Cah. Biol. Mar. (2006) 47 : 353-357

# Dispersal of vent-barnacle (genus *Neoverruca*) in the Western Pacific

Hiromi WATANABE[1], Ryusuke KADO[2], Moehiro KAIDA[2],
Shinji TSUCHIDA[3] and Shigeaki KOJIMA[1]
(1) *Ocean Research Institute, University of Tokyo, 1-15-1 Minamidai, Nakano, Tokyo 164-8639, Japan.*
*Fax: +81-3-5351-6470. E-mail: hwatanabe@ori.u-tokyo.ac.jp*
(2) *School of Fisheries Sciences, Kitasato University, 160-4 Okkirai, Sanriku, Ofunato, Iwate 022-0101, Japan.*
*Fax: +81-192-44-2125. E-mail: rukado@kitasato-u.ac.jp*
(3) *Extremobiosphere Research Center, Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushima, Yokosuka 237-0061, Japan. Fax: +81-46-867-9558. E-mail: tsuchidas@jamstec.go.jp*

**Abstract:** Dispersal of vent endemic animals is important in elucidating their evolution and adaptation to vent fields. Vent barnacles belonging to the family Neoverrucidae are widely distributed and abundant in Western Pacific vent fields. Larvae of these barnacles are relatively easy to rear under atmospheric pressure. Temperature stimulation, which is an important factor to control dispersal and settlement of the larvae of vent animals, was examined for larvae of *Neoverruca* sp. collected from the Myojin Knoll, off southeast Japan, to elucidate dispersal of this barnacle. The larvae were reared under three temperature conditions: 4°C, 10°C and 25°C. The larvae reared at 25°C died before metamorphosing into cyprids. This result suggests that larvae of *Neoverruca* sp. cannot disperse by means of high-temperature surface currents. Larvae reared at 10°C were successfully reared until the cyprid stage. The length of their larval period was significantly shortened compared to 4°C conditions when larvae stayed for more than a year in the cyprid stage. These results suggest that larvae of *Neoverruca* sp. can change their planktonic dispersal periods depending on temperature. This ability may allow them either to maintain populations within warm vent areas or to disperse long-distances in cold deep-sea water.

*Keywords*: Vent barnacle • *Neoverruca* • Dispersal • Hydrothermal vent • Western Pacific

## Introduction

Hydrothermal vent fields are unstable environments in the ocean, as they are ephemeral and distributed intermittently on the seafloor. Animal communities in vent fields consist of many vent-endemic species. To avoid extinction with the inevitable end of hydrothermalism, such vent endemic species must constantly disperse and settle on active vent fields. As most vent animals are benthos, dispersal is mainly limited to larval periods. Therefore, larval characteristics of vent animals are considered to be important in their dispersal. There are two main approaches to investigate larval dispersal of vent species: larval ecological studies and population genetic studies. In recent years, larval characteristics of some vent animals have been revealed by pressurized or non-pressurized rearing experiments

(Epifanio et al., 1999; Tyler & Dixon, 2000; Pradillon et al., 2001) and genetic population analyses (e.g. Hurtado et al., 2004). These larval studies suggest that temperature is an important factor in dispersal and settlement of larvae. The molecular studies suggest that transform faults, cross-axis flow and topographic depressions are dispersal barriers for some vent endemic species. Most studies on the dispersal of vent animals have been carried out at either the East Pacific Rise (EPR) or the Mid-Atlantic Ridge (MAR). Most hydrothermal vents in the Western Pacific, which are distinguished as different biogeographical regions from the EPR and the MAR (Van Dover et al., 2002), are located on arcs and in backarc basins, while most vents in EPR and MAR are located on ridges. Therefore, the factors restricting larval dispersal are expected to differ between these two tectonic systems.

