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EFFECT OF TEMPERATURE, DIET, LIGHT, AND CULTIVATION DENSITY ON GROWTH AND SURVIVAL OF LARVAL AND JUVENILE WHITE ABALONE *HALIOTIS SORENSENI* (BARTSCH, 1940)

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ABSTRACT White abalone *Haliotis sorenseni* was studied in the mariculture laboratory of the Channel Islands Marine Resource Institute in southern California to determine the effect of environmental factors such as temperature, diet, light, and cultivation density on growth and survival. Fertilized eggs and larvae were raised at water temperatures of 9°C, 12°C, 15°C, 18°C, and 21°C in two separate trials. The rate of larvae development increased significantly with each 3°C change in temperature. Survival from fertilization to settlement stage was greatest (56%) at 12°C, followed by survival of 23% at 15°C, and 2% at 18°C. Larvae raised at the extremes of 21°C and 9°C had 100% mortality by 90 and 100 h posthatch. The biological zero temperature, the point at which growth stops, is projected to be 3.04°C for white abalone, significantly lower than that of sympatric species. Fecundity was determined as 7,271 eggs/g for wild-caught abalone and 6,128 eggs/g for hatchery-reared abalone and was not significantly different from previous estimates based on gonad bulk index. The effect of feed and temperature on the growth of juvenile abalone was studied. Juvenile abalone 28 mm in length were held for 147 days at 12°C, 15°C, and 18°C and fed diets of kelps *Macrocystis pyriferia* (L.) C. Agardh, 1820; *Laminaria farlowii* (Setchell, 1893); *Chondracanthus exasperatus* (Harvey & Bailey, 1996); *Palmaria mollis* (Setchell & N. L. Gardner, 1903), or combinations of these algae. Juveniles displayed fastest growth at 15°C when fed *M. pyriferia*. Juvenile survival was highest at 12°C and lowest at 18°C, at which temperature animals succumbed to withering syndrome. Optimal seawater temperatures for both larval and juvenile white abalone were determined to be significantly lower than previously reported. In other experiments, animals 20 mm in length stocked at 25 gm/L grew at 41 μm/day versus 32 μm/day for those at 50 gm/L. No significant difference in growth was observed for abalone grown under low lighting conditions (3%–5% ambient) and almost complete darkness (1% ambient light).

KEY WORDS: *Haliotis sorenseni*, fecundity, larvae, cultivation, temperature, biological zero point, diet, density, light, endangered species

INTRODUCTION

White abalone *Haliotis sorenseni*, a large marine snail inhabiting coastal habitats from Point Conception, CA, to Baja, Mexico, and the offshore islands, was the first marine invertebrate to be added to the United States Federal List of Endangered Species in 2001 (NOAA 2001) as a result of its precipitous decline in the second half of the 20th century (Davis et al. 1996, Hobday et al. 2001). Environmental conditions, human exploitation, and environmentally influenced disease likely contributed to this decline (Friedman et al. 2007, Davis et al. 1996). Reports since the 2001 listing indicate that white abalone densities have continued to decline at several locations in southern California (Butler et al. 2006, Stierhoff et al. 2012, Stierhoff et al. 2014). Recent management recommendations emphasize that captive propagation and enhancement is the only mechanism to reduce the probability of extinction within a decade (Stierhoff et al. 2014).

Understanding tolerance ranges and optimal environmental parameters for cultivation and growth is the critical first step in a restoration effort to outplant laboratory-reared juveniles to natural habitats in southern California as described in the White Abalone Recovery Plan (National Marine Fisheries Service 2008). Information on environmental tolerances (Ben-Horin et al. 2013, Braid et al. 2005, Kimura et al. 2011, Moore et al. 2000, Pereria et al. 2007, Takami et al. 2002, Tutschulte 1976), larval development, and survival (Ebert & Houk 1984, Jaeckle & Manahan 1989, McCormick et al. 2012, Roberts & Lapworth 2001, Takami 2001) has been reported for several species of abalone but is limited for larval and juvenile white abalone.

White abalone have been estimated to live to between 20 and 40 y old (Tutschulte & Connell 1988b). By the last decades of the 20th century, southern California populations of white abalone had a distribution skewed toward older individuals, possibly indicating episodic recruitment as found in other species (McShane & Naylor 1996). Declines in populations may have stemmed from fishing take and irregular recruitment attributed to environmental variation (Hobday & Tegner 2000, Shepherd et al.1998). However, as Hobday and Tegner (2002) noted, long-lived adults in pre-exploitation abalone populations could have offset irregular recruitment.

Tutschulte and Connell (1981) found that wild white abalone populations off southern California had a short, highly synchronized spawning period when water temperatures were 12–14°C. In the laboratory, Leighton (1974) observed the highest survival of white abalone larvae at 16–18°C. White abalone are the deepest living of southern California abalone and found in rocky benthic habitats from 10 to 60 m in depth. As of the 1970s, they were most abundant at depths of 26 to 65 m (Davis et al. 1996). Tutschulte (1976) suggested that deeper fringe habitat, while somewhat food limited, provided white abalone

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with a refuge from more abundant pink abalone (*Haliotis corrugata*) and predation.

Abalone feed most actively under low light conditions, and work with other species has shown that increasing the length of darkness can lead to prolonged periods of feeding activity (Garcia-Esquivel et al. 2007, Pereira et al. 2007). Because white abalone live in deep habitats and feed mostly at night (Tutschulte & Connell 1988a), growth rates may also vary with light intensity. Abalone have been observed to consume some algae in the proportion it is found in drift algal samples whereas other species of algae may be selectively consumed or avoided in mixed algal drift (Tutschulte & Connell 1988a).

This article summarizes research intended to expand the knowledge of the biology of larval and juvenile white abalone. The following laboratory experiments with wild and hatchery-raised animals were quantified: fecundity and spawning duration; the effect of temperature on the rate of development and survival of eggs and larvae; the biological zero temperature (Seki & Kan-no 1977); the effect of temperature and food on the growth and survival of juvenile abalone; and the effect of density and light intensity on growth. In addition, data on overall growth rates under large-scale culture conditions are presented.

MATERIALS AND METHODS

Beginning in November 2000, wild adult white abalone were collected by the California Department of Fish and Game and transported to the Channel Islands Marine Resource Institute (CIMRI) in Port Hueneme, CA, for culture. Prior to this, California Department of Fish and Game had collected wild animals for the University of California at Santa Barbara (UCSB). In April 2001, two females and one male were successfully spawned in cooperation with UCSB, using hydrogen peroxide (Morse et al. 1977). In subsequent matings at CIMRI, abalone were induced to spawn using UV radiation (Kikuchi & Uki 1974) and raised using cultivation methods originally developed in Japan and summarized by McCormick (2000). Sexually mature offspring from this and subsequent spawns of wild and hatchery-raised white abalone (McCormick & Brogan 2003) were used to produce fertilized eggs, juveniles, and sexually mature adults for the research presented here. The main intent of the spawns was to produce abalone to enhance wild populations. Surplus animals were used for research.

