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NUMBER AND DURATION OF ZOEAL STAGES OF THE HYDROTHERMAL VENT CRAB *GANDALFUS YUNOHANA* FROM LABORATORY REARED SPECIMENS

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ABSTRACT

The hydrothermal vent crab *Gandalfus yunohana* is found along the Izu-Ogasawara Arc in the north-western Pacific at depths from 420 to 1400 m. To study the larval developmental characteristics of this vent endemic species, we collected adult crabs from a depth of 445 m in May 2005 from the Kaikata Seamount (26°42.607′N, 141°04.457′E). These individuals were maintained at atmospheric pressure and temperature (15 and 18°C) for several months, until two females spawned and released larvae. Larvae were maintained at atmospheric pressure and at five different temperatures ranging from ~18 to 30°C and fed *Artemia* sp. At ~18°C, no larvae survived until the second zoeal stage. Some larvae reached the second or third zoeal stages when reared at ~21°C. At 24-30°C, six individuals metamorphosed into the megalopal stage following a fifth or sixth zoeal stage 34-60 d after hatching. Megalopae swam actively, but they eventually died 58-104 d after hatching and showed no signs of moulting into the juvenile crab stage. Newly hatched first stage zoeae were phototactic, and we observed relatively high temperature requirements for larval survival and development. These facts suggest that zoeae may be distributed relatively high in the water column in warmer near-surface waters during their planktotrophic development. This is the first report of successful larval rearing of any species of bythograeid crabs. Our study establishes the conditions under which the megalopae moult to the first crab stage, laying the groundwork for future experiments.

KEY WORDS: deep sea, dispersal, hydrothermal vent crab, larval development, survivorship of larvae, temperature

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INTRODUCTION

Brachyuran crabs were first discovered at deep-sea hydrothermal vents on the Galapagos Rift at depths between 2400 and 2700 m. These organisms are characterised by a reduced external eye structure and a white or bone-coloured body (Williams, 1980; Martin and Haney, 2005; McLay, 2007). Williams (1980) described the vent-endemic species *Bythograea thermydron* Williams, 1980 as a representative of a new genus (*Bythograea*), new family (Bythograeidae), and new superfamily (Bythograeoidea). Since their discovery, bythograeid crabs have been found at a variety of vents around the world and now include six genera and 14 species (Martin and Haney, 2005; McLay, 2007; Ng et al., 2008).

Vent fields occur sporadically along active mid-ocean ridges and back-arc basins as well as at some seamounts, and they are generally active for no more than a decade (Haymon et al., 1993; Van Dover et al., 2002). Therefore, vent-endemic species must be able to effectively disperse and colonise new vents after locations become inactive. As bythograeid crabs are benthic, they must disperse through the water column during their larval stages. Therefore, studies on larval developmental characteristics are crucial in evaluating the larval dispersal ability of bythograeid crabs. Larval rearing experiments are useful tools in elucidating the larval developmental characteristics and dispersal capabilities of shallow water decapod crustacean species (Gore, 1985; Anger, 2001), and similar methods have been applied to deep-sea hydrothermal vent crab species. Epifanio et al. (1999) collected *B. thermydron* megalopae from vent fields and successfully reared them through juvenile moults in the laboratory at atmospheric pressure. Jinks et al. (2002) reported that zoea larvae hatched from a freshly collected ovigerous female and wild-caught megalopae possessed image-forming compound eyes. Dittel et al. (2008) kept an ovigerous female of *B. thermydron* under hyperbaric conditions and succeeded in hatching eggs, but they were unsuccessful in culturing newly hatched larvae. These larvae initially appeared to be similar in morphology to first stage zoea, but they showed undeveloped natatory setae of exopods of the maxillipeds. It was also reported that a bythograeid crab *Gandalfus yunohana* (Takeda, Hashimoto, and Ohta, 2000) has a first stage zoea with pigmented eyes (Miyake et al., 2007; Nakajima et al., in press). This species was recently reassigned from *Austinograea* Hessler and Martin, 1989 to *Gandalfus* McLay, 2007. *Gandalfus yunohana* is distributed throughout the Myojin Knoll and the Suiyo, Kaikata and Nikko Seamounts along the Izu-Ogasawara (Bonin) Arc in the north-western Pacific at depths from 420 to 1400 m (Fig. 1; Takeda et al., 2000; Kojima, 2002; McLay, 2007), and adult crabs may be kept in captivity at atmospheric pressure (Tsuchida et al., 1998; Miyake et al., 2007). Tsuchida et al. (1998) reported moulting and growth of adult *G. yunohana* reared in tanks for more than