Vent endemic barnacles of the family Neoverrucidae are widely distributed in the Western Pacific hydrothermal vent fields extending from the Lau Basin in the South to the Myojin Knoll in the North (Fig. 1). In the same way as other crustaceans, neoverrucid barnacles copulate and brood their eggs until hatching. Furthermore, they are sessile organisms and their dispersal-mediated gene flow is restricted to planktonic larval stages. Therefore, the neoverrucid barnacle is suitable to study the gene flow among populations and the dispersal process by using their planktonic larvae.

In a previous study, we successfully reared larvae of *Neoverruca* sp. under 4ºC and atmospheric pressure conditions (Watanabe et al., 2004). From this study, the larvae exhibited long planktonic periods extending to 108 days in average. The naupliar period of the last (sixth) instar was approximately four times longer than that of the fifth instar, whereas generally the last naupliar periods are twice as long as the former naupliar periods (Kado, 1982). Such a long larval period is considered to be unfavorable for the larvae to settle in the same vent field as inhabited by their parents in order to maintain the source population.

In this study, we focused on temperature conditions which are thought to play an important role in larval dispersal characteristics, and examined the effects of rearing temperature on the larvae of *Neoverruca* sp. Based on the comparison of durations and survival rates among larvae under various temperature conditions, the larval dispersal process of *Neoverruca* sp. among hydrothermal vent fields in the Western Pacific is discussed.

## Materials and Methods

During Dive#185 of Remotely Operated Vehicle (ROV) *HyperDolphin* of Japan Agency of Marine-Earth Science and Technology (JAMSTEC), adults of *Neoverruca* sp. were collected from the Myojin Knoll hydrothermal vent field (32°06'N, 139°52'E; depth 1290 m) on the Izu-Ogasawara Arc, off southeast Japan. Thirty-two larvae of *Neoverruca* sp. were collected from laboratory aquarium in which adult *Neoverruca* sp. were kept. Larvae were divided into three groups and reared under the following temperature conditions: 4°C, 10°C and 25°C. All larvae were kept in 12-well microplates (3810-0012, IWAKI Co., Tokyo) individually with 4 ml of filtered seawater (34.5 in salinity). The water was replaced every two days and, at the same time, instars of the larvae were checked and molts were collected.

Difference in durations of each larval period and survival rates among temperature groups were tested with a rank test (as mentioned in the results, the highest temperature group could not develop until cyprid larvae and Mann-Whitney's *U*-test was employed).

## Results

The duration of each larval period of each rearing group is shown in Table 1. The larvae did not reach the cyprid stage under 25°C and thus are not shown in Table 1. Comparisons of durations of periods and survival rates were conducted between groups reared at 4°C and 10°C (Table 1). Except for the first two naupliar periods, durations of larval periods significantly decreased in the group reared under 10°C conditions. Although the differences between durations were relatively small (3.59 - 5.95 days on average) during the third to the fifth naupliar instars (N3-N5), in the sixth naupliar instar, the difference in durations was up to 37 days on average.

The survival rate between groups reared at 4°C and 10°C conditions were similar (from 41.18 to 82.35% during N2-N6 periods). Under 4°C conditions, larvae survived for more than a year after metamorphosizing into cyprids, although all cyprids died within several months under 10°C. All cyprid larvae developed in the present rearing experiments indicated abnormal morphology, which is very similar to results observed in Watanabe et al. (2004).

## Discussion

Since the larvae of *Neoverruca* sp. can survive for a long period without effect by the hydrothermal fluid, they are able to disperse through the ordinary oceanic environment as well as within the vent fields (Watanabe et al., 2004). However, the present results indicate that the larvae of *Neoverruca* sp. can not survive in high temperatures (at least 25°C and above), therefore it seems that they can not disperse by high-temperature surface currents. Our previous molecular study revealed that genetic differentiations exist between populations of *Neoverruca* sp. in the