Fecundity and Spawning Duration

Previously reported fecundity of white abalone was an estimate based on soft tissue weight (Tutschulte 1976). However, in the estimate of fecundity, the number of eggs produced per female when abalone were stimulated to spawn in the hatchery were counted. Eggs were collected from sixteen wild adult abalone and sexually-mature, laboratory-reared offspring from CIMRI's hatchery and UCSB (McCormick & Brogan 2003). Prior to spawning, each of the sixteen female abalone was placed in a separate 10-L spawning container that received a steady flow of UV-irradiated seawater. Shell length (SL) and wet weight of each female was measured. The duration of spawning was noted by direct observation of animals during eleven spawns between April 2001 and May 2008. Eggs collected from these spawns were handled according to cultivation methods summarized by McCormick (2000). The number of eggs spawned by each female was estimated by counting eggs in multiple aliquots taken with large-bore 1-ml pipettes.

Larval Development and Survival Relative to Temperature

Two separate spawning trials were conducted to study the effect of temperature on larval development. Prior to spawning, adult abalone were held at 15°C in a flow-through culture system, where they were fed Giant Kelp (*Macrocystis pyrifera*) and Pacific Dulse (*Palmaria mollis*) *ad libitum*. During fertilization trials, eggs were held in water at 16°C for 30 min prior to and during exposure to addition of sperm. In the first trial, sperm from 20 hatchery-reared males were used to fertilize eggs from a single wild female. To maximize fertilization, sperm densities of 50,000–100,000 sperm/ml were used. These densities have been shown to produce optimal fertilization in three sympatric species (Mill & McCormick 1992). In the second trial, sperm from a wild adult and 25 hatchery-raised males were used to fertilize eggs from 37 hatchery-raised female abalone. In both spawning trials, the adults were unrelated, and the fertilization rates were over 98%.

After a rinse with seawater to remove sperm, fertilized eggs were held at a density of 50 eggs/ml. Replicates of 200 ml of seawater and eggs were added to 800 ml filtered seawater at 16°C in each of twenty-five 1,000-ml Azlon polypropylene beakers (BS5404 Part 1) to bring the total volume of each replicate to 1,000 ml (approximately 10,000 fertilized eggs/beaker). The number of fertilized eggs in each beaker was verified by counting the number of eggs in a 1-ml sample. Five beakers for each test temperature (9°C, 12°C, 15°C, 18°C, and 21°C ± 0.5°C) were immediately placed into separate water baths at five different water temperatures (Fig. 1). Stocking densities were based on an anticipated hatching rate of 50%, common in hatchery operations, yielding a larval density of 5 larvae/ml. Larval culture densities for other abalone species at commercial hatcheries are at least twice this amount (McCormick 2000).

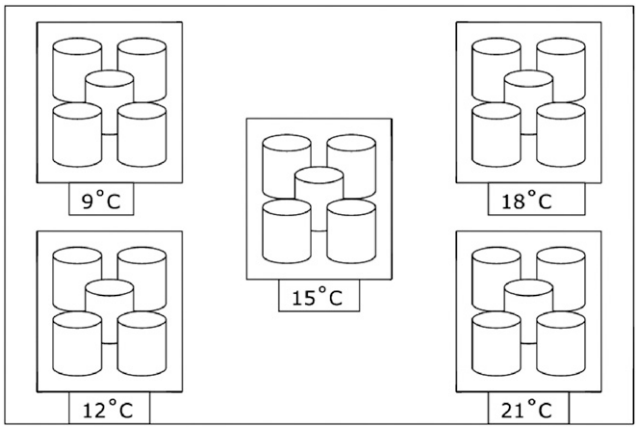

Figure 1. Diagram of larval temperature experiment. The large box represents a 360-l water bath at 6°C. Smaller boxes represent the five 24-l primary water baths immersed within the larger bath and warmed with immersion heaters. Each primary bath was warmed by an immersion heater to 9°C, 12°C, 15°C, 18°C, or 21°C, respectively. Five beakers, each containing 1 l of seawater and approximately 10,000 fertilized eggs, were held in each of the primary water baths.

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Larval Holding Methods

The five replicate beakers for each temperature treatment (9°C, 12°C, 15°C, 18°C, and 21°C ± 0.5°C) were held in separate 24-l primary water baths equipped with an immersion heater and thermostat set to the designated temperature. A small submersible magnetic drive pump provided constant water circulation within each water bath. The five primary water baths were held in a 360-l secondary water bath chilled to 6°C. Constant chilling of the secondary water bath and constant heating of the primary water baths minimized temperature variations in the test beakers. Water baths were set up 1 wk prior to each spawning event and monitored daily to verify that all temperatures were stable. A diagram of the experimental setup is shown in Figure 1.

The twenty-five larval rearing chambers received independent aeration via an air stone. Dissolved oxygen levels were checked daily and remained at saturation for the duration of the experiments. Beginning on the 2nd day after fertilization, water was exchanged twice a day by pouring water and larvae through a 60-µm sieve, wiping and rinsing the beaker with fresh water, then seawater, replacing the larvae and adding new seawater that had passed through a UV sterilizer and 5-µm filter. This rinsing method removed egg membranes, unhatched eggs, and dying larvae. Neither microalgae cultures nor antibiotics were added.

Developmental Stages of Larvae

Developmental rates were determined by sampling larvae from each beaker according to the schedule in Table 1 for the first trial.

In the second trial, the same schedule was followed, except that no samples were taken during the 1st 4 hours after fertilization. Larval samples were placed in 30% buffered formalin to halt development and later checked to note the developmental stage. For both experimental trials, 10 fertilized eggs or larvae were sampled from each beaker at each interval, to determine the developmental stage relative to temperature.

External and internal features of developing eggs and larvae for other species of *Haliotis* have been documented (Ino 1952, Seki 1980, Seki & Kan-no 1977, 1997, Courtois de Vicose et al. 2007). This study previously used features described by Seki and Kan-no (1977) as reliable markers in the development of green, pink, red, and white abalone larvae in the hatchery; Table 2 summarizes these stages of development.

Attainment of each developmental stage was noted when 50% of the larvae observed had features associated with that stage (Table 2). Larval development was considered complete with the appearance of the fourth tubule on the cephalic tentacle (Stage 41), just prior to settlement.

TABLE 1.

Sampling schedule for developmental assessment.

Time after fertilization (h)	Sample interval
0–4	Every ½ h
4–48	Every 4 h
48–180	Every 6 h

TABLE 2.

Abalone larval developmental stages.

