9 Distribution Expansion and Historical Population Outbreak Patterns of Crown-of-Thorns Starfish, *Acanthaster planci* sensu lato, in Japan from 1912 to 2015

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Abstract

The present chapter reviews the distribution and population outbreak records of the crown-of-thorns starfish, *Acanthaster planci* sensu lato, in Japan from 1912 to 2015. The literature survey suggests that *A. planci* sensu lato distribution has been extending northward since 1945 from Amami Oshima (its previous northernmost distribution) to Miyake Island and Goto Island. Genetic homogeneity within Japanese *A. planci* sensu lato populations indicates that larval dispersal has likely caused this poleward migration. Water temperatures have significantly increased in the temperate area of Japan, implying that global warming is partly responsible for this poleward migration. More frequent and intense population outbreaks in temperate areas were also observed, possibly in relation to increased water temperatures and successive larval dispersal from the south. Overall, complex and persistent patterns were observed for two major successive population outbreaks in Japan: from 1969 to 1991 and from 1995 to now. The evidence suggests that the western Okinawa populations are the most likely origin for secondary outbreaks within Japan. The Amami population is also likely to be an important source for outbreaks in temperate regions. However, no records of population outbreaks were found for least in two regions: Ogasawara and the Osumi Islands. Ogasawara is located approximately 1000 km south of the Kuroshio Current, so infestation via larval dispersal from other populations is more limited than in other Kuroshio regions. The Osumi Islands are, however, located in the middle of the Kuroshio Current, implying that insufficient corals are available for the growth of *A. planci* sensu lato or that unknown environment factors such as abundant predators of juvenile starfish suppress recruitment and juvenile survival.

Keywords

Crown-of-thorns starfish • Population outbreak • Genetic analysis • Mitochondrial DNA • Early life history • Microsatellite loci • Climate change • Larval dispersal • Global warming • Poleward migration

9.1 Introduction

9.1.1 *Acanthaster planci* sensu lato

Many detailed reviews are available about the biology and ecology of the crown-of-thorns starfish, *Acanthaster planci* sensu lato (e.g., Moran 1986; Birkeland and Lucas 1990; Pratchett et al. 2014). Therefore, I focus in the present chapter on reviewing key aspects of *A. planci* sensu lato

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associated with larval dispersal, drawing on information from Japanese-based literature and unpublished data to improve the understanding of previous population outbreak patterns in Japan. I was interested in the following three questions: (1) Is *A. planci* sensu lato migrating toward the north like other coral species? (2) Has the intensity of population outbreaks increased in recent years? (3) Is the western Okinawan population really the source of other population outbreaks in Japan?

9.1.2 Species Status

Currently, the genus *Acanthaster* contains five species in the Indo-Pacific Ocean, but only two official species names exist: (1) *A. brevispinus*, which is a single species, and (2) *A. planci* (East Indian Ocean species) and the others called *A. planci* sensu lato, which is a complex of three cryptic species (Haszprunar and Spies 2014).

Acanthaster planci **sensu lato**: *A. planci* is well-documented as a cause of coral-devastating population outbreaks in the Indian and Pacific Oceans (Pratchett et al. 2014). Vogler et al. (2008) showed that there are actually four closely related *A. planci* species complex. These four species include three genetically distinct species in the Indian Ocean and a single species in the Pacific Ocean, as determined by phylogenetic analysis using the mitochondrial CO1 region. One Indian Ocean *A. planci* lineage is distributed mainly in the western Indian Ocean, another lineage is mainly distributed in the Red Sea, and the last lineage is distributed in the eastern Indian Ocean. On Pari Island in northern Jakarta, the Pacific *A. planci* lineage (orange color morph) and eastern Indian Ocean *A. planci* lineage (purple color morph) are co-distributed (Yasuda et al. 2010). Although nuclear microsatellite analysis indicated distinct genotypes between the two *A. planci* lineages (*A. planci* and *A. planci* sensu lato) found on Pari Island and no intermediate color morphs were observed, one specimen had a mitochondrial haplotype incongruent with its color morph, implying that natural hybridization may have occurred between the two lineages in the past.

Acanthaster brevispinus: In contrast with *A. planci* species complex, *A. brevispinus* is relatively rare. The holotype specimen of *A. brevispinus* was collected at Sirun Island in the Philippines, with no subsequent documentation (Birkeland and Lucas 1990). In Japan, *A. brevispinus* was occasionally caught in lobster gill nets south of Wakayama between 2003 and 2005 (Saba and Iriyama 2002), and there was an initial report of *A. brevispinus* being detected in Sukumo (western Shikoku) during the removal of *A. planci* sensu lato in 2006 (Nakachi 2007), but there have been no subsequent reports. *A. brevispinus* was also collected in the Seychelles by Jangoux and Aziz (1984) in the western Indian Ocean. These reports imply that *A. brevispinus* is distributed in both the Indian (Seychelles) and Pacific Oceans (Japan, Philippines, and eastern Australia) but are seldom found (Birkeland and Lucas 1990). This huge difference in population density between *A. planci* species complex and *A. brevispinus* is surprising, given that *A. brevispinus* has a life cycle, fecundity, and spawning peak (Lucas and Jones 1976) similar to that of *A. planci* species complex. Unlike in the Great Barrier Reef (GBR, Australia), where *A. planci* sensu lato mainly appears around the reefs, while *A. brevispinus* is found in deeper lagoons, the habitat use of the two species partly overlaps to the south of Wakayama and in western Shikoku. Here, the total area is much smaller than that of the GBR, and the sea is shallow for some distance with a gentle slope from the shore. No real coral "reefs" exist in the temperate coral communities of Wakayama and Shikoku, but corals can be found in relatively shallow rocky areas near the shore. Corals, *A. planci* sensu lato, and *A. brevispinus* can thus be found in the same areas. Although *A. brevispinus* has never eaten corals in Australia (Lucas and Jones 1976), volunteer divers in Wakayama engaged in the control of *A. planci* sensu lato observed *A. brevispinus* digesting corals by baring its stomach, much like *A. planci* sensu lato. If *A. planci* and *A. brevispinus* with similar reproductive characteristics live in the same region and feed on the similar diet, differences between the two species (such as fertilization rates, larval behavior patterns, juvenile habitat use, and predators) should be examined to explain the difference in population density.

Acanthaster ellisii: Historically, the genus *Acanthaster* has contained three species separated by morphology: (1) *A. planci* species complex, found in the Indian Ocean and western and central Pacific Ocean (Pacific and Indian Ocean *A. planci* species complex was considered to be a single species), (2) *A. brevispinus*, and (3) *A. ellisii*, found only in the eastern Pacific Ocean (e.g., the Gulf of California).

