturity the abalone may be regarded as juvenile.

FIGURE 1.—1) Trochophore larva after hatching. 2) Cap-shell early veliger larva. 3) Inflate-shell veliger (torsion stage). 4) Early operculate veliger (preeye spot). 5) Incipient cephalic tentacle stage operculate veliger. 6) Midformed cephalic tentacle stage. 7) Digitate or branched cephalic tentacle stage. 8) Crawling and settling stage. 9) Peristomial shell stage postlarva. 10) Midasymmetric shell postlarva. 11) Circular-shell postlarva.

Labelled structures:

c.g.,	ciliated girdle
c.t.,	cephalic tentacle
cten.,	ctenidium
d.g.,	digestive gland
e.,	eye spot
e.t.,	epipodial tentacle
f.,	foot
int.,	intestine
l. sh.,	larval shell
m.,	mantle
m.o.,	mouth with odontophore
op.,	operculum
p.s.,	peristomial shell
r.m.,	retractor muscle
r.s.m.,	right shell muscle
v.,	velum
vis.,	viscera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RESULTS

In the course of the study six batches of larvae were obtained from *Haliotis rufescens,* while three productive spawnings occurred with *H. corrugata* and *H. fulgens.* Year-round spawning in *H. rufescens* was predicted by Boolootian, Farmanfarmaian, and Giese (1962) and Young and DeMartini (1970) from field sampling for gonad indices. I found spawning adults every month of the year (1969-71) in samples taken from Estero Bay (central California) and in the present study with *H. rufescens* from southern California, laboratory spawnings were obtained in January, February, April, September, November, and December. *Haliotis corrugata* and *H. fulgens* spawned only during the months of April, June, and October. Members of the shallowwater species, *H. cracherodii,* held in the laboratory for another study, spawned in early spring and early fall. *Haliotis sorenseni* produced viable gametes only during late winter (Leighton, 1972).

DEVELOPMENT AND HATCHING IN EGGS

At 14°-16°C (ambient for La Jolla during most of the year) eggs of all species hatched within 18-24 h. Generally, development to hatching appeared normal over a rather broad thermal range. At hatching, however, consequences of inappropriate incubation temperatures became pronounced as trochophore larvae at and near thermal limits became highly abnormal in appearance and behavior and usually succumbed within 48 h, particularly at higher temperatures. Bizarre ciliated bodies predominated at high extremes of temperature while retardation and paralysis occurred at lowest temperatures. Commonly torsion was incomplete in larvae held at subnormal temperatures. A consequence of ensuing abnormality and mortality near thermal limits is apparent in the series of curves generated for development during the first several days of larval life. Attrition at upper and lower extremes and relatively high survival and rapid growth at optimal temperatures is reflected in the sharply peaked curves for larval development rate versus temperature. In *H. rufescens,* for example, eggs developed in an apparently normal manner over the range 10°-23°C, but larval growth after hatching became restricted to the comparatively narrow range 13.5°-20.0°C (Figure 2). The apparent shift of the

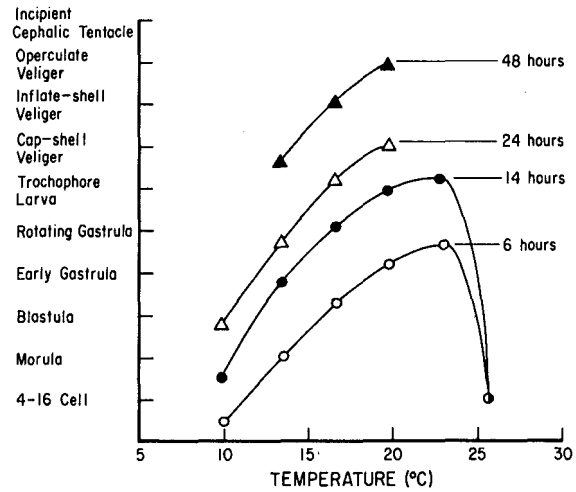

FIGURE 2.—Development of eggs of *Haliotis rufescens* held at different temperatures over a period of 48 h. Mortality occurred above 20°C after 14 h.