No.	Stage	Development stage (from Seki & Kan-no 1977)
1	Egg	Fertilization
2		First polar body
3		Second polar body
4		First cleavage
5		Second cleavage
6		Third cleavage to gastrula
7		Fourth cleavage
8	Morula	
9	Blastula	
10	Gastrula	
11		Appearance of prototrochal cilia
12	Trochophore	Stomodaeum
13		Formation of prototrochal girdle
14		**Bursting of egg membrane, hatching**
15		Beginning of larval shell formation
16	Veliger	Completion of velum
17		**Appearance of larval retractor muscle**
18		Formation of integumental attachment to shell
19		Protrusion of foot mass
20		Completion of larval shell
21		**Torsion: 90° twisting of cephalo-pedal mass**
22		Torsion complete; 180° rotation of foot mass
23		Spines on end of metapodium
24		Formation of operculum
25		Appearance of fine cilia on the sole of the foot
26		Vertical groove formation in the velum
27		Appearance of eyespot
28		Formation of propodium
29		Appearance of cephalic tentacle
30		Cilia growth on the propodium
31		Appearance of cilia in the mantle cavity
32		Formation of apophysis on the propodium
33		**Formation of first epipodal tentacle**
34		Appearance of otolith
35		Appearance of short spine on the cephalic tentacle
36		Snout protrusion
37		Appearance of two tubules on the cephalic tentacle
38		Ciliary process on the roof of the mantle cavity
39		Appearance of third tubule on the cephalic tentacle
40		Larval retractor muscle drawn into mantle cavity
41		**Appearance of fourth tubule on the cephalic tentacle**

Features of *Haliotis discus hannai* in egg and larval stages (Seki & Kan-no 1977, 1997) were used to track the development of *Haliotis sorenseni* eggs and larvae.

Larval Survival Relative to Cultivation Densities

In the first experimental trial, 10 fertilized eggs or larvae were sampled from each beaker at each interval, this number being sufficient to accurately determine the developmental stage and detect differences between test temperatures. Over the duration of the larval culture period, this sampling technique resulted in the removal of up to 4% of the fertilized eggs and larvae from

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each beaker. In addition, the numbers of abalone larvae within the beakers decreased at different rates over time, depending on temperature.

In the second experimental trial, the rate of development at different temperatures was once again recorded. In addition, the number of larvae, and thus survival, in each treatment was noted in addition to assessment of the rate of development. In the second trial, no sampling was done until 4 h after fertilization. When sampled, each beaker was mixed to evenly distribute larvae. A small plastic rod with a 5-cm-diameter plastic disk attached to one end was used as a stirring device to push water on one side of the beaker down, and pull it up on the opposite side. After mixing, three 1-ml replicate samples were taken. The developmental stage was noted and the number of individuals/ml was counted to estimate larval density. Cultivation densities were similar in both trials.

Juvenile Growth and Survival Relative to Temperature and Diet

Offspring resulting from the mating of a wild female abalone with hatchery-reared males were cultured on a production scale for 17 months in 1,360-l tanks, where they fed exclusively on microalgae cultures (McCormick 2000). A pool of 1,100 animals was graded by size to eliminate the largest and smallest abalone. From the remaining group of 840 animals, those with an average SL of 29.8 mm (SD 6.9, median 28.5 mm) and an average wet weight of 4 g were chosen for this experiment. Each test replicate consisted of five abalone placed in a plastic mesh bag (5-mm mesh size) that contained a PVC ring (50-mm diameter × 50-mm high) that served as a substrate for the abalone. The top and bottom of each bag was tied in a knot to retain abalone inside the bag. Each mesh bag and ring was placed in a polystyrene plastic beverage cup (Solos, Inc., 520 ml) and immersed to half its depth in a water bath. Each container received a constant flow of seawater at a rate of 18 ml/min. Seawater was filtered to 5 μm, and chilled or heated to a temperature of 12°C, 15°C, or 18°C ± 0.5°C in a 115-l aerated header tank. Seven replicate cups, each containing five abalone (total wet weight of approximately 20 g) were used for each test diet, at each test temperature. Abalone SL was measured to the nearest 0.1 mm at the beginning of the experiment and then at intervals of approximately 30 days for 144 days. Diets consisted of either Rhodophyta or Phaeophyta tested singly or in combination (Table 3).

Once a week, each mesh bag was opened, uneaten algae removed, and fresh algae added. Each alga was provided separately on alternate weeks. Abalone were fed *ad libitum* using enough algae to ensure that some remained at the end of each week. Algae moisture and protein content were determined by Michelson Laboratories Inc., Commerce, CA (Table 4).

Protein content was calculated as % nitrogen times 6.26. Protein content varied among algae tested in this project and has been reported at varying levels. Cultivated *Palmaria mollis* contains slightly higher levels of protein (11%–18%, Rosen et al. 2000) than *Macrocystis pyrifera* (5%–14%, Linder et al. 1977 and Hart et al. 1976; 11% Ortiz et al. 2009; 9% Correa et al. 2014).

Juvenile Growth and Survival Relative to Stocking Density

The effects of cultivation density on the growth and survival of juvenile white abalone were tested over a period of 8 mo.

TABLE 3.

Species list and algal combinations used in abalone growth trials.

Single-alga diet species	Two-algae diet species
Macrocystis pyrifera	*M. pyrifera* and *C. exasperatus*
Laminaria farlowii	*M. pyriferia* and *P. mollis*
Chondracanthus exasperatus	*L. farlowii* and *P. mollis*
Palmaria mollis	

Offspring resulting from the mating of wild female and male abalone were grown in 1,360-l tanks where they fed exclusively on microalgae cultures (McCormick 2000). A pool of 3,928 animals was graded by lengths to retain the middle third of the size range comprised of 1,323 animals (SL 17–24 mm, average SL 21 mm, average wet weight 0.84 g). For this experiment, animals were held in mini-raceway tanks (7.5-cm water depth × 7-cm wide × 50-cm length) made from sections of PVC rain gutter with PVC end pieces glued on each end. A 3-mm horizontal slit was made at the downstream end for outflowing water. The volume of each raceway was 1.3 l with a submerged surface area of 965 cm^2. A PVC LeafGuard grid was snapped onto the top of each raceway to prevent abalone from crawling out. A flow of 4.5 l/min of seawater filtered to 5 μm was periodically pulsed via a submersible pump from a 115-l aerated header tank into a manifold that delivered water to each raceway at a rate of 0.2 l/min, equivalent to an exchange rate of 3.9 raceway volumes/h. An air stone in each raceway provided supplemental aeration. Seven of the mini-raceways were stocked at a low density of 25 gm/L (63 abalone with a total weight range 72.7–90.2 g) and another seven were stocked at a high density of 50 gm/L (126 abalone with a total wet weight range 134.7–167.6 g). The range of weights was a function of variability in abalone size. Shell lengths of 50 abalone from each raceway were measured at approximately 35-day intervals over the course of 8 mo. Total weight of all abalone in each raceway was measured at the beginning and end of the experiment. Abalone were fed a diet of *Macrocystis pyrifera* and *Palmaria mollis*. These algae were offered separately on alternate weeks. Abalone were fed *ad libitum* using enough algae to ensure that some remained at the end of each week.

Juvenile Growth and Survival Relative to Light Intensity

Twenty-five abalone were placed in 14 mini-raceways. The average total weight of abalone in outdoor raceways was 100.5 g

TABLE 4.

Algal moisture and protein content.