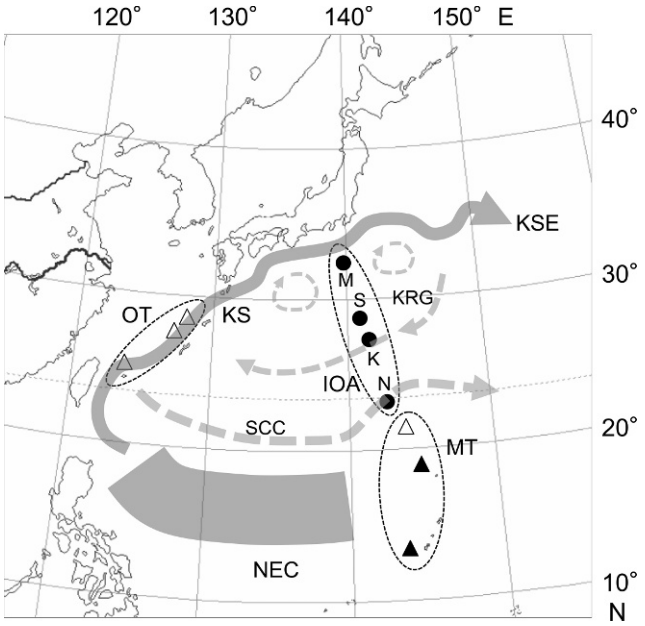

Fig. 1. Distribution of hydrothermal vent regions in the north-western Pacific (drawn from Kojima, 2002). MT, Mariana Trough; IOA, Izu-Ogasawara Arc; OT, Okinawa Trough. Black circles show the hydrothermal vent fields where *Gandalfus yunohana* has been reported: M, Myojin Knoll; S, Suiyo Seamount; K, Kaikata Seamount; N, Nikko Seamount. Black triangles show the hydrothermal vent fields where *Austinograea williamsi* has been reported in MT. Open triangles show some hydrothermal vent fields in MT and OT. Ocean currents are schematically illustrated as follows: KRG, Kuroshio recirculation gyres; KS, Kuroshio; KSE, Kuroshio Extension; NEC, North Equatorial Current; SCC, Subtropical Countercurrent.

six years. However, larvae of this species have never previously been successfully reared in a laboratory setting. Thus, several studies have suggested that bythograeid crabs have planktonic larval stages (Epifanio et al., 1999; Jinks et al., 2002; Miyake et al., 2007; Dittel et al., 2008). However, larval developmental characteristics, including the number of zoeal stages and the duration of the larval period, are not known for any species of bythograeid crab.

This study was undertaken to elucidate the larval developmental characteristics of *G. yunohana*. We maintained female individuals from spawning to hatching and successfully reared larvae from hatching to the megalopal stage. This is the first time that this has been accomplished for any bythograeid crabs. In this paper, we document the number of zoeal stages and larval duration until the megalopal stage of *G. yunohana*.

Materials and Methods

Larval Collection

Gandalfus yunohana were collected on May 26, 2005 at Kaikata Seamount (26°42.607′N, 141°04.457′E, at a depth of 445 m) in the Izu-Ogasawara Arc (Fig. 1) using the remotely operated vehicle (ROV) Hyper-Dolphin (Dive #418) belonging to the Japan Agency for Marine-Earth Science and Technology, Yokosuka. Five males and six females with carapace widths (CW) between 26.4-34.9 mm were collected and transported back to the laboratory at Tokyo University of Marine Science and Technology, Tokyo, where they were maintained in tanks with 30-60 L volume at ~12, 15 and 18°C according to the method of Tsuchida et al. (1998). Spawning and hatching occurred in two females reared in the 15°C and 18°C tanks. In the 18°C tank, hatching occurred on August 7, 2005, but newly hatched larvae were inadvertently taken up through the recirculation system of the tank and trapped by the filter. Larvae were carefully removed from the filter and transferred to another container, and first stage zoeae, excluding prezoeae (which did not swim and sank to the bottom of the container), were used for larval rearing experiments 1 and 2. In the 15°C tank, the recirculation system was halted before hatching, and the female hatched her larvae on October 12, 2005; first stage zoeae, excluding prezoeae, were used for larval rearing experiment 3.