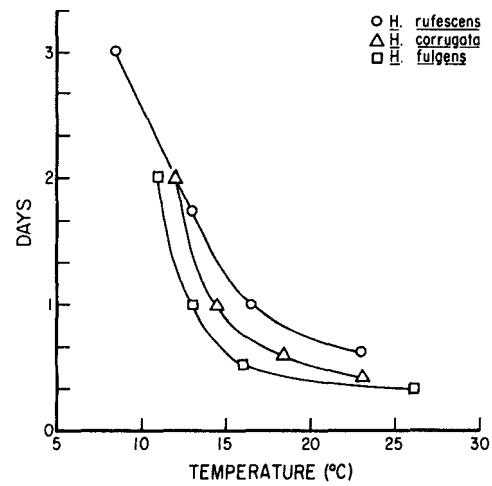

FIGURE 3.—Hatching time for eggs of three species of *Haliotis* incubated at several temperatures.

peaks of curves with time to suggest true optima at temperatures about 2°C lower than observed in trochophore larvae was found in all species studied due to supraoptimum mortality.

Hatching time was strongly dependent on temperature and ranged between 10 and 72 h. Both *H. corrugata* and *H. fulgens,* at temperatures supporting rapid but normal growth (their respective thermal optima), reached the point of hatching sooner than did *H. rufescens* (Figure 3). Strongest contrast in specific development rate is seen in the stage attained at supraoptimum temperatures (2°-3°C above optimum). In 2 days: *H.*

rufescens (near 19°C) reached the early (preeye spot) operculate stage, *H. corrugata* (near 23°C) had formed eyespots and cephalic tentacle buds, and *H. fulgens* (near 25°C) had become mid-cephalic tentacle operculates. In the latter, settling was observed as early as 3 days after fertilization.

OBSERVATIONS ON TROCHOPHORE LARVAE

When swimming trochophore larvae rather than developing eggs were introduced to the thermal gradient system, survival was improved. In experiments initiated with fertilized eggs, survival beyond 3 days in the 20-ml tubes was low despite routine addition of dihydrostreptomycin sulfate and sulfanilamide (to final concentration, 10 ppm). Substances within the perivitelline space (including excess sperm) are liberated at rupture of the albumen membrane, frequently promoting fouling. Temperature block studies in which trochophore or veliger larvae were freed of contaminants by repeated transfer and then admitted to the tubes showed reduced mortality.

Haliotis rufescens larvae settled approximately 4 days after fertilization (18°C). However, after 3 wk in the temperature block, only those groups between 14° and 18°C had reached advanced postlarval stages (Figure 4). Settling occurred in some *H. corrugata* larvae within 3.5 days, but postlarvae did not survive (22°-23°C). Most rapid growth and best survival in *H. corrugata* was at 21°-22°C; the circular-shell postlarval stage was reached in 17 days (Figure 5). Settlement began in larvae of *H. fulgens* at 25.5°C in slightly less than 3 days, but again, subsequent success was poor. Those at 22°-23°C, however, settled by the fourth day and progressed to the circular-shell stage in 15 days (Figure 6). There was a close correspondence of curves for development rate vs. temperature obtained with progeny from different spawnings and parentage. Optima described graphically for each species varied within only 1°C for *H. corrugata*, 1.5°C for *H. fulgens*, and 2°C for *H. rufescens*.

Larvae introduced to a thermal gradient as operculate veligers exhibited tolerance to a broader temperature range. Subsequent development rate was, however, slowed. The general retardation may be a shock response to environmental change. The greatly reduced volume provided in the 20-ml tubes and the totally darkened conditions in the temperature block contrast with

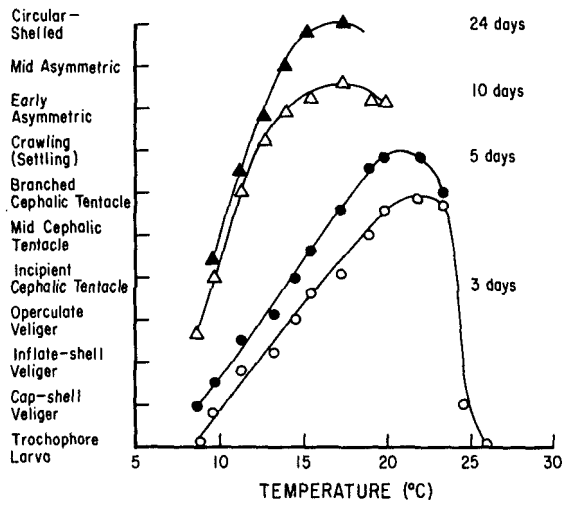

FIGURE 4.—Development of larvae of *Haliotis rufescens* at a series of temperatures when introduced to the thermal gradient as trochophores.