Algae	% Moisture	% Protein
Chondracanthus exasperates: Sample 1	81.43	1.59
Chondracanthus exasperates: Sample 2	81.46	1.97
Laminaria farlowii: Sample 1	79.59	2.5
L. farlowii: Sample 2	79.60	2.2
Macrocystis pyrifera: Sample 1	89.29	0.79
M. pyrifera: Sample 2	89.22	0.9

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(SD 12.9, equivalent to 32). For the indoor raceways, the average total weight was 103 g (SD 8.0, equivalent to 33). Seven raceways were placed in an outdoor cultivation area. The other seven were placed indoors under a black cover. For the outdoor raceways, two layers of shade cloth (light reduction of 75% and 80%) and the grid cover of the mini-raceway reduced maximum light levels at midday to 59,202 lumens/m^2 (approximately 3%–5% ambient light). Lighting levels in the indoor raceways were undetectable (<10 lumens/m^2). Seawater was cooled to 15°C and periodically pulsed into each 3.1-l raceway at a rate of 19 l/h. Abalone were fed a mixed diet of Giant Kelp (*Macrocystis pyrifera*) and Pacific Dulse (*Palmaria mollis*) weekly. Approximately once each month, the SL and total weight of 20 abalone from each raceway were measured. The growth trial was carried out over a period of 6 mo.

Juvenile and Young Adult Growth in the Hatchery

From 2001 to 2003, four crops of white abalone were produced in the CIMRI hatchery. Juvenile abalone were raised on a mixed diet of microalgae that included monostromatic microalgae such as *Myrionema* spp., diatoms such as *Cocconeis* spp., *Navicula* spp., and *Nitszchia* spp., grown on vertically oriented, corrugated fiberglass culture plates in outdoor tanks using cultivation methods originally developed in Japan and described by McCormick (2000). Abalone were weaned onto diets of *Macrocystis pyrifera* at SL between 15 and 35 mm. The initial crop resulted in over 100,000 abalone at a SL of 3–5 mm. Subsequent spawns in 2003 produced 4,400, 1,200, and 1,040 abalone of similar size. Shell lengths and weights of the four crops were measured monthly.

RESULTS

Fecundity and Spawning Duration

Fecundity data from spawning wild ($n = 10$) and hatchery-reared ($n = 85$) female white abalone (10–1,210 g total prespawn wet weight, and SL 40–192 mm) are summarized in Table 5 and Figure 2. Hatchery-raised white abalone were somewhat smaller (SL 40–111 mm) than wild abalone (SL 142–192 mm). For comparison, Tutschulte's (1976) estimates of fecundity from 197 wild animals are also included in Table 5 and Figure 2. Tutschulte's calculations on fecundity relative to weight were based on soft tissue weight, not total wet weight (including shell) as was done here. Tutschulte's count includes eggs that may never be released because the total number of eggs embedded in the gonad was counted through tissue sections; whereas, counts in this study were made after spawning and included only eggs released into the water column. Both methods yielded similar fecundity estimates.

The maximum number of eggs released by a single female in one spawning event was estimated at 13.14 million. Fecundity of female abalone in a single spawning event ranged from 1,037 eggs/g to 14,038 eggs/g with a statistically significant Pearson correlation coefficient between wet, prespawn weight, and fecundity [$r(12) = 0.87$, $P < 0.01$). As in most gastropods, there was a general trend of higher fecundities for larger females (Fig. 2).

A Mann–Whitney U test revealed no significant difference between the fecundities of wild and hatchery-reared animals ($U = 40$, $Z = -0.88$, $P = 0.37$). Tutschulte's data were excluded from the analysis of wild versus hatchery rearing because weight

TABLE 5.

White abalone fecundity.

Source	Average shell length (mm)	Average prespawn weight (g)	Eggs spawned per female	Eggs per gram	Number of individuals
CIMRI	40	10	57,667	5,767	30
CIMRI	40	10	49,100	4,910	30
CIMRI	72	47	170,000	3,617	20
UCSB	111	267	2,000,000	7,491	1
UCSB	111	267	1,500,000	5,618	2
UCSB	111	267	2,500,000	9,363	2
Wild	142	482	500,000	1,037	1
Wild	142	525	1,100,000	2,095	1
Wild	143	482	3,910,000	8,112	1
Wild	143	544	5,760,000	10,588	1
Wild	143	500	2,190,000	4,380	1
Wild	155	616	4,860,000	7,890	1
Wild	177	874	8,600,000	9,840	1
Wild	184	949	11,350,000	11,960	1
Wild†	185	1,210†	3,350,000†	2,769†	1†
Wild	192	936	13,140,000	14,038	1
Tutschulte	N/A	624*	5,180,000	8,301	Unknown
Tutschulte	N/A	615*	5,630,000	9,154	Unknown
Tutschulte	N/A	514*	3,690,000	7,179	Unknown
Tutschulte	N/A	416*	4,210,000	10,120	Unknown

Trials with abalone hatched and raised in captivity are identified by the acronym of their hatchery location (CIMRI or UCSB). Tutschulte data are included for comparison and based on trials with 197 wild animals (Tutschulte 1976).

* Weight calculated as soft tissue weight.

† Outlier excluded from analysis.

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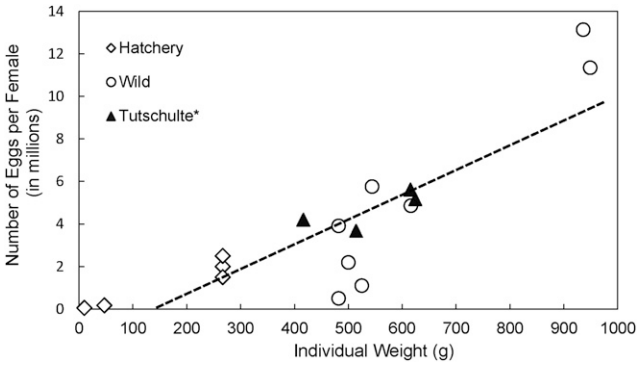

Figure 2. White abalone fecundity relative to weight. Number of eggs spawned versus total weight (g) for hatchery abalone (CIMRI & UCSB laboratories) and wild abalone; number of eggs calculated from gonad bulk by Tutschulte (1976) for comparison. Regression line ($y = 112{,}691 \times -1E+06$, $R^2 = 0.749$) is based on all samples. * Weight calculated as soft tissue weight.

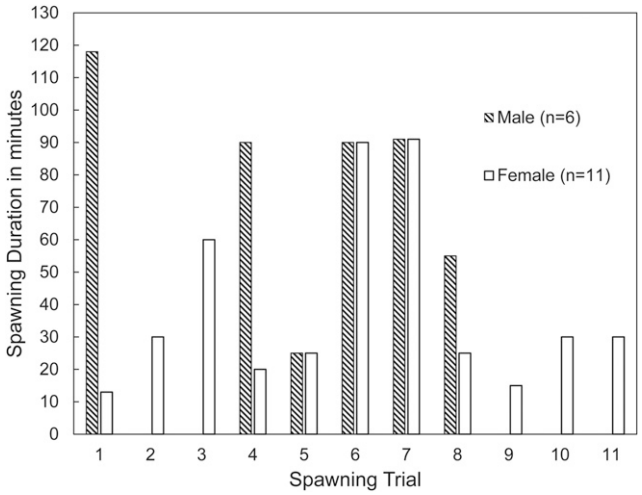

Figure 4. White abalone spawning duration. Data were collected during 11 spawning trials.

was calculated differently by Tutschulte than for abalone in this project. Figure 3 summarizes the results of these comparisons. Fecundity was determined as 7,271 eggs/g for wild-caught abalone and 6,128 eggs/g for hatchery-reared abalone and was not significantly different from previous estimates based on gonad bulk index (Tutschulte & Connell 1981).

