JARQ 44 (4), 375 – 382 (2010) http://www.jircas.affrc.go.jp

REVIEW

Reproduction and Early Life Ecology of Abalone *Haliotis diversicolor* in Sagami Bay, Japan

Toshihiro ONITSUKA[1,3]*, Tomohiko KAWAMURA[1] and Toyomitsu HORII[2]

[1] Ocean Research Institute, The University of Tokyo (Nakano, Tokyo 164–8639, Japan)
[2] National Research Institute of Fisheries Science, Fisheries Research Agency
(Yokosuka, Kanagawa 238–0316, Japan)

Abstract

Studies on the reproduction and early life ecology of an abalone, *Haliotis diversicolor*, are reviewed, especially focusing on the results of our recent field and laboratory studies in Sagami Bay, Japan. Our four-year monitoring of the occurrence of newly settled post-larvae and changes in adult gonads clearly indicates that the spawning of *H. diversicolor* in Sagami Bay was triggered by typhoon events with large-scale storms. The abalone could spawn at least twice in a single spawning season, but required an interval of at least 1 month between spawning events. The proportion of adults releasing gametes and the amount of released eggs/sperms from each individual tended to increase on the spawning events occurring later in a spawning season. Higher mortality rates of post-larvae and early juveniles were detected at places which had greater water turbulences and more frequent stone overturning caused by storms. A storm event caused by a typhoon appears to be a necessary cue triggering the synchronous spawning of *H. diversicolor*, but the violent water turbulence and overturning of stones caused by storms negatively affect the post-settlement survival. Cohorts experiencing lower seawater temperatures due to the later settlement in the spawning season tended to have a slower growth rate than those experiencing higher temperatures, suggesting the temperature-dependent growth of post-larval *H. diversicolor.* The timing of typhoon-triggered spawning in *H. diversicolor* was suggested to be an important factor affecting the growth and survival and eventual recruitment of the abalone.

Discipline: Fisheries
Additional key words: growth, post-larval abalone, settlement, spawning cue, survival

Introduction

Haliotis diversicolor is a relatively small abalone species (about 10 cm in the maximum shell length) that inhabits shallow subtidal areas in subtropical and temperate zones of the western North Pacific; southern Japan, southern Korea, Taiwan, and southern China[6]. In these countries, this species is an important fishery resource and a major target of aquaculture. In Japanese coastal waters, the reseeding of hatchery-reared *H. diversicolor* juveniles into wild populations has also been conducted for a long time, but the total catch of the species has been rapidly declining since the late 1980s. In general, the primary reason for the decrease in catch of abalone species in Japan has been considered to be poor recruitments in their natural habitats. This has presumably resulted mainly from too low densities of adult abalone for the successful reproduction due to longtime overfishing, and/or low survivals in the early life stages due to inappropriate environments in their nursery habitats[13,14]. To restore abalone stocks, natural recruitments need to be enhanced by appropriate stock management based on the reproductive and ecological characteristics of each abalone species, together with the reseeding of hatchery-reared juveniles. However, studies on reproduction and early life ecology of wild abalone, which include *H. diversicolor*, had been limited. Understanding processes of reproduction and recruitment of each abalone species and factors affecting those processes in the natural environment is

---

Present address:
[3] Hokkaido National Fisheries Research Institute, Fisheries Research Agency (Kushiro, Hokkaido 085–0802, Japan)
* Corresponding author: e-mail onitsuka@affrc. go. jp

Received 22 October 2009; accepted 14 January 2010.

important to improve the methods of reseeding of hatchery-reared abalone and to manage natural abalone stocks. Since 2001, therefore, we have been studying the adult maturation and spawning processes, larval and post-larval ecology of *H. diversicolor* in Sagami Bay, Japan, by both field observations and laboratory experiments. In this article, we review the previous studies on the reproduction and early life ecology of *H. diversicolor*, especially focusing on our recent studies in Sagami Bay.

In this paper, the transition from the post-larval to the juvenile stage in *H. diversicolor* is defined as the size at which the first respiratory pore is sealed [~2.5 mm in shell length (SL)[26]], following the definition for *H. discus hannai*[38]. Individuals smaller than 500 µm SL, within a week after settlement, are defined as newly settled post-larvae, and individuals larger than 35 mm SL, which are expected to have a mature gonad[22], are defined as adults.