The crown-of-thorns starfish in the Gulf of California, where it has short spines with short arms, was called *A. ellisii* and regarded as a different species from other Pacific crown-of-thorns starfish. However, population genetic analysis of *A. ellisii* and several Pacific *A. planci* sensu lato populations by Nishida and Lucas (1988) using allozyme markers showed that *A. ellisii* is genetically closer to other western Pacific crown-of-thorns starfish populations than to that in Hawaii. The result was unexpected because crown-of-thorns starfish in Hawaii has the same morphological features as its western Pacific counterpart. Given that the crown-of-thorns starfish in Hawaii is *A. planci*, *A. ellisii*, which is genetically closer to other Pacific *A. planci* than to *A. planci* in Hawaii, became synonymous with *A. planci*.

Two *Acanthaster* species are present in Japan: Pacific *A. planci* sensu lato and *A. brevispinus* (Fig. 9.1). *A. planci* sensu lato occurs in the Nansei Islands (all of the islands

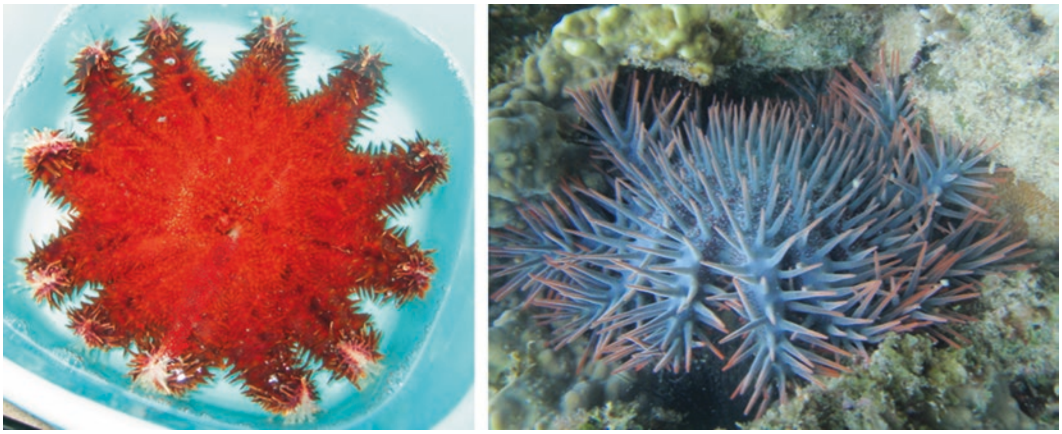

Fig. 9.1 Two *Acanthaster* species from Japan. *Left*, *Acanthaster brevispinus* collected in Susami, Wakayama, in 2004. *Right*, *A. planci* sensu lato collected from western Okinawa

Table 9.1 Summary of peak spawning periods of *Acanthaster planci* in Japan

Latitude (N)	Locality	Year	Apr	May	Jun	Jul	Aug	Sep	Oct	Source
33.5	Mainland Japan	1973				→	→			The Environmental Agancy (1974)
31.5	Kyushu South	2014 and 2015				→	→			Yasuda observation
28	Amami-Ohshima	2004				→	→			Yasuda et al. (2010)
26.5	Okinawa Mainland	2004				→	→			Yasuda et al. (2010)
26.5	Okinawa Mainland	2005				→	→			Yasuda unpublished data
26	Kerama Islands	2004			→	→				Yasuda et al. (2010)
24.5	Miyako Island	2004			→	→				Yasuda et al. (2010)
24	Sekisei-Lagoon	2004		→	→					Yasuda et al. (2010)
24	Iriomote Island	1984 and 1985			→	→				Yokochi and Ogura (1987)

between Kyushu and Taiwan) and the southern parts of Kyushu, Shikoku, and Honshu islands. *A. brevispinus* is much rarer than *A. planci* sensu lato and can be found in Shikoku and Wakayama, as noted above.

9.1.3 Life Cycle and Early Life Ecology

A. planci sensu lato is dioecious (i.e., contains both males and females) with high fecundity. *A. planci* sensu lato spawning in Japan is summarized in Table 9.1. Spawning starts from late May to early June in the southern part of its range, i.e., the Yaeyama region (24.31°N) of Japan. As spawning shifts to higher latitudes (e.g., Kushimoto, 33.48°N), the spawning period becomes shorter and occurs later. Because *A. planci* sensu lato spawning in Japan peaks when the water temperature exceeds approximately 28 °C in Japan (Yokochi and Ogura 1987; Yasuda et al. 2010), the timing and duration of spawning may change slightly at the same location across years. Such variations likely exist because 28 °C is the optimum temperature for *A. planci* sensu lato larvae, which have a relatively narrow temperature tolerance (26–31 °C; Lucas 1973). For example, on Okinawa Island (26.61°N), peak spawning was slightly delayed in 2005 compared to 2004 due to lower water temperatures (Table 9.1). While *A. planci* sensu lato spawning is not necessarily associated with the phase of the moon (Birkeland and Lucas 1990; Pratchett et al. 2014), *A. planci* sensu lato in a tank did spawn during the full moon in July and August near the northernmost part of their distribution range, in Wakayama (33.48°N) (Nature Conservation Bureau, Environment Agency 1974).

When the spawning peak starts, over half of both males and females have partially spawned or spent gonads, which are easily detected by dissecting the roots of their arms (Yasuda et al. 2010, Fig. 9.2). Each individual appears to spawn several times during the spawning period, because during the middle of a spawning period, a population contains individuals with full gonads, gonads at approximately