Figure 4 summarizes results on spawning duration. These data represent 11 spawning trials. The duration of gamete release by male and female abalone was recorded.

The duration of spawning by male white abalone when stimulated to spawn in the hatchery ranged from 25 to 118 min, with an average of 78 min. A significantly shorter spawning duration (Mann–Whitney U test, $P < 0.05$) was recorded for females of 13–91 min with an average of 39 min as depicted in Figure 5.

Larval Development and Survival Relative to Temperature

The rate of larval development varied with temperature; development was most rapid at 21°C and slowest at 9°C. Figure 6 shows the time required to reach each developmental stage for abalone raised at the five test temperatures. At 21°C, all larvae died within 84 h after fertilization at Stage 30 (cilia growth on the propodium of the veliger). Larvae raised at 9°C died at Stage 17 (appearance of the retractor muscle in the veliger larvae). This occurred after 102 h in the first trial and 90 h in the second trial. Larvae raised at 18°C reached Stage 41 (appearance of the fourth tubule on the cephalic tentacle), and were competent to settle at 126 and 120 h (5.25 and 5 days) in the two trials. At 15°C and 12°C, larvae attained Stage 41 after 132 h (5.5 days) and 180 h (7.5 days), respectively. The rate of larval development in the first and second spawning trials was similar. Developmental rate was affected by temperature. Results of the present study showed that for each 3°C change in temperature, there was a significant increase in the rate of development as determined with multiple regression analysis [$F_{(4162)} = 87.8$, $P < 0.001$].

Developmental and survival rates were lowest at 9°C. Optimal development occurred at 12°C as summarized in

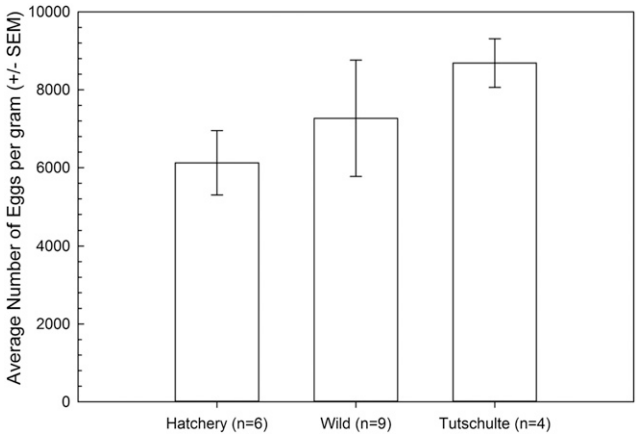

Figure 3. White abalone fecundity. Number of eggs spawned per gram of weight for wild-reared, hatchery-reared and Tutschulte's wild abalone. Differences were not significant ($U = 40$, $Z = -0.88$, $P = 0.37$). Tutschulte's data were treated separately because weight was calculated differently than for wild and hatchery abalone in this study.

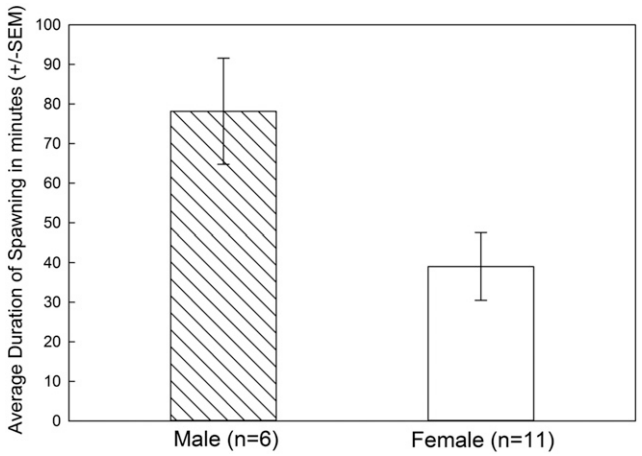

Figure 5. Average white abalone duration of spawning by gender. Non-parametric Mann–Whitney U test demonstrated a significant difference between male and female abalone, but small sample size should be noted ($U = 73.5$, $Z = 1.92$, $P = 0.05$).

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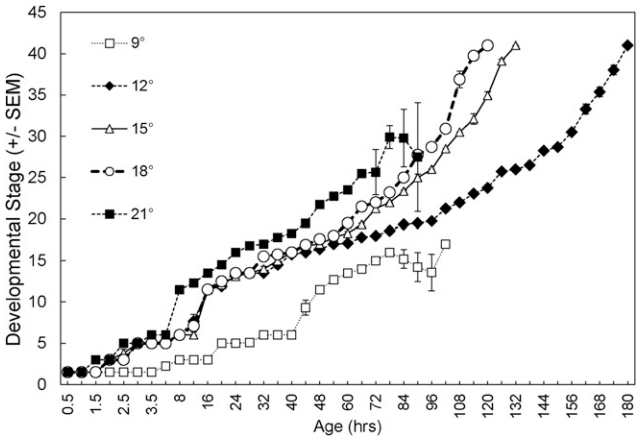

Figure 6. White abalone larval development relative to temperature. Results are pooled from two spawns. Developmental stages are from Seki and Kan-no (1977).

Figures 6 and 7. Figure 7 depicts the average number of hours for abalone to reach developmental stages: Stage 14 (hatch), Stage 17 (retractor muscle), Stage 21 (torsion), and Stage 33 (epipodal tentacle), at five temperatures of (9°C, 12°C, 15°C, 18°C, and 21°C). Data on time needed to reach certain developmental stages for each temperature treatment were treated with a repeated measures analysis of variance (ANOVA) with a Tukey's HSD *post hoc* test with Bonferroni corrections. This showed that the interaction of temperature and time significantly affected the time to reach a developmental stage [$F_{(37,134)} = 647.05$, $P < 0.01$). Comparison of the times required to reach a developmental stage using the repeated measures ANOVA indicates two instances where temperature had no significant effect on development: Stage 14 (hatch) at 12°C and 15°C, as well as 15°C and 18°C were similar; and at Stage 17 (retractor muscle development) where development times at 15°C and 18°C were similar.