Maturation process

The maturation processes of abalone are controlled by the water temperature, photoperiod and food conditions[45]. Therefore, the timing when abalone becomes possible to spawn is different among years or areas. The spawning season of *H. diversicolor* is between June and November at Honshu Island in Japan[22,24]. The ovary of *H. diversicolor* before spawning events has two oocyte cohorts; the primary cohort consists of well-developed oocytes and the secondary cohort consists of oocytes of early developmental stages[24]. The oocyte composition of the ovary is similar to that in *H. asinina*[8] and *H. discus hannai*[5,44], in which the secondary cohort begins to mature immediately after the primary cohort is released. The secondary cohort is ready to be spawned after at least 2 weeks at about 26°C in *H. asinina*[8], and after about 1 month at 20°C in *H. discus hannai*[5]. In the wild *H. diversicolor* in Sagami Bay, a new cohort of oocytes began to develop shortly after the previous oocyte cohort was spawned, and the secondary cohort was ready to be spawned after approximately 1 month, indicating that *H. diversicolor* requires an interval of at least 1 month between spawning events[24].

Spawning

Abalone are dioecious broadcast spawners. Eggs must encounter a high density of sperm within a short period of time after release to be fertilized[1]. Consequently, the synchronous spawning of neighboring males and females induced by distinctive external cues is important for the successful fertilization. The limited data available for abalone provide conflicting evidence regarding spawning cues. *Haliotis discus hannai* larvae are detected primarily after typhoons or minor storms[33] while *H. kamtschatkana* and *H. rubra* are suggested to spawn during calm periods[2,30]. Tanaka[43] concluded that sudden temperature changes induced the spawning of *H. discus discus*, *H. madaka* and *H. gigantea*, while the spawning of *H. asinina* appears to be triggered by the lunar cycle and/or tidal amplitude[4]. From our results, the spawning of *H. diversicolor* in Sagami Bay is strongly associated with typhoon events[24]. In Sagami Bay from 2001 to 2004, the occurrence of newly settled post-larval *H. diversicolor* was strictly limited to the periods just after typhoons passed (Fig. 1). The gonad index of both males and females also decreased only after typhoon events. The mature adult *H. diversicolor* experienced various changes in the seawater temperature, tidal height and lunar phase, but the evidence of spawning corresponding with those environmental changes was not found. Larvae of *H. discus hannai* often appeared following minor storms, as well as typhoons[33], but occurrences of newly settled *H. diversicolor* were not observed after minor storms. Unlike other abalone species studied to date, the spawning of *H. diversicolor* in Sagami Bay appears to be triggered only by typhoon-scale storms.

The maximum amount of gametes released from a population in a spawning event is determined both by the total number of mature adults and by the amount of eggs/sperms released from each individual. For *H. diversicolor* inhabiting Sagami Bay, the amount of released eggs/sperms from adults tended to increase on the spawning event occurring later in the spawning season (Fig. 2). Consequently, the timing of typhoon passage is an important factor varying the quantities of released gametes (Fig. 2) and then affecting the post-settlement survival and growth by changing physical and biological environmental conditions experienced by the abalone as discussed in detail below.

Larval settlement

In natural habitats, abalone larvae preferentially settle on crustose coralline algae (CCA), and grow on the CCA habitat for at least several months. The rapid larval attachment and metamorphosis induced by CCA have been previously shown for many abalone species[15,31]. The settlement of *H. diversicolor* is also induced by CCA[28]. It is considered that specific chemical materials secreted from CCA may induce the settlement of abalone larvae, but the chemical substances have not yet been completely identified. Other chemical materials such as the gamma-aminobutyric-acid (GABA) also induce the abalone settlement. However, these materials have weaker and un-