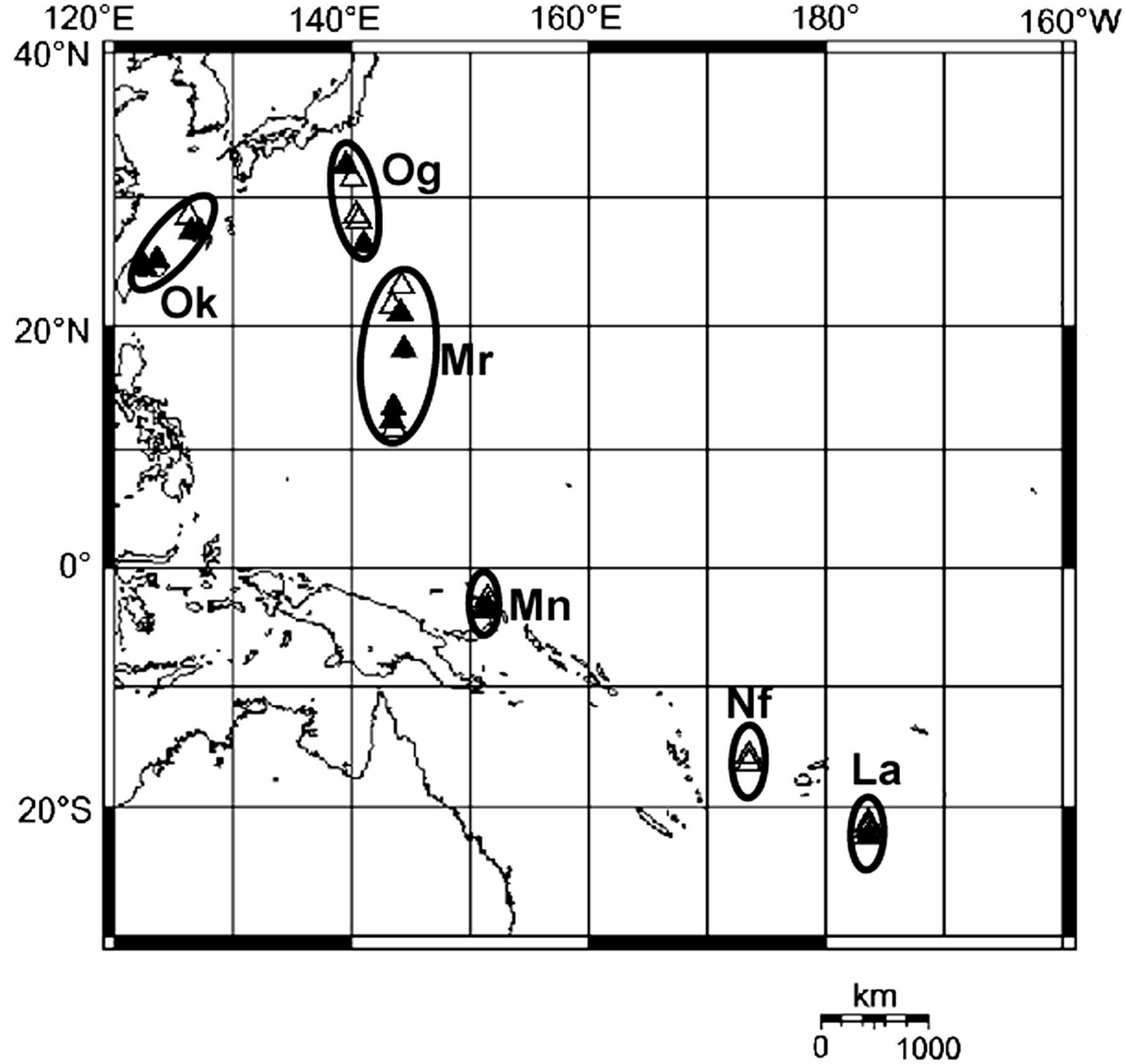


**Figure 1.** Distribution of hydrothermal vent fields in the Western Pacific. ▲: hydrothermal vent fields where neoverrucid barnacles have been reported; △: hydrothermal vent fields where neoverrucid barnacles have not been reported. Ellipses denote the hydrothermal vent regions as follows: Og, Izu-Ogasawara Arc; Ok, Okinawa Trough; Mr, Mariana Trough; Mn, Manus Basin; Nf, North Fiji Basin and La, Lau Basin.