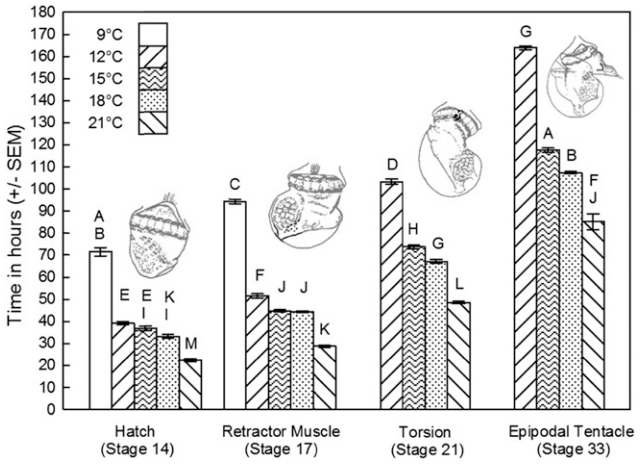

Figure 7. Abalone development relative to temperature. Bars not connected by same letter indicate significantly different values. [$F_{(37,134)} = 647.05$, $P < 0.01$: Repeated Measures ANOVA with Tukey's HSD *post hoc* test with Bonferroni corrections]. Larval stage drawings adapted from Seki and Kan-no (1977).

Biological zero temperature for larval white abalone was determined from the two experimental trials of larval development relative to water temperature using the combined rates of development to each of four stages (Fig. 7): Stage 14 (hatch), Stage 17 (appearance of larval retractor muscle), Stage 21 (torsion), and Stage 33 (formation of first epipodal tentacle). Biological zero point determined from combined data is 3.04°C.

Hatching success (Stage 14) was calculated by dividing the number of trochophores by the starting number of fertilized eggs. Hatching results were variable with no clear correlation to temperature as summarized in Table 6.

Temperature had a significant effect on the percent larval survival to the settlement stage (Kruskal–Wallis, $H(4) = 22.6$, $P < 0.001$). At 9°C and 21°C, all larvae died prior to completing development. At 18°C, only 2% larvae survived from fertilized eggs to Stage 41. Survival increased to 23% at 15°C with the highest being 56% at 12°C (Table 7).

Juvenile Growth and Survival Relative to Temperature and Diet

Diet and temperature affected the growth and survival of white abalone over the course of this 144-day (4.7 mo) trial. The interplay of these environmental factors is represented in Figures 8 and 9. Variance in the data, the number of dependent variables, and the combined effects of these factors prohibited statistical significance; however, some trends in the data may be important. Growth results were better on diets including *Macrocystis* and/or *Palmaria*. In early development, growth rates were highest at the higher temperatures (15°C and 18°C), but survival was lowest at 18°C.

Abalone that were raised at the extreme high or low temperatures and fed *Chondracanthus* showed minimal or negative changes in SL. Negative growth can result from erosion of the shell edge or from the largest abalone dying, shifting the average SL downward.

Juvenile Growth and Survival Relative to Stocking Density

The interaction of density and time depicted in Figure 10 had a significant effect on growth (determined by SL) as demonstrated by repeated measures ANOVA with Tukey's HSD *post hoc* test [$F_{(6,4695)} = 27.95$, $P < 0.001$]. Abalone stocked at a low density of 25 grew faster than at 50 (Fig. 10). In the low-density raceways, SL increased from an average of 19.6 ± 0.4 mm to 29.1 ± 0.9 mm, the equivalent of 46 μm/day. In the high-density raceways, SL increased from 20.0 ± 0.4 mm to 25.8 ± 1.0 mm, equivalent to 28 μm/day. At low stocking densities, wet weight per abalone increased from an average of 1.3–3.5 g wet weight, or 269%. Abalone stocked at twice this density increased from

TABLE 6.

Abalone hatching success by temperature.

Temperature (°C)	Hatching success (%)
9	43
12	74
15	80
18	56
21	86

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TABLE 7.

Abalone larval development and survivorship relative to temperature.

	Trial number					
			Spawn 2			
	Spawn 1				% Survival	
Temperature (°C)	Developmental stage	Hours	Developmental stage	Hours	From egg to hatch	From egg to Stage 41
9	17	102	17	90	43	0
12	41	180	41	180	74	56
15	41	132	41	132	80	23
18	41	126	41	120	56	2
21	30	84	31	84	86	0

Developmental stages of larvae are from Seki and Kan-no (1977). The last developmental stage attained in each temperature regime and the average number of hours to achieve that stage listed for two spawning trials. Percent survival to hatching and to Stage 41 is listed for the second spawning trial only.

an average weight of 1.2–2.5 g wet weight or 208%. Overall densities in the raceways increased from 25 to 64 at the low stocking density, and from 50 to 90 at the high stocking density. Survival averaged 90% for low-density raceways and 88% for high-density raceways. Growth at both low and high densities slowed as densities increased in the course of the experiment.

Juvenile Growth and Survival Relative to Light Intensity

Growth of abalone during the course of this 192-day (6.3 mo) experiment was similar in the two light regimes of this project. Outdoor raceways received a maximum of 59, 202 lumens/m^2 (approximately 3%–5% ambient light). Indoor raceways were received less than 10 lumens/m. Changes in SL and total wet weight of the 175 abalone per treatment of differing light regimes are shown in Figures 11 and 12. No significant relationship was found using repeated measures ANOVA with Tukey's HSD *post hoc* test.

The growth data from four hatchery-spawned crops of white abalone are graphed in Figure 13. Abalone were raised on microalgal cultures until reaching SL of 15–35 mm. Feed was then changed to *Macrocystis pyrifera*. Shell length (in mm) represents measurements from 50 animals per cultivation tank.

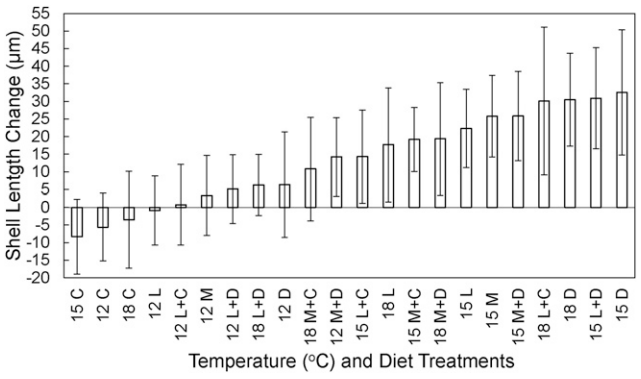

Figure 8. Juvenile abalone growth relative to temperature and diet. Change in SL in microns per day for juvenile white abalone with varied diet and water temperatures over 144-day period. Numbers represent water temperature and letters indicate diets of *Chondracanthus* (C), *Dulse* (D), *Laminara* (L), and *Macrocystis* (M).

Total number of abalone at SL of 3–5 mm was April 23, 2001 = 121,600; January 6, 2003 = 4,424; April 11, 2003 =1,040; and April 14, 2003 =1,200.

DISCUSSION

Larval Development

In these two experiments, the rate of larval development increased with temperature over the range of 9–21°C. For every 3°C change in temperature over this same range, the speed of development showed a significant increase [multiple regression, $F_{(4162)} = 87.8$, $P < 0.001$]. Larvae cultured at 12°C completed development and were competent to settle in 7.5 days, whereas those at 15°C required 5.6 days, and those at 18°C required 5.3 days. Extreme temperatures of 9°C and 21°C resulted in complete mortality prior to completion of larval development.