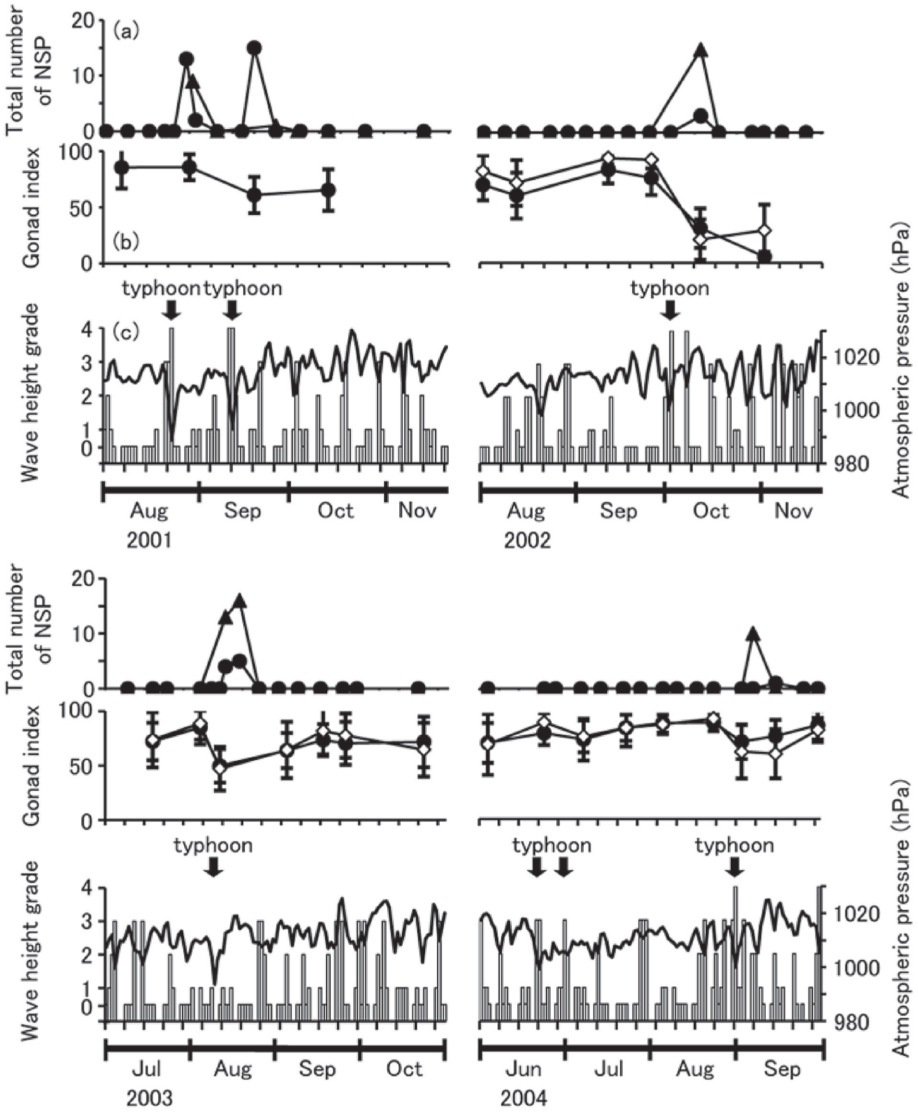

Fig. 1. The occurrence of newly settled post-larvae (NSP), changes in the gonad index (GI) of adult *H. diversicolor* and environmental factors in Sagami Bay from August to November 2001, August to November 2002, July to October 2003, and June to September 2004

(a): The total number of NSP collected at each of two locations in Sagami Bay. (b): The mean GI of adult abalone. GI was calculated as the ratio of the diameter of the gonad (excluding the digestive organ) to the diameter of the cross section at 1 cm from the tip of the gonad portion following the method of Ino & Harada[7]. Males and females are indicated by ● and ◇, respectively. Error bars indicate standard deviation. (c): The wave height grade (white box) and atmospheric pressure (solid line). Wave height grades were defined as: 0, calm sea; 1, little ground swell; 2, ground swell; 3, a few white-crested waves by a south wind; and 4, many white-crested waves by a strong south wind.

stable potency of inducing the abalone settlement compared to CCA[31], and the metamorphosis of *H. diversicolor* is not induced by GABA[3,16].

The abalone settlement is also affected by the species composition and density of microalgae such as benthic diatoms. Sessile organisms and microalgae covering the CCA surface often prevent larval abalone from metamorphosing[15,31]. Another possible factor inhibiting the abalone settlement is deposited sediments on settlement substrata. In Sagami Bay, densities of the newly settled *H. diversicolor* were lower in a thickly-sedimented area than in a thinly-sedimented area[28]. In a laboratory experiment using two substances (kaolin and clamshell powder) with different physical properties, the metamorphosis rate of *H. diversicolor* decreased as the sediment thickness on CCA increased in both the kaolin and clamshell powder treatments (Fig. 3). Then, larvae were trapped by the kaolin with a sticky property and most could not metamorphose successfully, but there were no larvae trapped by the clamshell powder[28]. These results indicate that the settlement of larval *H. diversicolor* in the natural habitat is influenced by the quantities and physical properties (stickiness and grain size) of the sediments deposited on CCA surfaces.

In the absence of the correct chemical cues, the larval metamorphosis is delayed[32,39]. In lecithotrophic abalone larvae, prolonged larval periods deplete the nutrient stores found in the egg yolk, leading to the nutritional stress and decreased the post-larval survival and growth. In *H. discus hannai*[39] and *H. iris*[32], the delayed larval metamorphosis has negative effects on the post-settlement survival and growth. If the larvae of these species undergo metamorphosis within approximately 2 weeks of fertilization, however, the resulting post-larvae are able to survive and grow normally if provided with an appropriate and sufficient diet. Similar negative effects by delaying metamorphosis were observed for *H. diversicolor*. However, larval *H. diversicolor* is more susceptible to the detrimental effects of delayed metamorphosis than *H. discus hannai* and *H. iris*[29].