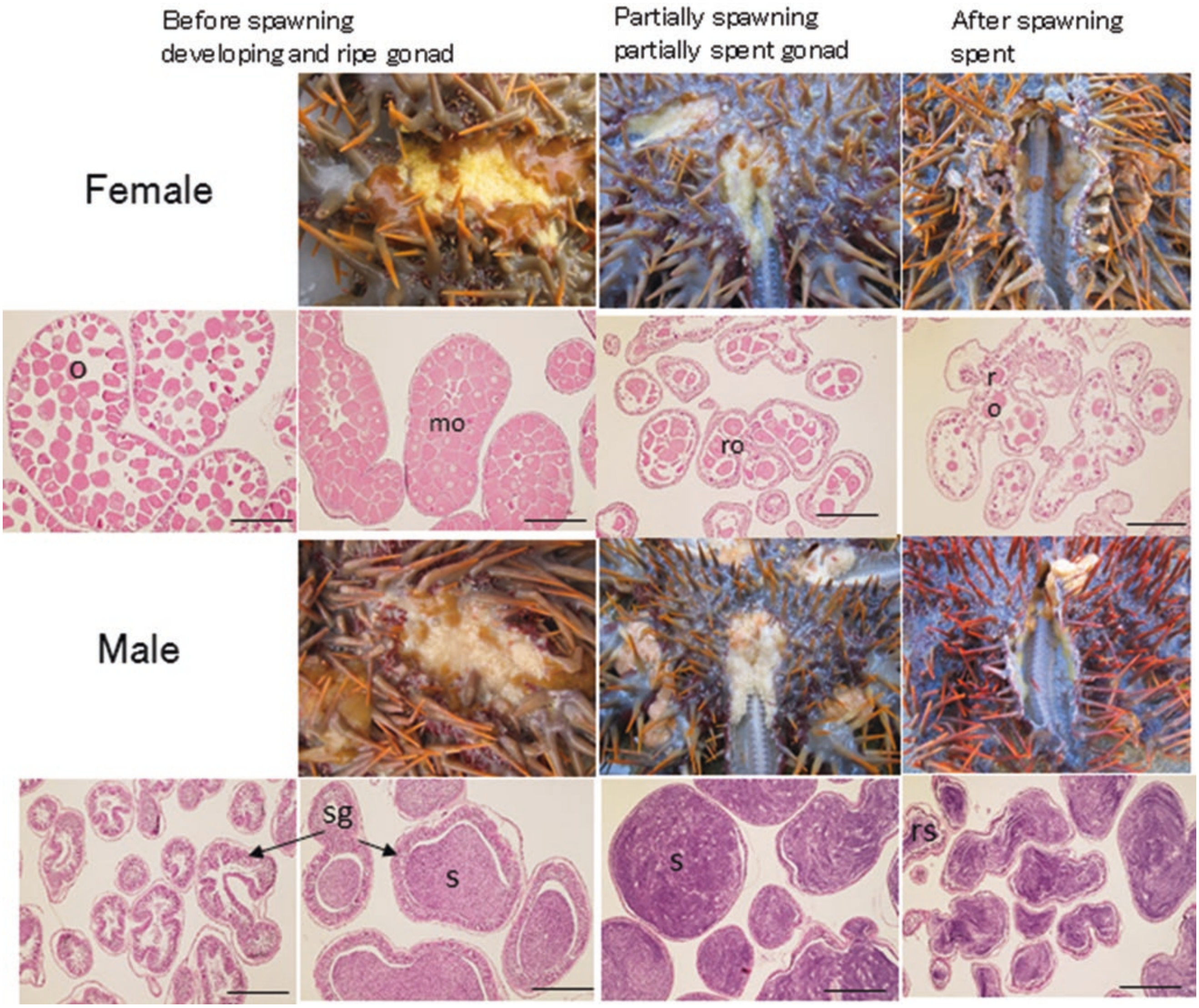

Fig. 9.2 Comparison of simple dissection and histological examinations during Japanese *Acanthaster planci* sensu lato gonad development and spawning (dissection pictures from Yasuda et al. 2010). *o* oocytes, *mo* mature oocytes, *ro* residual oocytes, *s* spermatozoa, *sg* spermatogenic layer, *rs* residual spermatozoa. Scale bars = 500 μm

60 % volume, gonads at approximately 30 %, and no gonads; all individuals eventually become spent (Yasuda et al. 2010). Surprisingly, while Environment Agency researchers observed the spawning activities during the summer, artificial fertilization was achieved in December (the middle of winter in Japan) but failed in May, even though the gonads appeared to be more mature at that point than in December (Nature Conservation Bureau, Environment Agency 1974). Mature gonads may have remained in the starfish until December from the preceding summer, whereas only immature eggs and sperm were present in May, as suggested by the histology images shown in Fig. 9.2 (left side of slide). Yamazato and Kiyan (1973) implied possible reproduction during September and October on Okinawa Island.

Eggs are fertilized in the water column, and the resultant larvae disperse over a 3–4-week period, depending primarily on food availability and temperature, before settling on the ocean floor (Yamaguchi 1973). Juvenile *A. planci* sensu lato start to eat coral from approximately 4 months in age (8 mm in diameter; Yamaguchi 1974). Before this stage, larval and juvenile *A. planci* sensu lato are often eaten or killed by corals (Yamaguchi 1981). Interestingly, Yamaguchi (1981) observed cauliflower corals, *Pocillopora* spp., catching and killing *A. planci* sensu lato larvae but not eating or digesting them.

In the northern regions (>31°N), at the periphery of their distribution range (e.g., south of Honshu, Shikoku, and Kyushu in Japan), *A. planci* sensu lato are subject to low temperatures during the winter (e.g., <18 °C). However, *A.*

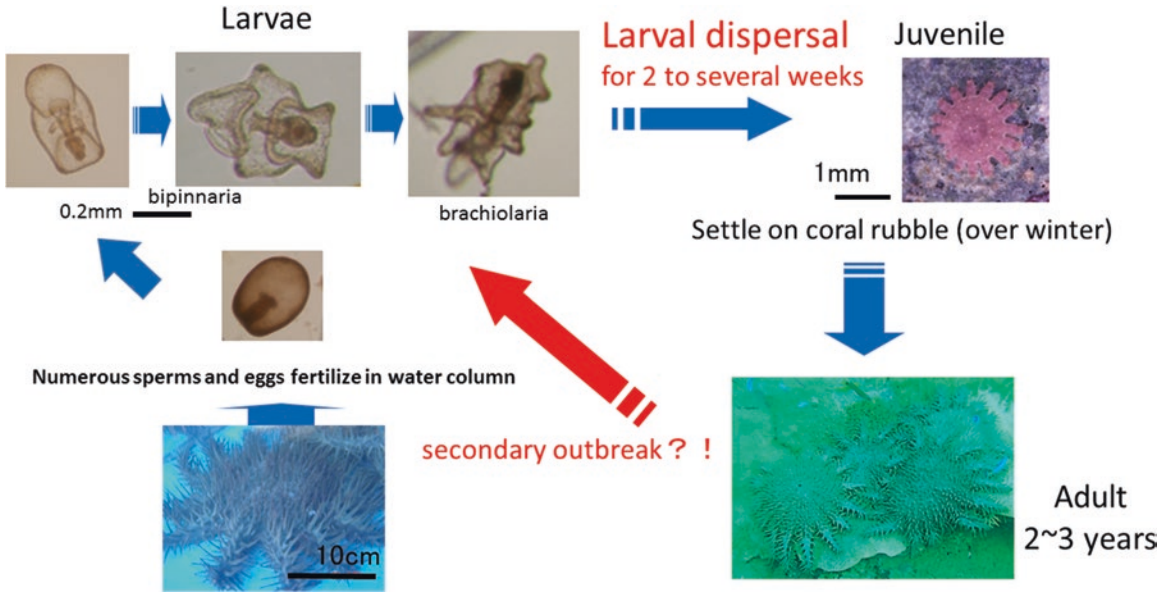

Fig. 9.3 Life cycle of *Acanthaster planci* sensu lato. *A. planci* sensu lato releases numerous eggs and sperm. After fertilization in the water column, larvae develop from bipinnaria to brachiolaria before settlement. When the juvenile becomes big enough to eat corals, *A. planci* sensu lato grows fast and becomes a mature adult in 2–3 years

planci sensu lato juveniles appear to have relatively wide temperature tolerance. Researchers in the 1970s showed that most adult *A. planci* sensu lato collected from Kushimoto, south of Honshu (33.48° N), survived when kept in a tank at 15 °C, the coldest water temperature observed around Kushimoto, suggesting that *A. planci* sensu lato can overwinter in this area (Nature Conservation Bureau, Environment Agency 1974). In Okinawa, however, Takahasi (1986) and Yamaguchi (1987) found that juvenile and subadult *A. planci* sensu lato behaved normally at 18 °C but stopped eating at approximately 16 °C. The starfish survived only for several days at 14 °C and lost their ability to hang on to the substrate. Generally, most adult *A. planci* sensu lato die at temperatures below 13–14 °C (Okaji personal communication). These results suggest that 17–18 °C is the cold-tolerance threshold for juvenile and subadult *A. planci* sensu lato, and 15 °C is the threshold for adult *A. planci* sensu lato.