Survival

Mortalities during the initial growth stage from fertilized egg to the hatch out of trochophore larvae (Stage 14) varied from 43% to 86%, with no correlation to temperature. Initial mortality within this range is often observed in abalone hatcheries.

Over the duration of the larval culture period, the sampling for development assessment resulted in the removal of up to 4% of the fertilized eggs and larvae from each beaker. In addition,

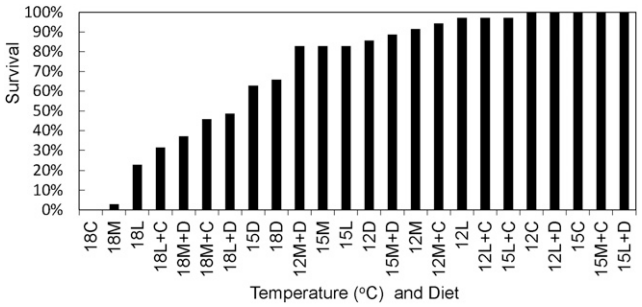

Figure 9. Juvenile abalone survival relative to temperature and diet. Abalone survival over 144 days of growth under different temperatures and diets. Numbers represent water temperature and letters indicate diets of *Chondracanthus* (C), *Dulse* (D), *Laminara* (L), and *Macrocystis* (M).

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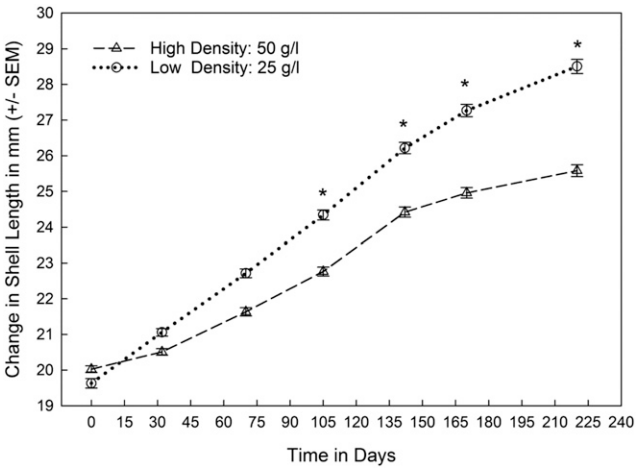

Figure 10. Juvenile abalone shell growth relative to stocking density. Change in SL of abalone grown in high densities (50 gm/L) and low densities (25 gm/L). The interaction of density and time had a significant effect on SL [$F_{(6,4695)} = 27.95$, $P < 0.001$). * Indicates significantly different lengths for the time per Tukey's HSD *post hoc* test.

the numbers of abalone larvae within the beakers decreased at different rates over time, as a result of temperature-dependent mortality. Changes in the number of larvae per beaker may have affected the rate of development. Fewer individuals within the tank would result in an increase in available nutrients per larva. Lecithotropic abalone larvae do not consume microalgae or other particulates, but can absorb dissolved organic material in the form of amino acids directly from seawater (Jaeckle & Manahan 1989).

Temperature had a significant (Kruskal–Wallis, $H(4) = 22.6$, $P < 0.001$) impact on survival of larvae from hatch out to fully developed veligers. At 9°C, the number of larvae steadily declined to zero by 90–102 h in the first and second spawns. The number of larvae in the 12°C treatment remained constant throughout development with 56% of the fertilized eggs surviving to settling competency. At 15°C, initially high mortalities continued until formation of the operculum (Stage 23) at 72 h, then survival rates stabilized. At this temperature, only 23% of the initial number of eggs survived. At 18°C, only 2% survived until settlement. Steady mortality was also seen at

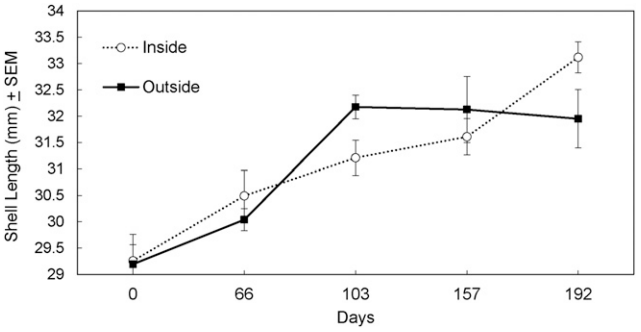

Figure 11. Juvenile abalone shell growth relative to light intensity. Shell length of abalone grown at two lighting levels in outside and inside raceways. Lengths were not significantly affected by light intensity [$F_{(1,12)} = 0.013$, $P = 0.91$], or the interaction of time and light intensity [$F_{(4,48)} = 2.55$, $P = 0.051$]. Time was a significant factor [$F_{(4,48)} = 26.56$, $P < 0.001$].

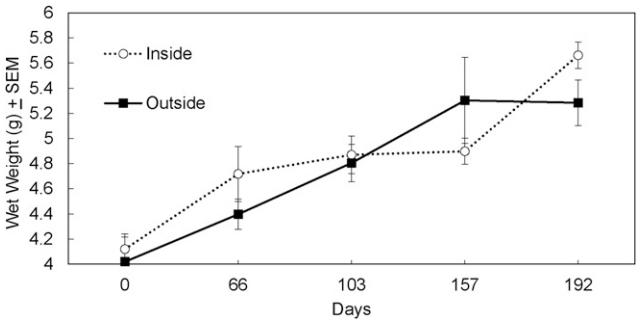

Figure 12. Juvenile abalone growth in mass relative to light intensity. Wet weight of abalone grown in two different levels of light intensity (indoor and outdoor) raceways. Time was the only significant factor in wet weight [$F_{(4,48)} = 21.96$, $P < 0.001$]. Light intensity and the interaction of light intensity did not significantly affect wet weight [light intensity: $F_{(1,12)} = 0.293$, $P = 0.60$], light × time interaction: $F_{(4,48)} = 1.71$, $P = 0.16$].

21°C where all larvae died 84 h after fertilization having reached Stage 30, the growth of cilia on the propodium. This work indicates that 12°C is the optimal temperature for survival of white abalone larvae.

The study by Leighton (1974) is the only other study on the effects of temperature on growth and survival of white abalone larvae that found best survival at 16°C and 18°C. At 15°C, he observed settlement at 9–10 days. At temperatures of 14°C, 12°C, and 10°C, he found that survival decreased rapidly. Leighton's methods were different from the present work and may account for the differing results. In Leighton's work, eggs from a single pair mating had a fertilization rate of 5% or less. Eggs and larvae were held at 12°C (±2°C) for 72 h posthatch (approximately 96 h after fertilization), prior to placement in test temperatures. Larvae raised at 12°C for 72 h posthatch would already be well developed, having completed formation of the larval shell (Stage 20). Transfer to different temperatures at this point would have an impact on developmental rate and temperature shock would reduce survival. Subsequent development was only checked every other day.