First stage zoeae of *G. yunohana* proved to be phototactic when a torch light was focused onto the side of a rearing container.

Larval Rearing Experiments

Temperature is one of the most important environmental factors affecting survival, development and growth of decapod crustacean larvae under culture conditions and larval dynamics in the field (Anger, 2001). To improve the likelihood of survival and growth of *G. yunohana*, larval rearing experiments were conducted at different temperatures ranging from ~18 to 30°C in a multi-thermo incubator (MTI-201; Tokyo Rikakikai Co., Ltd., Tokyo, Japan).

In experiment 1, larvae were reared at three temperature levels: 17.9 ± 0.4, 21.3 ± 0.2 and 24.2 ± 0.3°C (mean ± SD, recorded daily during the course of the experiment). Selected minimum (~18°C) rearing temperatures coincide with the hatching temperature of the female. At each test temperature, 30 first stage zoeae were stocked in a 1-L white plastic beaker with filtered seawater (pore size, 1 μm). In addition, 10 first stage zoeae were stocked in a 350-mL glass container and reared under starved conditions at 17.9°C. In experiment 2, 12 first stage zoeae were stocked individually in two 6-well plates (Microplate 3810-006; IWAKI Co., Ltd., Tokyo, Japan) with 5 mL of filtered seawater at each test temperature as in experiment 1. Because no larvae moulted to the second zoeal stage at 17.9°C in experiment 1 or 2, elevated rearing temperatures were adopted in experiment 3; larvae were reared at four temperature levels: 21.0 ± 0.4, 24.0 ± 0.2, 27.0 ± 0.2 and 30.0 ± 0.3°C in a similar manner to experiment 1, but we added continuous gentle aeration in rearing beakers using Pasteur pipettes. Selected maximum (30°C) rearing temperatures coincide with the highest temperature in the water column around the distribution area of adult *G. yunohana* (Fig. 1) (Japan Oceanographic Data Center; http://jdoss1.jodc.go.jp/cgi-bin/1997/bts.jp; accessed 6 July 2009). Replicated rearing beakers at each test temperature could not be prepared in experiments 1 and 3 because of the limited number of first stage zoeae. The photoperiod was maintained at 14 h light (6:00-20:00, ~500 Lx): 10 h dark using a fluorescent lamp. *Artemia* nauplii (Utah Strain; INVE Ltd., Phichit, Thailand) fed the larvae at a density of 4 ind mL^{-1} except for a starvation treatment. Each morning, larvae were transferred to newly prepared rearing beakers with fresh filtered seawater (salinity, 32‰) and prey using a large-mouthed pipette. Dead larvae were removed from the rearing beakers. After transferring the larvae, dihydrostreptomycin sulphate was added to the rearing water at 10 mg L^{-1} to prevent bacterial attachment to the larvae. The larvae were observed daily, and the number of larvae moulted to the next stage was examined. The mean number of days to reach each larval stage was determined at each test temperature. Larval moulting and developmental stages were confirmed by observing moulted exoskeletons. To allow the description and illustration of the complete larval development of *G. yunohana* in a future study, larvae at each zoeal stage (N = 2-11) were sampled from rearing beakers and fixed with 5% neutral formalin for one day and then preserved in 70% ethanol solution. Larval rearing was terminated when all larvae died.