9.1.4 Genetic Structure of *A. planci* sensu lato in Japan

When fertilization is successful and more larvae and juveniles survive than usual, population outbreaks occur (Fig. 9.3). If no prior population outbreaks have occurred around that area and the population outbreak appears suddenly, it is designated as a primary population outbreak. Once a population outbreak has started in an area, the population will likely continue to produce large numbers of larvae. Successive population outbreaks will be caused by the recruitment of larvae produced by upstream population outbreaks, and these are designated as secondary outbreaks (Endean 1974). Secondary population outbreaks are suspected to have occurred in the GBR, Japan, and French Polynesia.

To test the secondary population outbreak hypothesis and estimate larval dispersal, many population genetic analyses have been conducted. Indeed, the genetic structure of *A. planci* sensu lato has been the most intensively and widely studied of all coral reef invertebrate species (Benzie 1999; Volger et al. 2008; Yasuda et al. 2009, 2011, 2013, 2014; Timmers et al. 2011, 2012). Significant genetic isolation by distance across remote Pacific Islands (Yasuda et al. 2009; Vogler et al. 2013) and North Indian Ocean species (Vogler et al. 2012) has been found using mitochondrial and nuclear microsatellite DNA.

In Japan, genetic homogeneity between different populations has been reported for different times and sites. Interestingly, genetic similarity between two outbreak populations 15 years apart examined using allozyme loci in Okinawa implied that relatively large populations are maintained during non-population outbreak (Katoh and Hashimoto 2003). Population genetic analysis using seven highly polymorphic nuclear microsatellite markers (Yasuda et al. 2006) from ten *A. planci* sensu lato populations extending from Sekisei Lagoon (24.31°N, near Taiwan; see Fig. 9.5) to the southern part of Wakayama (33.48°N, south of Honshu) showed no population differentiation based on traditional *F* statistics (Yasuda et al. 2009). Subsequent analysis using 14 microsatellite markers and mitochondrial control

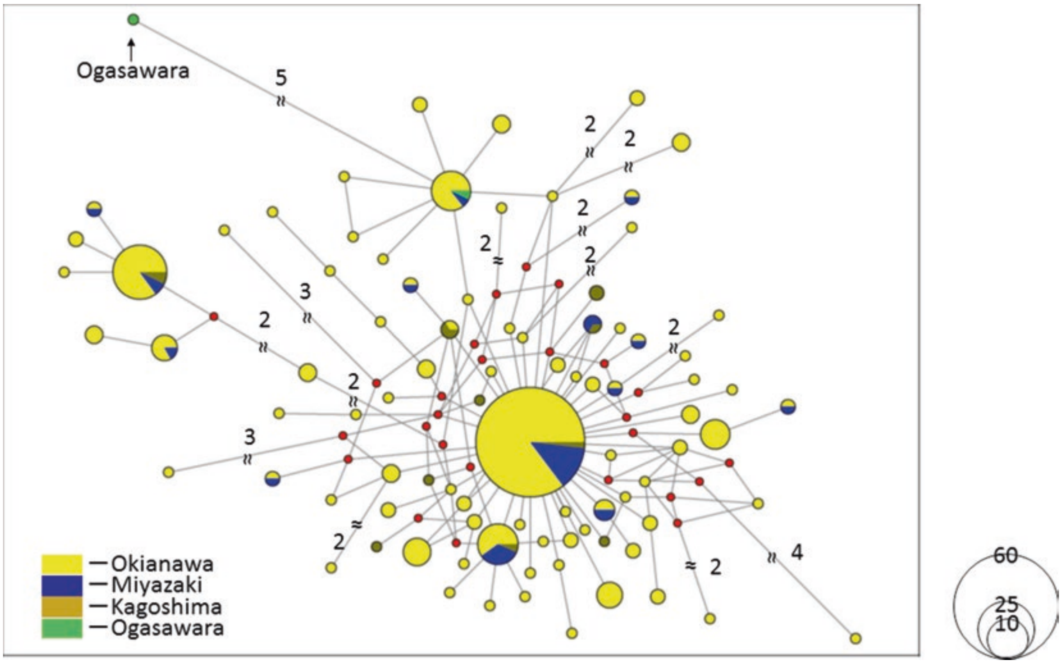

Fig. 9.4 Mitochondrial DNA haplotype network in Japan. Each *circle* represents a different haplotype, and size is proportional to haplotype frequency. Node *numbers* indicate the number of substitutions between haplotypes

region analysis also showed genetic homogeneity among four of the populations (Miyazaki, Okinawa mainland, Miyako, and Yaeyama). Haplotype network analysis of two individuals from Ogasawara (approximately 1400 km east from Okinawa) suggested that one shared the same haplotype with the Okinawan population while the other differed (Fig. 9.4). Therefore, *A. planci* sensu lato in Ogasawara may originate from both the Kuroshio region (which is equivalent to all of the Japanese population) and another region. Although it is difficult to find many *A. planci* sensu lato from Ogasawara, analyzing further samples will be interesting to trace their origin. While just five individuals were obtained from Miyake Island, population differentiation and microsatellite private alleles were not observed when they were compared with other Japanese *A. planci* sensu lato populations along the Kuroshio Current (Yasuda unpublished data). This observation implies that the Miyake Island population is genetically similar to the Okinawa populations. Additional samples are required to statistically prove a genetic relationship between the Miyake Island and other Japanese populations.

9.1.5 Definition of Population Outbreaks

A. planci sensu lato population outbreaks are not consistently defined. For example, Moran and De'ath (1992) defined population outbreaks of *A. planci* sensu lato as occurring at a density of 1500 individuals per km^2. Coral coverage is expected to decline above that density because the starfish's eating rate exceeds coral growth in the GBR. However, the rate of coral consumption may be different in Japan, because the average size of *A. planci* sensu lato is larger (approximately 40 cm) in the GBR than in Japan (<35 cm), and Japanese *A. planci* sensu lato are thought to eat less coral per individual. The growth rate and composition of coral species also vary across reefs in Japan; consequently, the tolerance threshold of *Acanthaster* density for corals also varies depending on sites. In addition, the water temperature in northern temperate Japan during winter is lower than that in the GBR. For conveniences, a density of 4,000 individuals per km^2 has been defined as the tolerance threshold in Japan, as calculated from a survey conducted by Kushimoto Marine Park (Nomura et al. 2001). Thus, the health of coral reefs is conveniently examined by monitoring *A. planci* sensu lato impact based on the criteria in the spot-check manual (Nomura et al. 2001; Ministry of the Environment, Natural Environmental Bureau 2005). The expected area for this spot check is approximately 2500 m^2 (50 × 50 m), covered by 15 min of swimming. The manual defines spotting fewer than one *A. planci* sensu lato per 15-min swim per person as normal density, two to four individuals as relatively high density requiring caution, five to nine individuals as a semi-population outbreak, and >10 individuals as an outbreak.