The present results are supported by the experience of raising white abalone larvae and juveniles on a hatchery scale. Over the course of six spawns that produced more than 35 million eggs, the cultivation of larval and early juvenile abalone was successful only if water temperatures averaged 12–14.5°C. In one spawn, larvae grew normally and had high survival at 15.5°C to Stage 27 (appearance of the eyespot). When temperatures

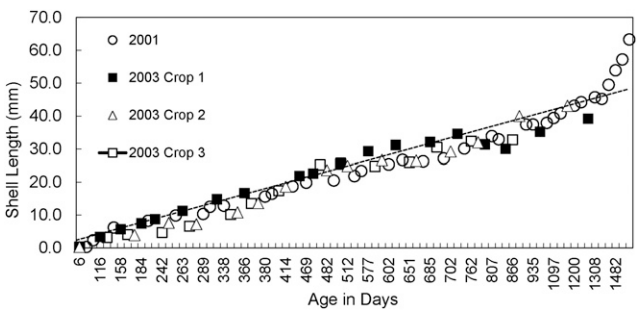

Figure 13. Juvenile abalone growth. Growth of four crops of white abalone in the nursery. The regression line ($y = 0.0356x + 2.0726$, $R^2 = 0.95$) was calculated with all crops pooled.

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increased to 16°C for the remainder of the culture period, mortalities reached 55%. Of the remaining larvae, 33%–50% were abnormal. In another instance, the failure of a chiller that kept water in larval culture tanks at 12°C resulted in total mortalities when water temperatures climbed to 18°C. Water temperatures in habitat known to support white abalone populations are optimal for survival of white abalone larvae when they are at their annual minimums in late winter and early spring. As an example, Figure 14 shows 10 y of temperature data at a depth of 47 feet (14 m) off Santa Cruz Island, CA, an area that traditionally supported populations of white pink (*Haliotis corrugata*) and red abalone (*Haliotis rufescens*). In 9 of the 10 years, water temperatures were within one degree of 12°C, the optimal temperature for maximum survival of white abalone larvae.

Variation in seawater temperature can have an impact on successful reproduction and recruitment in broadcast spawning invertebrates such as abalone. Temperature variations outside a narrow range can result in recruitment failure for abalone (Shepherd et al. 1998). This study has shown that optimal temperatures for the growth of white abalone larvae are significantly lower than previously published. This information may help restoration managers in both cultivation and restocking efforts of an endangered species to develop new models for the biology of this species.

Biological Minimum Temperature

Using developmental data from white abalone larval growth at five temperatures, it has been determined that the biological minimum temperature, the point at which growth stops, is 3.0°C for this species. This temperature is much lower than those of sympatric green *Haliotis fulgens* (9.9°C), red *Haliotis rufescens* (8.5°C), and pink *Haliotis corrugata* (5.7°C) abalone calculated by Seki (T. Seki, National Research Institute of Aquaculture, Japan. May 1993, lecture at UCSB, CA) using data from Leighton (1974). The biological minimum temperature for white abalone is also lower than values of 7.6°C, 8.5°C, and 9.0°C for *Haliotis discus hannai*; *Haliotis discus* (Reeve, 1846); and *Haliotis gigantea* (Gmelin, 1791), determined by Seki and Kan-no (1977).

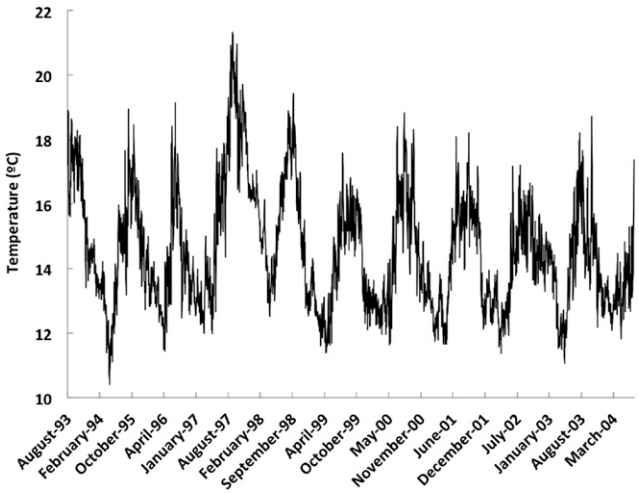

Figure 14. Seawater temperatures at a depth of 47 feet off Yellowbanks, Santa Cruz Island. (Data from D. Kushner, Kelp Forest Monitoring Program, Channel Islands National Park (2004).

The lower biological minimum temperature of white abalone may help explain its status as the deepest living abalone on the west coast of North America (Hobday & Tegner 2000). This species may be limited to habitat where seawater temperatures range from 12°C to 15°C during the late winter spawning period. Tutschulte (1976) found that spawning of white abalone off Catalina Island occurred in March, when temperatures at 30–40 m depth averaged 12°C. Based on Leighton's (1974) early results, Tutschulte (1976) postulated that the 10–12°C isotherm during spawning season set the lower depth limit for white abalone. In light of the present work, it appears that the 12°C isotherm indicates the optimal depth for larvae of this species with a lower limit being set by the 9°C isotherm and upper limit greater than 15°C. Suitable habitat might look similar to waters off Yellowbanks, off Santa Cruz Island, CA, at depths where late winter seawater temperatures are 12–15°C. An example of seasonal and annual variations in water temperatures at 15 m off Santa Cruz Island in southern California is shown in Figure 14.

White abalone, native to coastal waters off southern California and Baja California, Mexico, was one of six abalone species that contributed to valuable sport and commercial fisheries for much of the 20th century. Work on extant populations of white abalone off Catalina Island, CA, in the 1970s (Tutschulte 1976) found that white abalone specialized in deep-water habitats from 15 to 35 m with food availability and possibly temperature being limiting factors at the deeper margin of their distribution. Irregular recruitment under colder temperature and food limiting environments found at greater depths likely resulted in the observed strong dominant age classes (Tutschulte 1976, Hobday & Tegner 2000). Loss of white abalone habitat may have resulted from long-term increases in seawater temperature resulting from climate change and shorter fluctuations attributed to multidecadal events such as the Pacific Decadal Oscillation (PDO). A PDO warming period from 1977 to the 1990s (Mantura & Hare 2002, Hare & Mantua 2000) may have raised seawater temperatures to levels that were disadvantageous for survival of some abalone species (Mantua et al. 1997), including white abalone. Since the 1970s, it is estimated that white abalone populations dropped by 90% (Hobday & Tegner 2000). Population models for abalone, such as the one developed by Hobday and Tegner (2002) for *Haliotis rufescens* in southern California, have shown that variations in water temperatures of only a few degrees can lead to recruitment failures and population collapse. Optimal seawater temperatures for white abalone were found to be significantly lower than previously reported; however, it is difficult to discern the effect of the PDO in light of intense fishing pressure, which reduced densities of the dominant age classes to levels of unavoidable recruitment failure.

With the white abalone considered critically endangered throughout its range (Stierhoff et al. 2014), efforts in captive breeding, culture, and outplanting have never been more important. It is hoped that the data herein will enhance success of abalone mariculture programs to prevent the extinction of this once abundant and economically important animal.

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