Statistical Analyses

Differences in the mean number of days to reach each larval stage between temperature groups were tested with a pairwise t-test, based on Welch's t test without an assumption of variance homogeneity between compared groups. A Welch's t test was employed when mean values were compared between two groups. The relationship between temperature (x) and the intermoult period of zoeal stages (y) was analysed using a power function, $y = ax^b$, as reported for many decapod crustacean species (e.g., Anger, 2001). The intermoult period for each larval stage was calculated as the difference of mean values between successive stages in each rearing beaker. Data sets were fitted to the log-transformed linear regression model, $\ln y = \ln a + b \ln x$, and the parameters ($\ln a$, b) were estimated by the method of ordinal least squares. Analysis of covariance was employed to compare differences in slopes and y-intercepts between linear regression

Table 1. Number of *Gandalfus yunohana* larvae moulted to each stage at different temperatures. Z1-6, first to sixth stage zoeae; MZ5, megalopa metamorphosed from Z5; MZ6, megalopa metamorphosed from Z6. Figures in parentheses are number of larvae sampled at each stage.

Expt. no.	Water temperature (°C)	Number of larvae							
		Initial (Z1)	Z2	Z3	Z4	Z5	Z6	MZ5	MZ6
1	17.9	30	0	0	0	0	0	0	0
	21.3	30	3 (2)	0	0	0	0	0	0
	24.2	30	10 (2)	2	2	1	0	0	0
2	17.9	12	0	0	0	0	0	0	0
	21.3	12	3	0	0	0	0	0	0
	24.2	12	3	3	3	3	0	1	0
3	21.0	30	5 (1)	2	0	0	0	0	0
	24.0	30	17 (2)	10 (2)	7 (2)	5 (2)	2	1	1
	27.0	30	22 (2)	14 (2)	10 (2)	7 (2)	5 (2)	0	3
	30.0	30	16 (2)	12 (2)	9 (2)	6 (2)	3	1	2

equations. All statistical procedures were performed in R-language (R Development Core Team, 2009), and the level of significance was assessed at $\alpha = 0.05$. To control type I error in pairwise comparisons, the significance level was adjusted by the Holm-Bonferroni method (Holm, 1979).

Results

In experiment 1, larvae did not moult to second stage zoeae at 17.9°C (Table 1), but the mean survival time for these larvae (12.5 d) was significantly higher than that for larvae at an identical temperature under starvation (8.3 d; $P < 0.05$). This indicates that *G. yunohana* larvae are planktotrophic. Larvae did not reach the third zoeal stage at 21.3°C, whereas one larva survived to the fifth zoeal stage at 24.2°C. In experiment 2, a similar result was obtained to experiment 1, and one larva metamorphosed to the megalopal stage from the fifth zoeal stage at 24.2°C. In experiment 3, larvae did not survive to the fourth zoeal stage at 21.0°C, whereas larvae metamorphosed to the megalopal stage through the fifth or sixth zoeal stage at 24.0-30.0°C. Megalopae were active swimmers but eventually died 58-104 d after hatching, without any sign of morphological characters of the pre-moulting stage in the moulting cycle (Anger, 1983) before the first crab stage.

All larvae were bright red and had pigmented compound eyes (Fig. 2). The first stage zoeae showed strong positive phototaxis; they immediately moved towards a light source when a pocket torch was turned on the side of a rearing beaker.

The larval duration (days) from hatching to each progressive larval stage tended to decrease with increasing temperature (Table 2). The time until the megalopal stage ranged between 34 and 60 d at 24.0-30.0°C. The relationships between temperature and the intermoult period of zoeal stages tended to be divided into two groups: first and sixth zoeal stages and the second to fifth zoeal stages (Fig. 3). Because of the limited data set for each zoeal stage, the log-transformed linear regression model of the power function was applied to the two groups as follows: first and sixth zoeal stages, $\ln y = 8.6511 - 1.9053 \ln x$ ($N = 11$, $R^2 = 0.8315$, $F_{1,9} = 44.41$, $P = 9.227 \times 10^{-5}$); second to fifth zoeal stages, $\ln y = 8.2679 - 1.9400 \ln x$ ($N = 19$, $R^2 = 0.4953$, $F_{1,17} = 16.69$, $P = 7.717 \times 10^{-4}$). We found no significant difference in slopes ($F_{1,26} = 0.0033$, $P = 0.9549$), but a significant difference was found between the *y*-intercepts ($F_{1,27} = 54.43$, $P = 6.176 \times 10^{-8}$) of the two equations. Maximum survival duration of larvae after metamorphosis to the megalopal stage was ~60 d at 27.0-30.0°C.

Fig. 2. *Gandalfus yunohana* (Takeda, Hashimoto, and Ohta, 2000): a, lateral view of first stage zoea; b, dorsal view of megalopa. Scale bars = 0.5 mm.