A variety of sources exist regarding the information for *A. planci* sensu lato population outbreaks in Japan. These include anecdotal reports by old fishermen or locals, observation records from fishermen and coral reef researchers, and monitoring data obtained by the Ministry of the Environment

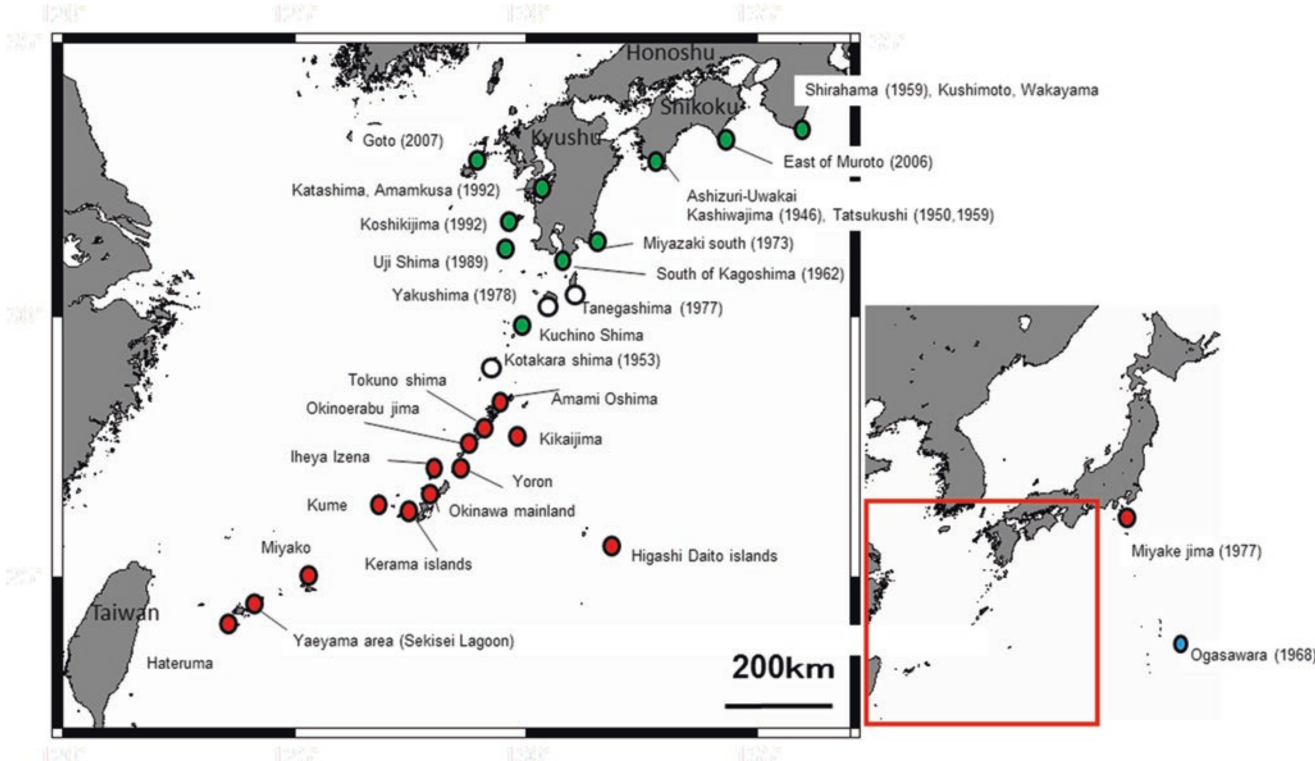

Fig. 9.5 Places in Japan where *Acanthaster planci* sensu lato was observed before WWII (*red*), observed after WWII (*green*), and where population outbreaks have never been reported (*white*). *Numbers in parentheses* indicate the years in which *A. planci* sensu lato was first observed

and other local government agencies. Intensive control efforts have been led by national and local government agencies, local volunteer divers, and fishermen over seven decades. However, the success rate of removal depends on the number of participants, required effort, detectability of *A. planci* sensu lato individuals, and target area. In particular, it is often difficult to estimate the intensity of population outbreaks based on *A. planci* sensu lato numbers alone.

To clarify the patterns of population outbreaks from the past to the present and to see if the intensity of population outbreaks has increased in recent years, I visualized the intensity of previous population outbreaks in Japan. I used the spot-check manual criteria and an overview of available outbreak information to define the intensity of *A. planci* sensu lato population outbreaks, as shown in Table 9.2.

9.2 Review of A. planci sensu lato Occurrence and Population Outbreaks in Japan from 1912 to 2015

Here, I have accumulated and summarized all existing records I could find about this phenomenon. Reports about *A. planci* sensu lato population outbreaks were based on published reports (e.g., Yamaguchi 1986, 1987), survey reports (e.g., Ministry of the Environment), control program reports (e.g., Okinawa Prefectural Government), newspapers, information from local fishermen and professional divers, and other anecdotal information such as blogs with photographs. The oldest written record of *A. planci* sensu lato in Japan was published in 1903: the species was on Amami Oshima by Mitsukuri (1903), who named it Onihitode (demon starfish in English). The oldest anecdotal record of a population outbreak in Japan is sometime between 1912 and 1926 in Yoron (Marine Parks Center of Japan 1987). All of these sources are integrated in Fig. 9.5 and Table 9.3.

9.2.1 Before 1960: Population Outbreaks Around the Ryukyu Islands with Relatively Low Human Impact

It was challenging to find official written information on population outbreaks of *A. planci* sensu lato before World War II (WWII). However, because of the starfish's toxic spine and unusual appearance in the sea, local people, especially fishermen, often remember if a population outbreak of *A. planci* sensu lato occurred at least once, and each island often has a local name for *A. planci* sensu lato (Birkeland 1982; Marine Parks Center of Japan 1987). Inquiry surveys were conducted from 1984 to 1987 by the Marine Parks Center of Japan (1987), asking local elders (fishermen's