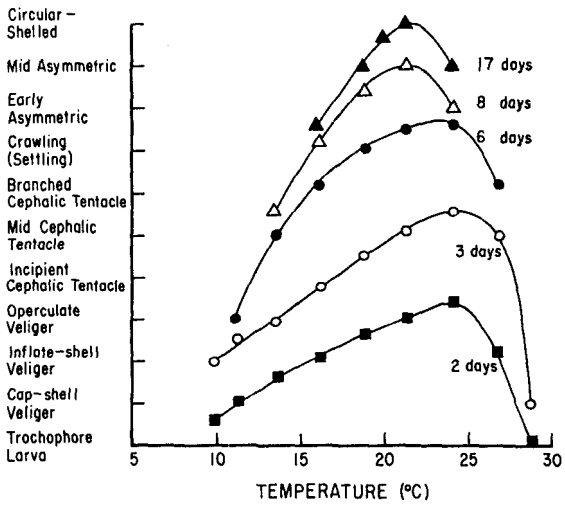

FIGURE 5.—Stages attained by larvae of *Haliotis corrugata* over a period of 17 days. Larvae were placed in the thermal gradient at the trochophore stage.

the 10-liter volume and illumination in the plastic rearing containers. In an experiment illustrating the point, *H. corrugata* eggs, trochophores and operculate veligers were placed in the gradient for 5 days in each case. At 20°-22°C, eggs developed rapidly and early postlarval stages reached in 5 days. However, operculate veligers had not yet reached the crawling stage at an age of 7 days (Figure 7).

In temperature block experiments, survival through settling usually ranged between 50 and

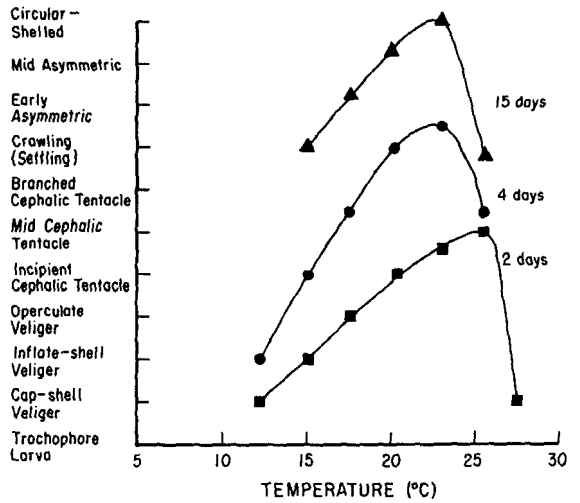

FIGURE 6.—Stages attained by *Haliotis fulgens* larvae incubated at several temperatures for 15 days. The experiment was initiated with trochophore larvae.

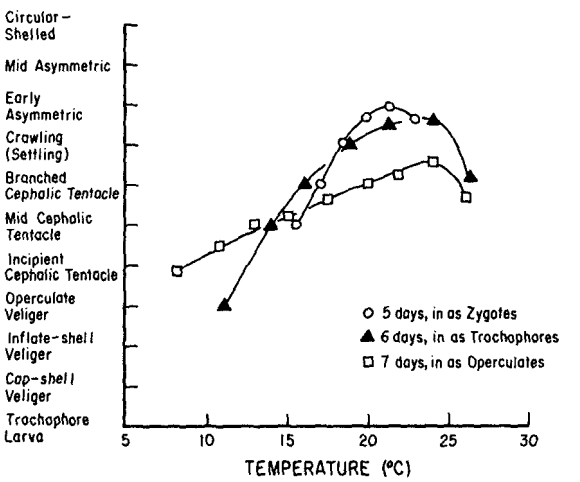

FIGURE 7.—Comparison of development rate and tolerated thermal range in larvae of *Haliotis corrugata* placed in the temperature block at 1, 20, and 48 h after fertilization.

80% within the physiologically acceptable temperature range. High mortality near the upper limit might have been due, in part, to oxygen exhaustion. This was tested by sampling open-top tubes in the block at 22° and 24°C for oxygen content after holding approximately 150 larvae (*H. rufescens*) for 48 h. A decline from 5.8 to 2.9 ml O_2/liter was observed at 22°C in 48 h. Routinely, therefore, only 25 to 50 larvae or eggs were admitted to each tube and once daily tubes were mixed to assure adequate oxygen was available. Subsequently oxygen depletion was not a cause of mortality.

THERMAL TOLERANCE OF POSTLARVAE

Postlarvae ranging in age from 1 to 2 mo were placed (2-5/tube) in the thermal gradient block and provided each 3-4 days a mixture of three species of diatoms (*Nitzschia* spp.). Tubes were checked for survival and growth of postlarvae over periods of 2 wk. Survival was good in all species at colder temperatures, but those at 10°-12°C invariably were lethargic and could not right themselves once overturned. *Haliotis rufescens* survived over the range 10°-19.5°C. *Haliotis corrugata* and *H. fulgens* were tolerant to the same lower temperatures but had different upper limits, 23.5° and 26.0°C, respectively. Typically survival was nearly 100% over a broad intermediate range of temperatures, but declined sharply within 2° of the extremes.