Discussion

We successfully reared larvae from hatching to the megalopal stage of *G. yunohana*. Individuals were observed to have five or six planktotrophic zoeal stages. This finding provides the first information on the number of zoeal stages in any bythograeid crabs. Intraspecific variability in larval developmental pathways has been observed in many decapod crustaceans, both in the laboratory and in the field (Anger, 2001). This variability has been attributed to genetic, maternal and environmental factors (Anger, 2001). Although

Table 2. Duration in days from hatching to each developmental stage of *Gandalfus yunohana* larvae reared at different temperatures. Z1-6, first to sixth stage zoeae; MZ5, megalopa metamorphosed from Z5; MZ6, megalopa metamorphosed from Z6. Number of larvae to calculate the mean and standard deviation (SD) equals the number of larvae moulted to each stage in Table 1. Significant differences were found between temperature groups with different superscripts in the same column of each experiment (pairwise *t* test or Welch's *t* test, $P < 0.05$).

Expt. no.	Water temperature (°C)	Days to reach each larval stage													
		Z2		Z3		Z4		Z5		Z6		MZ5		MZ6	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	21.3	15.7[a]	1.5	–	–	–	–	–	–	–	–	–	–	–	–
	24.2	12.4[a]	3.7	20.0	0.0	28.5	3.5	34.0	–	–	–	–	–	–	–
2	21.3	14.7[a]	1.2	–	–	–	–	–	–	–	–	–	–	–	–
	24.2	12.3[a]	1.5	24.0	2.0	32.7	2.1	41.0	2.0	–	–	48.0	–	–	–
3	21.0	20.8[a]	3.3	33.5[a]	3.5	–	–	–	–	–	–	–	–	–	–
	24.0	14.7[b]	1.8	22.9[b]	2.3	31.7[a]	3.5	41.6[a]	4.3	46.5[a]	0.7	57.0	–	60.0	–
	27.0	11.7[c]	1.4	18.3[c]	2.6	24.2[b]	2.5	29.4[b]	1.4	36.2[b]	1.8	–	–	48.0[a]	1.7
	30.0	9.4[d]	0.7	15.3[d]	1.7	20.9[c]	1.6	26.5[b]	1.6	32.0[c]	3.0	34.0	–	39.5[b]	2.1

the factors affecting the variability in number of zoeal stages of *G. yunohana* are unknown, the larval developmental sequence found in this vent endemic species was not unique and appears to be common in brachyuran crabs (Gore, 1985).

Larval survival rates were lower in experiments 1 and 2 than experiment 3, probably because of poor hatching conditions for larvae used in experiments 1 and 2, while a similar trend was found in larval survival in all experiments. We found that temperature largely affected larval survival and rate of development in *G. yunohana*, as shown for many decapod crustaceans (e.g., Anger, 2001). Larvae moulted to second or third stage zoeae at ≥ 21.0°C, but not at 17.9°C. At 24.0-30.0°C, larvae survived and metamorphosed to the megalopal stage in 34-60 d. Thus, *G. yunohana* apparently requires higher temperatures for larval survival and development than the temperatures experienced by adults, determined to range between 8-22°C in several abyssal surveys (Mitsuzawa et al., 1989; Ono et al., 1996; Iizasa et al., 1997; Tsuchida et al., 2001; Watanabe et al., 2003). Relatively high temperature requirements for larval survival and development of *G. yunohana* are similar to subtropical and tropical crab species for which the optimal temperature range for rearing larvae is usually > 25°C, whereas temperatures < 20°C decrease larval survival (Anger, 2001).

Newly hatched first stage zoeae of *G. yunohana* were phototactic, and this, together with the relatively high temperature requirements for larval survival and development, suggests that zoeae may be distributed relatively high in the water column in warmer near-surface waters during their planktotrophic development. The intermoult period is longest at the first and sixth zoeal stages in *G. yunohana*, although it appears to be longer in the later larval stages in certain decapod crustaceans (Harms and Seeger, 1989). This feature may allow larvae to move into the phase of the water column most suitable for their development, while they show strong positive phototactic behaviour during the first zoeal stage. Future studies will test this hypothesis by examining phototactic behaviour in all larval stages.