**Figure 1.** Distribution des sources hydrothermales dans la zone ouest Pacifique. ▲: sources hydrothermales où les balanes neoverrucidae ont été signalées; △: sources hydrothermales où les balanes neoverrucidae n'ont pas été signalées. Les ellipses définissent les régions des sources hydrothermales : Og, Izu-Ogasawara Arc; Ok, Okinawa Trough; Mr, Mariana Trough; Mn, Manus Basin; Nf, North Fiji Basin et La, Lau Basin.

Izu-Ogasawara Arc (including the Myojin Knoll) and the Okinawa Trough (Watanabe et al., 2005). Thus, these two neoverrucid populations around Japan appear to be isolated from each other although they may have a long enough planktonic period to have dispersal between these two populations. Molecular analyses also suggest that neoverrucid populations in the Mariana Trough and the Manus Basin are also isolated from each other, as well as from those in Japanese waters (Watanabe et al., unpublished data). Therefore, a common mechanism might be behind the isolation of neoverrucids within single backarc basins.

Most hydrothermal vents in the Western Pacific are located in backarc basins (Fig. 1). Backarc basins, which are formed in association with island arcs, are topographic depressions along island arcs. The displacement of larvae of vent endemic animals from these topographic depres-

**Table 1.** Comparison of durations (days) of each larval instar between rearing group.
**Tableau 1.** Comparaison des durées (jours) de chaque stade larvaire élevé respectivement à 4 et 10°C.

| Instar | 4ºC | | | | 10ºC | | | | *P* value of *U*-test |
|---|---|---|---|---|---|---|---|---|---|
| | mean duration (days) | SE | *N* | survival rate (%) | mean duration (days) | SE | *N* | survival rate (%) | for durations |
| N1 | - | - | 15 | 100.00 | 3.41 | 0.81 | 17 | 100.00 | - |
| N2 | 10.40 | 0.62 | 12 | 80.00 | 9.21 | 1.01 | 14 | 82.35 | $P > 0.05$ |
| N3 | 10.36 | 0.24 | 10 | 66.67 | 6.77 | 1.33 | 13 | 76.47 | $P < 0.01$ |
| N4 | 12.91 | 0.41 | 10 | 66.67 | 8.38 | 1.19 | 13 | 76.47 | $P < 0.01$ |
| N5 | 15.50 | 0.56 | 10 | 66.67 | 9.55 | 1.03 | 11 | 64.71 | $P < 0.01$ |
| N6 | 50.00 | 0.76 | 10 | 66.67 | 13.00 | 1.57 | 7 | 41.18 | $P < 0.01$ |
| Total | 99,17 | 0.68 | 10 | - | 50,32 | 3.40 | 7 | - | $P < 0.01$ |

sions in the absence of a strong buoyant flow, such as megaplume, is considered to be a rare event. Since arcs are formed as a topographic rise and they sometimes form an archipelago (e.g. the Ryukyu Archipelago), larvae of vent animals must be exposed to shallow-water environments with low hydrostatic pressure and high temperature when they disperse out of the backarc basins. The survival of the larvae of *Neoverruca* sp. at surface-water temperature near vent fields is considered to be difficult as their habitats are located in the subtropics and tropics. Even if larvae survive in the surface layer, the length of their planktonic periods is decreased by high water temperatures. Therefore, under present oceanic conditions, larvae most likely metamorphose into cyprids and die prior to possible migration to other backarc basins.