Post-settlement survival and growth

Following settlement, *H. diversicolor* in Sagami Bay appears to grow on CCA surfaces at least for several months. The mortality of *H. diversicolor* in their natural habitats in Sagami Bay was highest during the initial month following settlement, and low from 6 to 9 months after settlement (Fig. 4)[27].

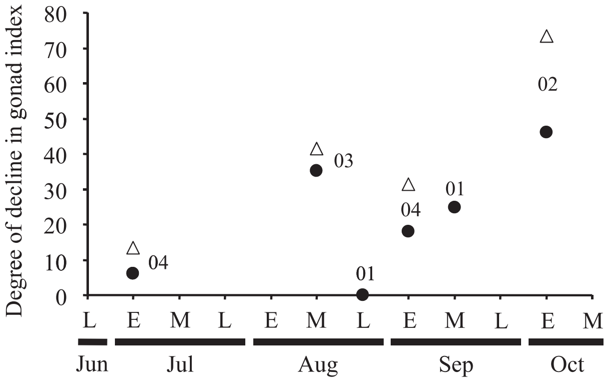

Fig. 2. The relationship between the timing of spawning and the degree of decline in the gonad index (GI) after each spawning event of *H. diversicolor* in Sagami Bay from 2001 to 2004

The degree of decline in GI is shown as the difference in GI between pre-spawning and post-spawning. ● and △ indicate males and females, respectively. Each number indicates the year of each spawning event. E: early in the month, M: middle in the month, L: late in the month.

Growth rates of post-larval *H. diversicolor* in Sagami Bay were 35–62 µm day^{-1} during a month following settlement[27]. However, the post-larval growth rates differed among the cohorts appearing in between 2001 and 2004 in Sagami Bay. Cohorts experiencing lower seawater temperatures (18–22°C) due to the later settlement in a spawning season tended to have a slower growth rate than those experiencing higher temperatures (23–26°C), suggesting the temperature-dependent growth of wild post-larval *H. diversicolor*[27].

Growth rates of post-larval *H. diversicolor*, which were reared in aquaria under ambient seawater temperatures (23.5–29.0°C) and fed on benthic diatoms, were ~80 µm day^{-1} during 30 days following settlement[46], which is higher than those in the natural habitat in Sagami Bay[27]. This difference may be due to the lower food availability

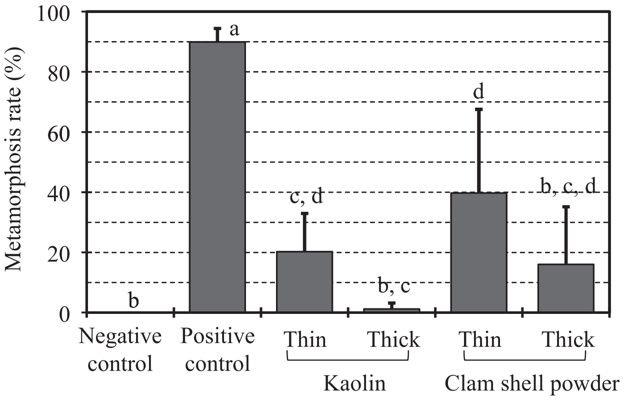

Fig. 3. The mean metamorphosis rate of larval *H. diversicolor* in the six treatments below

In all the treatments, larvae were placed in a Petri dish filled with the filtered seawater, with or without a CCA plate.

(1) without a CCA plate (negative control); (2) with a CCA plate (positive control); (3) with a CCA plate covered with a 20 µm thick kaolin coating (thin kaolin treatment); (4) with a CCA plate covered with a 100 µm thick kaolin coating (thick kaolin treatment); (5) with a CCA plate covered with a 20 µm layer of clamshell powder (thin clam shell powder treatment); and (6) with a CCA plate covered with a 100 µm thick layer of clamshell powder (thick clam shell powder treatment). Six replicates were assigned to each treatment. Different letters indicate that significant differences were detected among the treatments (Steel-Dwass test, $p < 0.05$). Error bars indicate standard deviation (N = 6).

in the natural habitat than in the culture condition.

Growths of the cohorts occurring in Sagami Bay in between 2001 and 2004 were monitored over a long period of time. The cohorts attained 17–40 mm SL in about 1 year after settlement. To estimate the size and age at the first stage of maturation, the increase in shell length and gonad development of a single cohort occurring in September 2001 were measured during ~2 years following settlement. This cohort attained 30–55 mm SL and showed a high gonad index at 22 months after settlement (Fig. 5), indicating the first stage of maturation of *H. diversicolor* is achieved at age 2[27].

Factors affecting post-settlement survival

Insufficient food availability, detachment by local water turbulence, predation, and low seawater temperatures in winter are considered as major factors reducing the abalone survival during the initial several months following settlement[11].