Table 9.2 Criteria for the intensity of population outbreak used in this study

	Intensity	15 min observation by a diver	per control effort by 3-10 divers with different detactability	Control effort per year per region (e.g. 20 times at 1-25 sites by 10 divers per effort)
Not distributed	0	Not distributed		
Very low	1	0 - 1	< 5	< 100
Sign of increasing	2	2 - 4	6 - 49	100 - 2,000
Semi-outbreak	3	5 -9	50 -100	2,000 - 10,000
Outbreak	4	10 - 49	100 - 500	10,000 - 100,000
Massive outbreak	5	50 <	500 <	100,000 <

unions, fisheries divisions, and directors of community centers) about local names and known population outbreaks of *A. planci* sensu lato on 11 Okinawan Islands, five Amami Islands, and two sites south of Shikoku. This survey clearly showed the presence of local names for *A. planci* sensu lato on tropical islands such as the Okinawan and Amami Islands; however, this was not the case in Shikoku, one of Japan's temperate areas. The oldest anecdotal evidence of *A. planci* sensu lato population outbreaks was observed by local fishermen sometime between 1912 and 1926 on Yoron Island (27.05°N), one of the Nansei Islands in Japan (Marine Parks Center of Japan 1987). Based on the talk from the head of the Yoron fisherman's cooperative association, Mr. Tokuzo Sako, at least three *A. planci* sensu lato population outbreaks were reported to occur around Yoron Island: sometime between 1912 and 1926, 1939–1940, and 1950–1951 (Marine Parks Center of Japan 1987). Mr. Sako remembered that removed starfish were piled up on a sabani, a traditional small fishing boat from Okinawa Island, within an hour during the severest population outbreak in 1950–1951. In Yoron, the removed *A. planci* sensu lato was used as fertilizer for sugarcane farming. A localized *A. planci* sensu lato population outbreak (inferred intensity 4 in Table 9.2) was detected at Amami Oshima (28.48°N) in 1955 (Shirai 1956; see also the oldest *Acanthaster* picture on record, Fig. 9.6). In a questionnaire, Mr. Katsuki Oki, an old local fisherman from Amami Oshima, mentioned a large number of dead *A. planci* sensu lato being washed ashore after a typhoon in 1955, which was then used as fertilizer for pumpkins, supporting the suggestion that a severe outbreak occurred at that time (Oki 2014). Local people from the Amami Islands called *A. planci* sensu lato "America Yui (Friend)" at that time because they believed that the starfish were being transported by the many boats traveling from Okinawa to the Amami Islands during the US administration after WWII. Another anecdotal record of an *A. planci* sensu lato population outbreak was reported from Sesoko (26.63° N), near the Okinawa mainland, in 1942 (Okinawa Prefectural Tourism Development Corporation 1976, Marine Parks Center of Japan 1987). The intensity of this population outbreak was almost the same as that in the 1970s. Anecdotal reports of population outbreaks were also obtained from Hatoma (24.47°N, in 1952 and 1953) and Kabira Bay (24.45°N, in 1958) in the Yaeyama region (see Fig. 9.5, Okinawa Prefectural Tourism Development Bureau 1976; Nature Conservation Division, Department of Cultural and Environmental Affairs, Okinawa Prefectural Government 2006). During the 1953 population outbreak at Hatoma Island, a truckload of starfish was seen almost every day (Nature Conservation Bureau, Environment Agency 1973, 1974). Almost at the same time as the events documented in the Yaeyama region and a few years after the Yoron (27.05°N) population outbreak, an *A. planci* sensu lato population outbreak was reported on Miyako Island (24.90°N, Fig. 9.5) from 1958 to 1959, with 212,700 individuals being removed in 1957 (Yamazato 1969; Nature Conservation Bureau, Environment Agency 1973). Reports of *A. planci* sensu lato population outbreaks were limited before World War II, partly because scuba diving was not as common as it is today, and no one knew that *A. planci* sensu lato ate corals at that time. However, outbreaks of *A. planci* sensu lato populations have been historically reported in Japan (as documented on the Nansei Islands) before the anthropogenic impact became as high as it is today.

Notably, the possible first population outbreak of *A. planci* sensu lato in a temperate region (Kashiwa Island, 32.76°N) occurred in 1946 (Tada 1982). No one in the region, including old fishermen, had seen that animal before. The inquiry survey conducted in 1986 indicated that *A. planci* sensu lato was locally called Genbaku (atomic bomb in English) at that time because skin injuries due to stings by the crown-of-thorns starfish look like radiation sickness (Marine Parks Center of Japan 1987).

Table 9.3 Population outbreak of *Acanthaster planci* in Japan

	Region	Latitude	Longtitude	1912	1913	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937
Honshu	Choshi	35.70433	140.87738	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Honshu	Tateyama	34.98333	139.81667	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyusuh NW	Tsushima	34.26697	129.32529	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu NE	Nobeoka	32.58912	131.72087	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oagasawara	Chichijima	27.04727	142.18268	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Izu	Niijima	34.35587	139.24278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Izu	Miyake	34.04719	139.49619	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Izu	Hachijyo Jima	33.14901	139.74068	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Honshu	Kushimoto	33.47767	135.72431	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Shikoku E	Muroto	33.27030	134.15907	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Shikoku W	Ashizuri-uwakai	32.76247	132.86831	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu W	Goto(Fukue)	32.74684	128.86777	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu W	Amakusa	32.19311	129.99381	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu W	Koshikijima	31.84601	129.90373	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu W	Ujishima	31.20592	129.47001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu E	Miyazaki south	31.46933	131.39251	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu S	South Kagoshima	30.99628	130.67078	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ohsumi	Tanegashima	30.39915	130.98550	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ohsumi	Yakushima	30.46281	130.49343	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tokara	Kodakara	29.22063	129.32215	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amami	Kikaijima	28.33752	129.96209	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Amami	28.47767	129.60981	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Tokunoshima	27.86615	128.96590																										
Amami	Okinoerabu	27.41105	128.63056																										
Amami	Yoron	27.05149	128.45914	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	1	1	1	1	1	1	1	1	1	1
Okinawa	Izena/Iheyajima	26.96472	127.92218																										
Okinawa	Daito-shoto	25.87377	131.24963																										
Okinawa	Okinawa E	26.29749	127.82141																										
Okinawa	Okinawa W	26.50742	127.85324																										
Okinawa	Kerama	26.20314	127.26717																										
Okinawa	Kume	26.33156	126.82681																										
Miyako	Miyako	24.99089	125.28617																										
Yaeyama	Yaeyama (Hatoma, Ishigaki, Sekisei)	24.31366	124.02195																										
Yaeyama	Hateruma	24.07135	123.77215																										

(continued)

Table 9.3 (continued)