Under 4°C conditions, larvae can survive more than a year. This is the longest survival period recorded among known barnacle larvae. Since the larvae can survive for a long period of time without being affected by hydrothermal fluid, they are able to disperse through the ordinary oceanic environment unless temperatures become higher than 4°C. On the other hand, the length of the larval period decreases to approximately 50 days at 10°C. This reduction of duration is most remarkable in the last naupliar period (N6 instar), which was shortened 37 days on average from 4°C to 10°C conditions. At 10°C, the duration of the sixth instar was approximately 1.3 times longer than the one of the former (N5) naupliar period, similar as in other most barnacles (Kado, 1982).

With regard to the hydrothermal vent fields, Kim & Mullineaux (1998) have suggested two main flow systems for larval dispersal: the buoyant plume flow and near-bottom current. The former rises from the hydrothermal vent due to its buoyancy and spreads horizontally within the layer where the hydrothermal plume has a neutral buoyancy (believed to be a few hundred meters above the sea floor), thereby facilitating larval dispersal to other vent fields. The latter is driven by the plume flow and circulates in the vicinity of the hydrothermal vent fields, thereby facilitating population maintenance via recruitment of the larvae to the source population. When larvae of *Neoverruca* sp. were caught in the buoyant plume flow, they were transported outside of the hydrothermal vent field where the water temperature was lower (2°C-5°C) than that in the hydrothermal vent field (Van Dover, 2000). Therefore, under lower temperature conditions, larvae extend their planktonic larval periods, and this enables them to disperse over a longer distance. On the other hand, when larvae are transported by the near-bottom current, they remain in the immediate vicinity of the original hydrothermal vent field, and length of their planktonic larval periods are thus decreased due to the high temperature (4°C-10°C); this facilitates settling within the vent field inhabited by their source population. Thus, the temperature-dependent variations in the length of the planktonic larval period of *Neoverruca* sp. play an important role in larval dispersal and population maintenance in hydrothermal vent fields.

In the Western Pacific, some vent animals are endemic to a single backarc basin. For example, the galatheid crab *Shinkaia crosnieri* (Baba & Williams, 1998) is endemic only to the Okinawa Trough, and hairy gastropods of *Alviniconcha* are genetically deviated among some backarc basins (Kojima, 2002). It appears that these vent animals have restricted dispersals to arcs surrounding backarc basins. However, this does not apply to all vent animals in the Western Pacific. For example, genetic divergence has not been detected between *Bathymodiolus* populations inside and outside of the Okinawa Trough (Miyazaki et al., 2004). The larvae of *Bathymodiolus* are presumed to have planktotrophic larvae (Tyler & Young, 1999), which are thought to be able to disperse long distances. On the other hand, although vesicomyid clams are thought to be lecithotrophic larvae (Tyler & Young, 1999), some vesicomyid species showed little genetic difference between distant areas (e. g. Kojima et al., 2004). Lecithotrophic larvae which hatched from large yolky eggs are believed to have little dispersal ability (e.g. Gage & Tyler, 1991). However, the present study suggests that dispersal of lecithotrophic larvae of *Neoverruca* sp. is restricted due to their low tolerance for temperature. In addition to larval type, physiological characteristics of larvae are also important as a determinant of the dispersal abilities of vent animals.

In summary, larval dispersal patterns and genetic differentiations are variable with various combinations of type of larval dispersion and topographic features of their habitats. Most hydrothermal vent fields in the Eastern Pacific and the Atlantic Ocean are distributed along mid-ocean ridge axes, where transform faults, cross-axis flows and topographic depressions are dispersal barriers for some vent endemic species. In the backarc basins of the Western Pacific, the present study shows that arcs act as dispersal barriers for vent barnacles that have a low tolerance for high temperature.