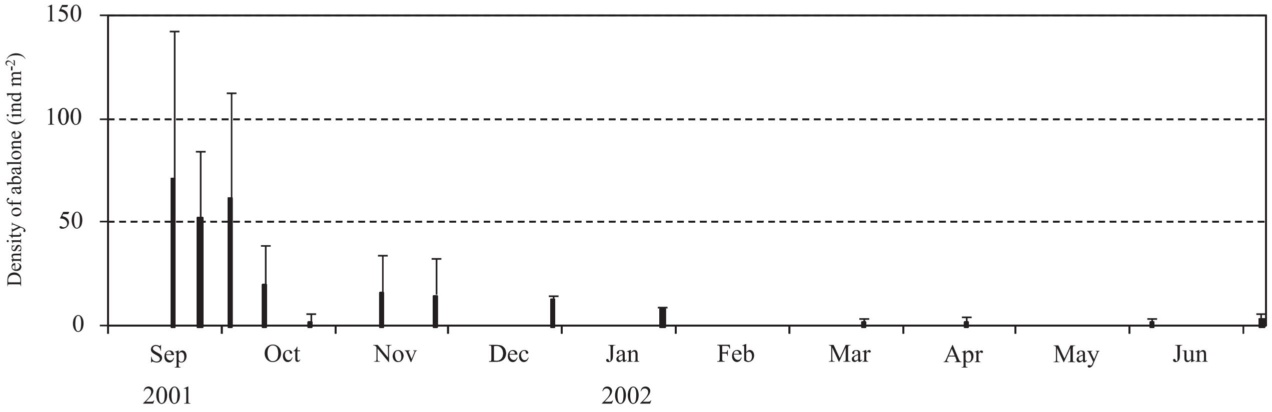

Fig. 4. Changes in density of a single cohort of *H. diversicolor* occurring in Sagami Bay in September 2001
Error bars indicate standard deviation.

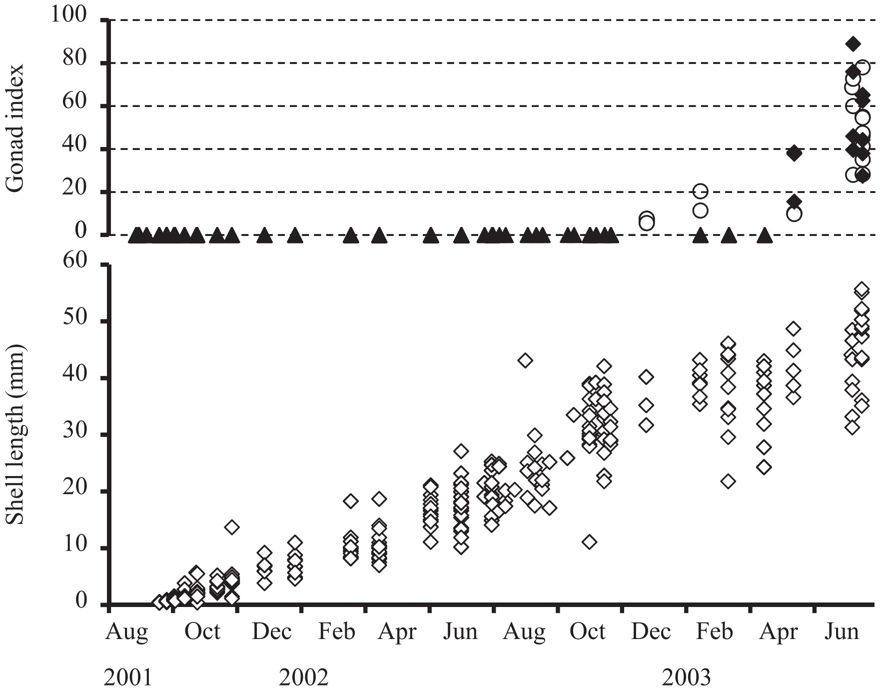

Fig. 5. Changes in gonad index (GI) and in shell length of a single cohort occurring in September 2001
The GI of males and females are indicated by ○ and ◆, respectively. Individuals of which sex could not be identified by their gonad color are indicated by ▲.