	Region	Latitude	Longtitude	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
Honshu	Choshi	35.70433	140.87738	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Honshu	Tateyama	34.98333	139.81667	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyusuh NW	Tsushima	34.26697	129.32529	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu NE	Nobeoka	32.58912	131.72087	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Oagasawara	Chichijima	27.04727	142.18268	0	0	0	0	0	0	0	0																		
Izu	Niijima	34.35587	139.24278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Izu	Miyake	34.04719	139.49619	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Izu	Hachijyo Jima	33.14901	139.74068	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Honshu	Kushimoto	33.47767	135.72431	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Shikoku E	Muroto	33.27030	134.15907	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
Shikoku W	Ashizuri-uwakai	32.76247	132.86831	0	0	0	0	0	0	0	0	3	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Kyushu W	Goto(Fukue)	32.74684	128.86777	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				0	0	0	0	0
Kyushu W	Amakusa	32.19311	129.99381	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				0	0	0	0	0
Kyushu W	Koshikijima	31.84601	129.90373	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
Kyushu W	Ujishima	31.20592	129.47001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
Kyushu E	Miyazaki south	31.46933	131.39251	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0								
Kyushu S	South Kagoshima	30.99628	130.67078	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0							1	1
Ohsumi	Tanegashima	30.39915	130.98550	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0							1	1
Ohsumi	Yakushima	30.46281	130.49343	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0							1	1
Tokara	Kodakara	29.22063	129.32215	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Kikaijima	28.33752	129.96209	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Amami	28.47767	129.60981	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	1	1	1	1	1	1	1	1
Amami	Tokunoshima	27.86615	128.96590																										
Amami	Okinoerabu	27.41105	128.63056																										
Amami	Yoron	27.05149	128.45914	1	3	3	1	1	1	1	1	1	1	1	1	4	4	1	1	1	1	1	1	1	1	1	1	1	1
Okinawa	Izena/Iheyajima	26.96472	127.92218													2	3	3	3	3	2								
Okinawa	Daito-shoto	25.87377	131.24963																						1				
Okinawa	Okinawa E	26.29749	127.82141																					1	1	1	1	1	1
Okinawa	Okinawa W	26.50742	127.85324					5														1	5	1	1	1	1	1	1
Okinawa	Kerama	26.20314	127.26717																				1	1	1	1	1	1	1
Okinawa	Kume	26.33156	126.82681																					4	1	1	1	1	1
Miyako	Miyako	24.99089	125.28617																				5	5	1	1	1	1	1
Yaeyama	Yaeyama (Hatoma, Ishigaki, Sekisei)	24.31366	124.02195											4				4						4	1	1	1	1	1
Yaeyama	Hateruma	24.07135	123.77215																										

	Region	Latitude	Longtitude	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
Honshu	Choshi	35.70433	140.87738	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Honshu	Tateyama	34.98333	139.81667	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyusuh NW	Tsushima	34.26697	129.32529	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu NE	Nobeoka	32.58912	131.72087										1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Oagasawara	Chichijima	27.04727	142.18268					1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1
Izu	Niijima	34.35587	139.24278	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Izu	Miyake	34.04719	139.49619	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	3	3	1	1	1	1	1	1	1	1	1
Izu	Hachijyo Jima	33.14901	139.74068	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Honshu	Kushimoto	33.47767	135.72431	1	1	1	1	1	1	1	1	1	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Shikoku E	Muroto	33.27030	134.15907																	1	1	1	1	1	1	1	1	1	1
Shikoku W	Ashizuri-uwakai	32.76247	132.86831	1	1	1	1	1	1	1	1	1	4	3	3	3	4	4	4	3	3	2	1	1	1	1	1	1	1
Kyushu W	Goto(Fukue)	32.74684	128.86777	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu W	Amakusa	32.19311	129.99381	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu W	Koshikijima	31.84601	129.90373																										
Kyushu W	Ujishima	31.20592	129.47001																								2	1	1
Kyushu E	Miyazaki south	31.46933	131.39251										2	2	2	2	2	3	2	2	2	2	2	2	2	1	1	1	1
Kyushu S	South Kagoshima	30.99628	130.67078	1	1	1	1	1	1	1	1	1	1	1	1	2	2	3	2	2	2	2	2	2	2	1	1	1	1
Ohsumi	Tanegashima	30.39915	130.98550	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ohsumi	Yakushima	30.46281	130.49343	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tokara	Kodakara	29.22063	129.32215	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Kikaijima	28.33752	129.96209	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Amami	28.47767	129.60981	1	1	1	1	1	1	1	1	1	4	4	4	4	4	4	4	5	4	4	4	4	4	4	3	3	3
Amami	Tokunoshima	27.86615	128.96590										1	1	1	3	3	2	3	3	2	3	3	2	3	3	3	3	3
Amami	Okinoerabu	27.41105	128.63056																			4	4	4					
Amami	Yoron	27.05149	128.45914	1	1	1	1	1	1	1	1		5	5	4	4	4	4	4	4	4	4	4	3	3	2	2	2	2
Okinawa	Izena/Iheyajima	26.96472	127.92218										4	4	5	5	5	5	5										
Okinawa	Daito-shoto	25.87377	131.24963																	1	1	1	1	1	1	1	1	1	1
Okinawa	Okinawa E	26.29749	127.82141	1	1	1	1	1	1	1	1	1	1	1	4	4	5	5	5	4	4	4	4						
Okinawa	Okinawa W	26.50742	127.85324	1	1	1	1	1	3	4	5	5	5	5	5	5	5						3	4	3	3	2	2	2
Okinawa	Kerama	26.20314	127.26717	1	1	1	1	1	1	1	1	3	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4
Okinawa	Kume	26.33156	126.82681	1	1	1	1	1	2	3	3	5	5	3	3														
Miyako	Miyako	24.99089	125.28617	1	1	1	1	1	1	1	1	1	4						5	5	5	5	5	4					
Yaeyama	Yaeyama (Hatoma, Ishigaki, Sekisei)	24.31366	124.02195	1	1	1	1	1	2	3	4	4	4	4	4	4	4	4	4	5	5	5	5	5	4	3	3	3	3
Yaeyama	Hateruma	24.07135	123.77215																					5	4	3	2	1	

(continued)

Table 9.3 (continued)

	Region	Latitude	Longtitude	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Honshu	Choshi	35.70433	140.87738	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Honshu	Tateyama	34.98333	139.81667	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyusuh NW	Tsushima	34.26697	129.32529	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kyushu NE	Nobeoka	32.58912	131.72087	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Oagasawara	Chichijima	27.04727	142.18268	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Izu	Niijima	34.35587	139.24278	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Izu	Miyake	34.04719	139.49619	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1
Izu	Hachijyo Jima	33.14901	139.74068	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Honshu	Kushimoto	33.47767	135.72431	1	1	1	1	1	1	1	1	1	1	1	1	2	1	4	4	4	3	4	2	1	2	2	2	2	2
Shikoku E	Muroto	33.27030	134.15907	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	
Shikoku W	Ashizuri-uwakai	32.76247	132.86831	1	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3	3	3	3	3	4	5	4	3	3	
Kyushu W	Goto(Fukue)	32.74684	128.86777	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	1	1	1	1
Kyushu W	Amakusa	32.19311	129.99381	0	0	0	0	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	3	3	2	2	1	1	1
Kyushu W	Koshikijima	31.84601	129.90373	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	3	2	2	2	1
Kyushu W	Ujishima	31.20592	129.47001	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Kyushu E	Miyazaki south	31.46933	131.39251	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	3	2	2	2
Kyushu S	South Kagoshima	30.99628	130.67078	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	4	3	1	2	5	4	3	3	
Ohsumi	Tanegashima	30.39915	130.98550	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ohsumi	Yakushima	30.46281	130.49343	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tokara	Kodakara	29.22063	129.32215	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Kikaijima	28.33752	129.96209	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amami	Amami	28.47767	129.60981	3	3	3	3	3	3	3	3	3	3	4	5	5	4	2	3	4	3	1	1	1	1	1	1	1	1
Amami	Tokunoshima	27.86615	128.96590	3	3	3	3	3	2	2	2	2	2	2	2	3	3	3	2	3	3	3	1	1	1	1	1	1	1
Amami	Okinoerabu	27.41105	128.63056																2	2	2	2	1	1	1	1	1	1	1
Amami	Yoron	27.05149	128.45914	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	2	1	1	1	2	1	2	2	2		
Okinawa	Izena/Iheyajima	26.96472	127.92218	3	3											3	3			1	1	1	1	1	1	1	1	1	1
Okinawa	Daito-shoto	25.87377	131.24963	1	1	1	1	1	1	1	1	1	1	1				3	3	3	3				1				
Okinawa	Okinawa E	26.29749	127.82141		4						5					4	4	3	3	1	1	1	1	1	1	1			
Okinawa	Okinawa W	26.50742	127.85324	1	1	1	1	1	1	4	5	5	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Okinawa	Kerama	26.20314	127.26717	3	3	3	3	3	3	4	3	3	3	3	4	5	4	4	4	3	1	1	1	1	2	2			
Okinawa	Kume	26.33156	126.82681	4		1											1	4	3	1	1	1	1	1	1	1	1	1	
Miyako	Miyako	24.99089	125.28617															4	4	4	5	4	4	4	5	4	4	3	
Yaeyama	Yaeyama (Hatoma, Ishigaki, Sekisei)	24.31366	124.02195	2	2	2	2	2	1	1	1	1	1	1	1	1	3	3	3	3	3	4	4	5	5	5	4	4	3
Yaeyama	Hateruma	24.07135	123.77215						1	1	1	1	1	1	1	1	1	1			3	3	4						