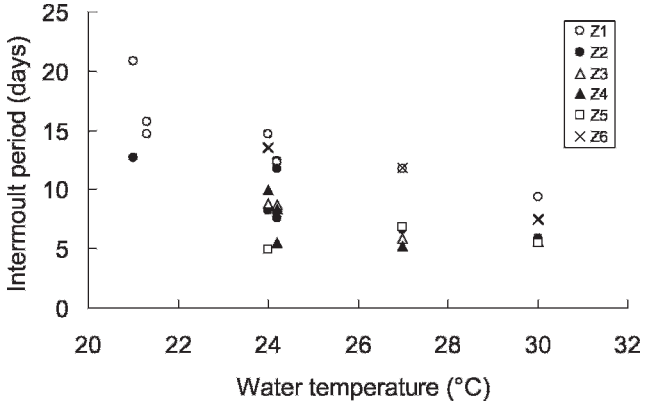

Fig. 3. Intermoult periods of larval *Gandalfus yunohana* plotted against the mean rearing temperatures. Z1-6 refers to the first to sixth zoeal stage.

The known distribution of *G. yunohana* is limited to the Myojin Knoll and several seamounts at depths ~420-1400 m, ranging from ~23°04′N to 32°06′N and from ~139°52′E to 142°20′E, along the Izu-Ogasawara Arc in the north-western Pacific (Fig. 1; Takeda et al., 2000; Kojima, 2002; McLay, 2007). Another bythograeid crab, *Austinograea williamsi* Hessler and Martin, 1989, is found at vent sites at a depth ~3600 m (~18°10-13′N, ~144°42-43′E) and at a depth ~1450 m (13°24′N, 143°55′E) in the Mariana Trough, south of the Izu Ogasawara Arc (Fig. 1; Hessler and Martin, 1989; Tsuchida and Fujikura, 2000); this closely related species may have a larval developmental sequence similar to *G. yunohana*. Zoeal dispersal may be largely influenced by passive transport in ambient currents. The Kuroshio, a warm-water current originating from the North Equatorial Current, flows from the East China Sea along the southern coast of Japan to the coast of Boso Peninsula (35°42′N, 140°52′E) and forms the Kuroshio Extension in the Pacific (Fig. 1). The effects of this strong current reach several thousand metres below the sea surface. Recirculation gyres circulate south of the Kuroshio and the Kuroshio Extension, as well as on both sides of the Izu-Ogasawara Arc, and the Subtropical Countercurrent circulates north of the North Equatorial Current (Fig. 1; see also Uda and Hasunuma, 1969; Sakamoto et al., 2005; Qiu et al., 2005; The Nippon Foundation Library, http://nippon.zaidan.info/seikabutsu/1999/00621/contents/004.htm [accessed on July 6, 2009]). These currents, recirculation gyres and countercurrents must affect the distribution of bythograeid crabs, *G. yunohana* and *A. williamsi*, at the hydrothermal vent fields in the north-western Pacific by driving zoeal dispersal.

In *B. thermydron*, selection of settlement sites may rely on active swimming by megalopae and recruitment to the

vent sites occurring during the megalopal stage (Epifanio et al., 1999; Dittel et al., 2008). Indeed, megalopae of this species have been collected at vent sites (e.g., Epifanio et al., 1999; Dittel et al., 2005). A megalopa tentatively assigned to *G. yunohana* was also collected at a vent site (Ono et al., 1996). In the present study, megalopae survived for a maximum of 60 d at 27.0-30.0°C, but they did not metamorphose and showed no sign of moulting to the first crab stage. Epifanio et al. (1999) reported a similar phenomenon while rearing megalopae of *B. thermydron* collected from the wild. Although it is possible that megalopal development requires several more months of larval development (Epifanio et al., 1999), the specific environment at vent sites could serve as cues for megalopal larvae to progress their moulting cycle and metamorphose into the first crab stage. We can now culture the larvae of *G. yunohana*, allowing future studies to prepare experimental animals to examine the environmental cues that stimulate the moulting cycle of the megalopae. These studies will greatly contribute to our understanding of the biology and ecology of larval dispersal and recruitment in bythograeid crabs.

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