For *H. discus hannai*, three major changes in the feeding are identified in early life stages[9,40]. The first change, shifting from the lecithotrophy to the particulate feeding, occurs just after metamorphosis. Mucous materials, such as the diatom extracellular substances, are likely to be used as major nutritional sources in this initial period. As the next change, post-larvae attained to 600–800 µm SL become capable of digesting diatom cell contents and they grow more rapidly on efficiently digested diatoms. Mucous materials only are not able to sustain the favorable growth of this size of post-larvae. The final change consisted of a shift from the biofilm diet to the macroalgal diet. When post-larval abalone attain to ~1.8 mm SL, they are able to efficiently utilize juvenile macroalgae[41]. These transitions in the feeding habit are closely associated with ontogenetic changes in the digestive enzyme activity[36] and in the radula morphology[10]. Ontogenetic changes in the radula morphology of *H. diversicolor* are similar to those of *H. discus hannai*, suggesting that similar feeding transitions occur in *H. diversicolor* in early life stages[23]. Feeding experiments for *H. diversicolor* using some benthic diatoms as foods showed that particulate foods such as diatom extracellular substances were principally utilized from post-settlement to 800 µm SL, and diatom cell contents were required to produce rapid growths of larger post-larvae (> 800 µm SL). Moreover, the availability of each diatom for post-larval *H. diversicolor* is affected by the diatom morphology, attachment strength, frustule strength, and post-larval size[25]. Thus, standing crops of the highly-available diatoms, which are determined by the diatom multiplication rate and/or the grazing pressure by benthic animals[12], potentially influence the survival and growth of post-larval *H. diversicolor*. A laboratory experiment with post-larval *H. diversicolor* showed that post-settlement starvation of longer than 6 days dramatically depressed the subsequent survival rates[29], even if the larval metamorphosis was successful and rapid. Takami et al.[37] showed that survival rates of post-larval *H. discus hannai* were decreased by the food competition with *Homalopoma amussitatum*, which was a dominant small gastropod and a co-habitant with post-larval abalone in CCA habitats. Potential competitors for post-larval *H. diversicolor* in Sagami Bay were estimated by stable isotope analyses[47], but impacts of the food competition on the post-larval survival and growth has never been verified.

The local water turbulence is also one of the important factors affecting the survival of abalone in early life stages[21]. In our study in Sagami Bay, mortality rates of post-larval *H. diversicolor* were higher in the area with greater water turbulences and more frequent overturning of stones under storm events than in the area with weaker water movements[27]. While the storm event caused by a typhoon appears to be the necessary cue triggering the synchronous spawning of *H. diversicolor* as described above, the violent water turbulence and overturning of stones caused by storms negatively affect the survival of post-larval and juvenile abalone. Consequently, successive passages of typhoons in a spawning season may result in the failure of the abalone recruitment.

Predation is another important factor affecting the survival of post-larval and juvenile abalone. Post-larval and juvenile abalone in the wild are potentially preyed upon by various carnivorous animals, such as polychaetes[20], fishes[34,35], crabs[19,35], and starfishes[17]. The species composition and density of benthic animals (annelids, arthropods, cnidarians, echinoderms, and mollusks) were examined in habitats of *H. diversicolor* in Sagami Bay, and the trophic structure of each species or taxon was estimated using stable isotope analyses[47]. These results suggest that Muricidae gastropod species, sea urchins and polychaetes are potential predators for *H. diversicolor*. Especially, a Muricidae gastropod, *Ergalatax contractus* is the most dominant potential predator in Sagami Bay. However, there is no information about the impacts of the predation by those carnivores and omnivores on the survival of post-larval *H. diversicolor*.

In *H. discus hannai*, the low seawater temperature in winter is suggested to result in the high mortality of post-larvae and early juveniles[42]. The size attained by juveniles by the end of autumn appears to be an important factor determining their overwintering survival, since larger juveniles of *H. discus hannai* are less vulnerable to low temperatures[18,48]. Although the lowest winter water temperature in the areas which *H. diversicolor* inhabits (~12°C in Sagami Bay) is apparently higher than that of *H. discus hannai* (~5°C), low winter water temperatures may affect the post-larval and juvenile survival of *H. diversicolor*. The timing of settlement and subsequent growth rate influenced by the water temperature and/or food availability are regarded as potential factors controlling the overwinter mortality of *H. diversicolor*.

References

1. Babcock, R. & Keesing, J. (1999) Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. *Can. J. Fish. Aquat. Sci.*, **56**, 1668–1678.
2. Breen, P.A. & Adkins, B.E. (1980) Spawning in a British Columbia population of northern abalone, *Haliotis kamtschatkana*. *Veliger*, **23**, 177–179.
3. Bryan, P.J. & Qian, P.Y. (1998) Induction of larval attachment and metamorphosis in the abalone *Haliotis diversicolor* (Reeve). *J. Exp. Mar. Biol. Ecol.*, **223**, 39–51.
4. Counihan, R.T. et al. (2001) Pattern, synchrony and pre-

dictability of spawning of the tropical abalone *Haliotis asinina* from Heron Reef, Australia. *Mar. Ecol. Prog. Ser.*, **213**, 193–202.