### Acknowledgements

We greatly appreciate the operation team of the ROV "*HyperDolphin*"; the crew of the R/V *Natsushima*; the members of the Laboratory of Marine Primary Production, Kitasato University; Benthos Laboratory, Ocean Research Institute, University of Tokyo; the Research Program for Marine Biology and Ecology, Japan Agency for Marine-Earth Science and Technology (JAMSTEC); and especially for Dr. James Reimer in JAMSTEC and Prof. W. A. Newman in Scripps Institution of Oceanography, who encouraged and gave us much useful advice. This study was supported by the Ministry of Education, Culture, Sports, Science and Technology of Japan (No. 12NP0201), and the Research Institute of Marine Invertebrates Foundation (Tokyo, Japan) provided funds for conducting this study.

## References

**Epifanio C.E., Perovich G., Dittel A.I. & Cary S.C. 1999.** Development and behavior of megalopa larvae and juveniles of the hydrothermal vent crab *Bythograea thermydron*. *Marine Ecology Progress Series*, **185**: 147-154.

**Gage J.D. & Tyler P.A. 1991.** *Deep-sea biology. A natural history of organisms at the deep-sea floor.* pp. 504. Cambridge University Press, Cambridge.

**Hurtado L.A., Lutz R.A. & Vrijenhoek R.C. 2004.** Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. *Molecular Ecology*, **13**: 2603-2615.

**Kado R. 1982.** Ecological and taxonomical studies on the free-living nauplius of barnacles (Crustacea, Cirripedia). *PhD thesis, University of Tokyo, Tokyo, Japan.* (Japanese text with English figures and tables).

**Kim S.L. & Mullineaux L.S. 1998.** Distribution and near-bottom transport of larvae and other plankton at hydrothermal vents. *Deep-Sea Research II*, **45**: 423-440.

**Kojima S. 2002.** Deep-sea chemosynthesis-based communities in the Northwestern Pacific. *Journal of Oceanography*, **58**: 343-363.

**Kojima S., Fujikura K. & Okutani T. 2004.** Multiple trans-Pacific migrations of deep-sea vent/seep-endemic bivalves in the family Vesicomyidae. *Molecular Phylogenetics and Evolution*, **32**: 396-406.

**Miyazaki J.I., Shintaku M., Kyuno A., Fujiwara Y., Hashimoto J. & Iwasaki H. 2004.** Phylogenetic relationships of deep-sea mussels of the genus *Bathymodiolus* (Bivalvia: Mytilidae). *Marine Biology*, **144**: 527-535.

**Pradillon F., Shillito B., Young C.M. & Gaill F. 2001.** Developmental arrest in vent worm embryos. *Nature*, **413**: 698-699.

**Tyler P.A. & Young C.M. 1999.** Reproduction and dispersal at vent and cold seeps. *Journal of the Marine Biological Association of the United Kingdom* **79**: 193-208.

**Tyler P.A. & Dixon D.R. 2000.** Temperature/pressure tolerance of the first larval stage of *Mirocaris fortunata* from Lucky Strike hydrothermal vent fields. *Journal of the Marine Biological Association of the United Kingdom*, **80**: 739-740.

**Van Dover C.L. 2000.** *The ecology of deep-sea hydrothermal vents*. Princeton University Press, New Jersey.

**Van Dover C.L., German C.R., Speer K.G., Parson L.M. & Vrijenhoek R.C. 2002.** Evolution and biogeography of deep-sea vent and seep invertebrates. *Science*, **295**: 1253-1257.

**Watanabe H., Kado R., Tsuchida S., Miyake H., Kyo M. & Kojima S. 2004.** Larval development and intermoult period of the hydrothermal vent barnacle *Neoverruca* sp. *Journal of the Marine Biological Association of the United Kingdom*, **84**: 743-745.

**Watanabe H., Tsuchida S., Fujikura K., Yamamoto H., Inagaki F., Kyo M. & Kojima S. 2005.** Population history associated with hydrothermal vent activity inferred from the genetic structure of neoverrucid barnacles around Japan. *Marine Ecology Progress Series*, **288**: 233-240.