POSTLARVAL AND JUVENILE GROWTH

Specific differences in growth rate of both postlarvae and juveniles under laboratory conditions were measured. When its postlarvae were provided near optimal thermal and feeding environments, *H. fulgens* formed the first respiratory pore in about half the time required by the other species. As the pore is formed, a notch is first seen on the anterior right shell margin. The feature is conspicuous and serves as a convenient point of comparison. The "notch stage" was reached in some rapid-growing *H. fulgens* at an age of 30 days (Table 1).

Variability in growth rate was marked. Groups of juveniles of identical parentage, age, and rearing environment sampled periodically for shell length distribution reflected a broad range and age-increasing standard deviation (Table 2). Shell

TABLE 1.—Age and shell length of postlarval *Haliotis* at formation of the first respiratory pore.

Species	Age (days)	Shell length (mm)	Temperature (°C)
H. rufescens	60-70	1.5-1.8	14-18
H. corrugata	50-60	2.0-2.5	15-22
H. fulgens	30-40	1.7-2.0	16-24
H. sorenseni	55-65	2.0-2.1	[1]14-18

[1]Leighton, 1972.

length at 1 yr of age in four species reared in the laboratory varied over a range greater than 10mm (Table 3).

INFLUENCE OF TEMPERATURE ON GROWTH RATE OF JUVENILES

Several growth experiments were conducted with juveniles of the three species of abalones to gain comparative data and to establish respective temperatures of maximum growth rate. Juveniles were reared for month-long periods in 10-liter plastic containers held at six temperatures between 12° and 30°C. Both *H. corrugata* and *H. fulgens* displayed enhanced growth rate above 20°C. *Haliotis rufescens,* however, grew best below 20°C and, in fact, grew but slightly less at the coldest temperature, 12.5°C (Table 4, Figure 8). *H. fulgens* again showed a superior growth rate. While a mean daily shell growth approaching 90 μ was observed at its temperature of maximum growth rate (26°C), some individuals increased in shell length as much as 130 μ per day.

DISCUSSION

Seven species of *Haliotis* occur in southern California waters ranging vertically from the intertidal to depths over 35 m. Depth distribution is stratified specifically, although in certain areas (i.e., in the presence of localized upwelling) overlapping does occur. Vertical and latitudinal distribution appears most closely related to temperature. The Point Loma (San Diego) shelf from 0 to 35 m supports all California abalone species (Table 5). Colder water species may be found intertidally in northern California (*H. rufescens, H.*

TABLE 2.—Variation in size of juvenile *Haliotis* of identical parentage, age, and growing environment.

Species	Age (months)	Number	Shell length (mm) Mean	Range	SD
H. rufescens	3.7	18	4.4	2.6-6.1	1.06
H. corrugata	5.0	27	9.2	6.8-14.1	2.42
H. fulgens	4.7	70	7.1	3.6-12.0	2.00
H. sorenseni	3.3	19	4.3	3.0-5.6	0.64

TABLE 3.—Size of *Haliotis* at completion of first year growth in the laboratory.

Species	Shell length (mm) Mean	Range	Number
H. rufescens	15.6	9.9-20.0	50
H. corrugata	18.3	12.2-26.4	18
H. fulgens	32.8	30.5-38.9	[1]3
H. sorenseni	13.4	8.0-21.0	19

[1]Recent observations on growth of over 100 juvenile *H. fulgens* suggest the three individuals represented here were exceptionally rapid growers. Projection of growth of juveniles presently 8 mo old suggest the mean size at 1 yr under laboratory conditions may fall closer to 25 mm.

TABLE 4.—Daily shell elongation rate for groups of juvenile *Haliotis* reared for month-long periods at different temperatures (microns/day).

Species and date	Temperature (°C ± 1.5°) 12	15	18	21	24	27	30
H. rufescens							
Oct. 1971	91	61	90	45	32	([1])	
Jan. 1972	36	41	68	61	29		
Mar. 1972	70	64	84	79	35		
Dec. 1972	46	92	67	95	13		
Mean	60.9	64.5	77.3	70.0	27.3		
H. corrugata							
Jun. 1972	26	29	30	46	53		
May 1973	57	55	62	54	60	28	
Jun. 1973		45	72	91	63	68	14
Mean	41.5	43.0	54.7	63.7	58.7	48.0	14.0
H. fulgens							
Mar. 1973	23	29	63	77	119	64	
May 1973	21	21	55	74	88	114	
Jun. 1973		21	56	60	50	86	54
Mean	22.0	23.7	58.0	70.3	85.8	88.0	54.0

[1]*H. rufescens* did not survive in the 27°C containers.