5. Fukazawa, H. et al. (2007) Oogenesis and relevant changes in egg quality of abalone *Haliotis discus hannai* during a single spawning season. *Aquaculture*, **270**, 265–275.
6. Geiger, D. L. (1999) A total evidence cladistic analysis of the Haliotidae (gastropoda: vetigastropoda). Ph. D. Thesis, Univ. Southern California. pp.375.
7. Ino, T. & Harada, K. (1961) Spawning season of abalone in Ibaraki prefecture. *Bull. Tokai Reg. Fish. Res. Lab.*, **31**, 275–281 [In Japanese].
8. Jebreen, E. J. et al. (2000) Synchronous oogenesis during the semilunar spawning cycle of the tropical abalone *Haliotis asinina*. *J. Shellfish Res.*, **19**, 845–851.
9. Kawamura, T., Roberts, R. D. & Takami, H. (1998) A review of the feeding and growth of postlarval abalone. *J. Shellfish Res.*, **17**, 615–625.
10. Kawamura, T. et al. (2001) Radula development in abalone *Haliotis discus hannai* from larva to adult in relation to feeding transitions. *Fisheries Sci.*, **67**, 596–605.
11. Kawamura, T., Takami, H. & Saido, T. (2002) What are the factors determining abalone natural recruitment? *Kaiyo Monthly*, **34**, 529–534 [In Japanese].
12. Kawamura, T., Takami, H. & Yamashita, Y. (2004) Effect of grazing by a herbivorous gastropod *Homalopoma amussitatum*, a competitor for food with post-larval abalone, on a community of benthic diatoms. *J. Shellfish Res.*, **23**, 989–993.
13. Kawamura, T. & Takami, H. (2005) Ecology and recruitment fluctuations of abalone. *In* Living marine resources: How do they fluctuate in the ocean? ed. Watanabe, Y., Tokai University Press, Tokyo, Japan, 286–303 [In Japanese].
14. Kawamura, T. (2007) Stock management and enhancement of abalone species based on their ecological characteristics. *Kaiyo Monthly*, **39**, 240–247 [In Japanese].
15. Kawamura, T. (2007) Selective settlement of abalone larvae and its ecological implications. *Sessile Organisms*, **24**, 95–102 [In Japanese with English summary].
16. Liu, L. L. et al. (1986) Negative effect of gamma-aminobutyric-acid (GABA) on the settlement of larvae of the small abalone, *Haliotis diversicolor supertexta* Lischke. *Bull. Inst. Zool. Acad. Sin.*, **25**, 1–5.
17. McShane, P. E. & Naylor, J. R. (1997) Direct estimation of natural mortality of the New Zealand abalone, *Haliotis iris*. *N. Z. J. Mar. Freshw. Res.*, **31**, 135–137.
18. Miyamoto, T. & Nozawa, Y. (1996) The study of reproductive mechanism of abalone. *Sci. Rep. Hokkaido Hakodate Fish. Exp. Stn.*, 118–130 [In Japanese].
19. Mower, A. G. J. & Shepherd, S. A. (1988) The crab fauna of West Island, South Australia: their abundance, diet, and role as predators of abalone. *Trans. R. Soc. S. Aust.*, **112**, 83–86.
20. Naylor, J. R. & McShane, P. E. (1997a) Predation by polychaete worms on larval and post-settlement abalone *Haliotis iris* (Mollusca:Gastropoda). *J. Exp. Mar. Biol. Ecol.*, **214**, 283–290.
21. Naylor, J. R. & McShane, P. E. (1997b) Post-settlement survival of abalone (*Haliotis irs*, *H. australis*) in turbulent flows. *Moll. Res.*, **18**, 227–232.
22. Oba, T. (1964) Studies on the propagation of an abalone, *Haliotis diversicolor supertexta* Lischke – I. On the spawning habits. *Bull. Jpn. Soc. Sci. Fish.*, **30**, 742–748 [In Japanese with English summary].
23. Onitsuka, T. et al. (2004) Morphological changes in the radula of abalone *Haliotis diversicolor aquatilis* from post-larva to adult. *J. Shellfish Res.*, **23**, 1079–1085.
24. Onitsuka, T. et al. (2007) Synchronized spawning of abalone *Haliotis diversicolor* triggered by typhoon events in Sagami Bay, Japan. *Mar. Ecol. Prog. Ser.*, **351**, 129–138.
25. Onitsuka, T. et al. (2007) Dietary value of benthic diatoms for post-larval abalone *Haliotis diversicolor* associated with feeding transitions. *Fisheries Sci.*, **73**, 295–302.
26. Onitsuka, T. et al. (2007) Identification of juvenile abalone *Haliotis diversicolor* based on the number of open and sealed respiratory pores. *Fisheries Sci.*, **73**, 995–1000.
27. Onitsuka, T. et al. (2008) Survival, growth and recruitment of abalone *Haliotis diversicolor* in Sagami Bay, Japan. *J. Shellfish Res.*, **27**, 843–855.
28. Onitsuka, T. et al. (2008) Effects of sediments on larval settlement of abalone *Haliotis diversicolor*. *J. Exp. Mar. Biol. Ecol.*, **365**, 53–58.
29. Onitsuka, T. et al. (2010) Effects of delayed metamorphosis and delayed post-settlement feeding on post-larval survival and growth of the abalone *Haliotis diversicolor*. *Aquaculture*, **298**, 239–244.
30. Prince, J. D. et al. (1987) Experimental-Evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.*, **106**, 243–263.
31. Roberts, R. D. (2001) A review of settlement cues for larval abalone (*Haliotis* spp.). *J. Shellfish Res.*, **20**, 571–586.
32. Roberts, R. D. & Lapworth, C. (2001) Effect of delayed metamorphosis on larval competence, and post-larval survival and growth, in the abalone *Haliotis iris* Gmelin. *J. Exp. Mar. Biol. Ecol.*, **258**, 1–13.
33. Sasaki, R. & Shepherd, S. A. (1995) Larval dispersal and recruitment of *Haliotis discus hannai* and *Tegula* spp. on Miyagi Coasts, Japan. *Mar. Freshw. Res.*, **46**, 519–529.
34. Shepherd, S. A. & Turner, J. A. (1985) Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference and abundance and predators of Juveniles. *J. Exp. Mar. Biol. Ecol.*, **93**, 285–298.
35. Shibui, T. (1971) Experimental studies on the predatory animals of young abalone. *Bull. Jpn. Soc. Sci. Fish.*, **37**, 1173–1176 [In Japanese with English summary].
36. Takami, H., Kawamura, T. & Yamashita, Y. (1998) Development of polysaccharide degradation activity in postlarval abalone *Haliotis discus hannai*. *J. Shellfish Res.*, **17**, 723–727.
37. Takami, H. et al. (2001) Competition for food between postlarval abalone and two species of herbivorous gastropods. *Bull. Tohoku Natl. Fish. Res. Inst.*, **64**, 43–51 [In Japanese with English summary].
38. Takami, H. (2002) Studies on the feeding, growth and survival in early life stages of an abalone *Haliotis discus hannai*. Ph. D. Thesis, The Univ. Tokyo, pp.220 [In Japanese].
39. Takami, H., Kawamura, T. & Yamashita, Y. (2002) Effects of delayed metamorphosis on larval competence, and postlarval survival and growth of abalone *Haliotis discus hannai*. *Aquaculture*, **213**, 311–322.
40. Takami, H. & Kawamura, T. (2003) Dietary changes in the

abalone, *Haliotis discus hannai*, and relationship with the development of the digestive organ. *JARQ*, **37**, 89–98.

41. Takami, H. et al. (2003) When is the abalone *Haliotis discus hannai* Ino 1953 first able to use brown macroalgae? *J. Shellfish Res*., **22**, 795–800.
42. Takami, H. et al. (2008) Overwinter mortality of young-of-the-year Ezo abalone in relation to seawater temperature on the North Pacific coast of Japan. *Mar. Ecol. Prog. Ser*., **367**, 203–212.
43. Tanaka, K. et al. (1986) On the distribution of swimming and deposited larvae of nursery ground of abalone at the southern coast of Chiba prefecture. *Bull. Jpn. Soc. Sci. Fish*., **52**, 1525–1532 [In Japanese with English summary].
44. Tomita, K. (1967) The maturation of the ovaries of the abalone, *Haliotis discus hannai* Ino, in Rebun Island, Hokkaido, Japan. *Sci. Rep. Hokkaido Fish. Exp. Stn*. **7**, 1–7 [In Japanese with English summary].
45. Uki, N. & Kikuchi, S. (1984) Regulation of maturation and spawning of an abalone, *Haliotis* (Gastropoda) by external environmental-factors. *Aquaculture*, **39**, 247–261.
46. Washiyama, H. & Ishida, T. (1999) Growth of juvenile abalone *Haliotis diversicolor aquatilis* under cultivation. *Saibai gyogyo gijutsu kaihatsu kenkyu*, **27**, 53–57 [In Japanese].
47. Won, N-I. et al. (2007) Community and trophic structures of abalone (*Haliotis diversicolor*) habitat in Sagami Bay, Japan. *Fisheries Sci*., **73**, 1123–1136.
48. Yamaguchi, H. & Inoguchi, N. (1991) An experiment on the low water temperature tolerance of juveniles Ezo abalone. *Business Report of South Iwate Sea-Farming Centre*, 22–25 [In Japanese].