These data are averages for groups of 8 to 15 individuals reared in each of six 10-liter plastic drums. In the case of *H. corrugata* and *H. fulgens*, temperatures were raised throughout for the third experiment to cover the supraoptimal range. Juveniles used in these experiments ranged from 5 to 20 mm.

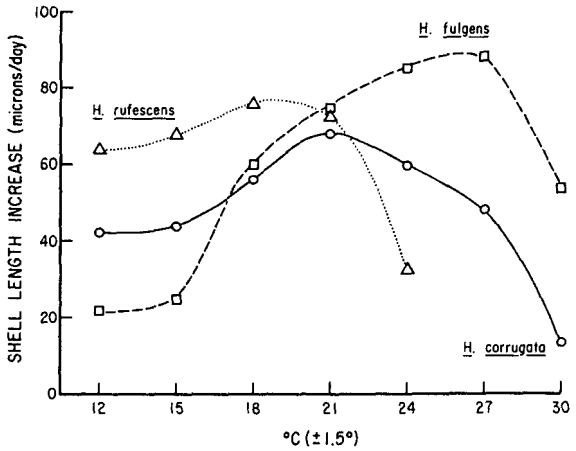

FIGURE 8.—Growth rate of juvenile abalone held for month-long periods at different temperatures. Points are averages for groups of 8 to 15 individuals (see Table 4).

TABLE 5.—Approximate depth distribution of *Haliotis* species off Point Loma (San Diego, Calif.).

Species	Depth range (m)
H. cracherodii	0-2
H. fulgens	0-5
H. corrugata	1-20
H. rufescens	10-25
H. k. assimilis	10-30
H. sorenseni	15-35
H. walallensis	15-35

kamtschatkana, and *H. walallensis* together with the generally shallow water and intertidal *H. cracherodii*). *Haliotis sorenseni*, *H. corrugata*, and *H. fulgens* range from Pt. Conception to central Baja California. *Haliotis cracherodii* and *H. rufescens* occur throughout California and northern Baja California, while *H. k. assimilis* replaces *H. kamtschatkana* in southern California (McLean, 1966).

This study has shown that the thermal requirements, particularly for eggs and early larvae, are exacting. Field distribution of juvenile and adult members of each species correspond with the thermal tolerance range observed in larvae in the laboratory. The range of tolerance increased with larval age. Larvae of *H. corrugata* placed in the thermal gradient as operculate veligers survived a range of 18° (from 8° to 26°C), while those resulting from eggs placed in the same situation were tolerant of a range of only 8° (from 15° to 23°C). The observation is not new nor limited to *Haliotis* (Loosanoff and Davis, 1963). Thus, survival of larvae dispersed in nature is likely dependent on their remaining within a water mass of appropriate temperature and further, settling in areas over which temperature change will not be extreme. Recruitment to marginal environments may rely on the timely influx of advanced veliger larvae. The situation is complicated, no doubt, by acclimation of mature adults near distribution limits.

Most studies in abalone culture have been conducted by Japanese workers concentrating on the species native to northern Japan, *H. discus hannai*. Its broad thermal tolerance (approximately 5°-30°C) and relatively rapid growth at elevated temperatures have attracted the interest of mariculturists. The species exhibits rapid larval development, settling in 3 days at 25°C and reaching the notch stage in 42 days (Kan-no and Kikuchi, 1962). When reared at five temperatures between 5° and 25°C, juvenile *H. d. hannai* displayed daily increments in shell length of 1, 2, 32, 68, and 95 μ, respectively, according to the same report. During winter months when sea temperatures at the coastal hatchery drop below 10°C, cultured juvenile abalone are transferred to a site adjacent the Yogasaki Electric Generating Plant using 26°C water detoured from the effluent stream (Kan-no, pers. commun., McBeth, 1972).

Thermal tolerance and growth characteristics of larvae and juveniles of the Japanese species are similar to that observed in the present study in *H. fulgens*. Of the American species considered here, only *H. fulgens* could be recommended for heated effluent mariculture.

First year growth measured in this study is not considered to approximate growth in nature. Artificial lighting, synthetic materials in rearing tanks, and other factors may have influenced growth, and the growth rate estimates are likely conservative. The general observation of rapid, moderate, and slow growth in *H. fulgens*, *H. rufescens* and *H. corrugata*, respectively, is concluded to reflect specific differences in growth potential.

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