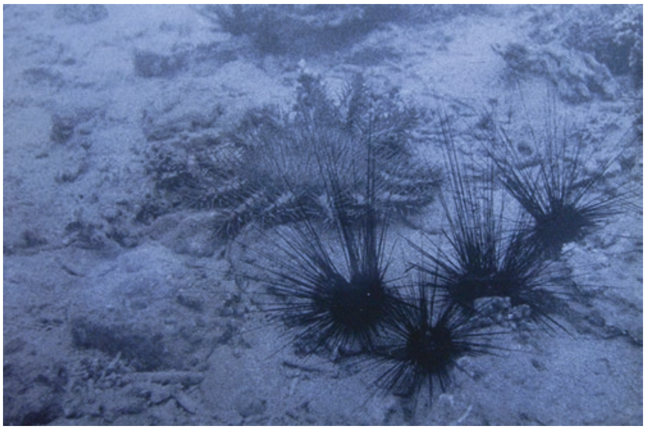

Fig. 9.6 The oldest picture of *Acanthaster planci* sensu lato, taken at Yuikojima, Amami Oshima, in 1956, courtesy of Dr. Shohei Shirai

9.2.2 The 1960s: No *A. planci* sensu lato Population Outbreaks but Possible Northward Migration (>29° N)

In the 1960s, people first became aware of the value and importance of coral reefs as a source of leisure activities for tourists. In parallel, anthropogenic impact on coral reefs dramatically increased due to coastal development (Oki 2014). Agriculture in the catchment areas changed from pineapple to sugarcane fields, and severe terrestrial sediment discharge emerged. In the middle of the high-economic growth period of the 1960s, the coral of the Nansei Islands was in recovery, because no intensive *A. planci* sensu lato population outbreaks occurred during this period (Ministry of the Environment and Japanese Coral Reef Society 2004; Oki 2014).

While no intensive *A. planci* sensu lato population outbreaks took place in Japan during the 1960s, possible northward migration occurred in northern temperate areas. For example, no official record of *A. planci* sensu lato existed in areas further north of Amami Oshima before the first *A. planci* sensu lato was found at Kodakara Island (29.21°N) and Nakanoshima on the Tokara Islands in 1953 (Tokioka 1953), although the inquiry survey revealed a small outbreak around Kashiwa Island (33.77°N), southwest Shikoku, in 1946. *A. planci* sensu lato was first officially recorded at Okinoshima (32.70°N), the southeastern most part of Shikoku Island, by Mr. Shohei Shirai in 1959 (Uchinomi 1962). In the same year, a small juvenile *A. planci* sensu lato was also found at Shirahama (33.65°N) in the south of Wakayama by Mr. Torao Yamamoto (Uchinomi 1962). Subsequently, however, neither juvenile nor adult *A. planci* sensu lato were observed in Wakayama until 1970 (Nature Conservation Bureau, Environment Agency 1974). Similarly, the first *A. planci* sensu lato was found in Cape Sata (30.98°N), the southernmost part of Kyushu Island, in 1962 (Kurata 1982). Around the same time, the possible northward migrations of other coral reef organisms, such as *Protoreaster nodosus*, *Ferdina ocellata*, *Phyllacanthus dubis*, *Salmacis bicolor*, *Toxopneustes elegans*, *Hoterocentrotus mamillatus*, *Metalia spartacus*, *Phyrella fragilis* (Uchinomi 1962), and *Culcita novaeguineae* (Nikaido 1963), were also observed in the south of Shikoku and Honshu.

According to the Japan Meteorological Agency website (*Web site 1), which summarizes annual average surface water temperature data from around Japan from 1914 to 2014, the temperature around Kyushu and Shikoku has increased by 1.2 °C over that 100-year period. The increase in water temperature is more remarkable during the winter (almost 1.5 °C around Shikoku and Tokai). Figure 9.7a, b shows these winter water temperature trends at a regional scale over this 100-year period in comparison to the first observations and population outbreaks of *A. planci* sensu lato in temperate areas. Note that the temperature is averaged over a relatively large marine area (Fig. 9.7c), and absolute water temperature values are not directly correlated with *A. planci* sensu lato survival. Overall, the increase in water temperature seems to coincide with the first observations of *A. planci* sensu lato and higher population outbreak frequency in temperate areas in Japan. However, the local temperature greatly depends on the path of the Kuroshio Current in a given year. Many coral reef organisms around the Ryukyu Islands that have relatively long larval durations (2–7 weeks, Yamguchi 1973), such as *A. planci* sensu lato and *C. novaeguineae*, spawn during summer when the water temperature exceeds 28 °C (e.g., Yasuda et al. 2009, 2010). After the settlement, at least 2 years are required for *A. planci* sensu lato to mature into adults (Yamaguchi 1974); therefore, juveniles must survive the cold winter. Yamaguchi (1987) speculated that even though the actual lethal temperature for *A. planci* sensu lato juveniles is not known, it should be roughly 14–15 °C. Therefore, winter temperatures may regulate the survival of nonadult *Acanthaster* populations at the northern limits of its distribution (Yamaguchi 1987). The recent increase in water temperature may have facilitated *A. planci* sensu lato migration northward, together with that of other marine animals, including corals (Yamano et al. 2011).

9.2.3 The 1970s and 1980s: The First "Confirmed" Successive *A. planci* sensu lato Population Outbreaks in Japan

A. planci sensu lato population outbreaks in Japan became more intensive and extensive in the 1970s. Although the Japanese government spent over 600 million yen to remove *A. planci* sensu lato during this period (Yamaguchi 1986), killing over ten million starfish (see the summary of control

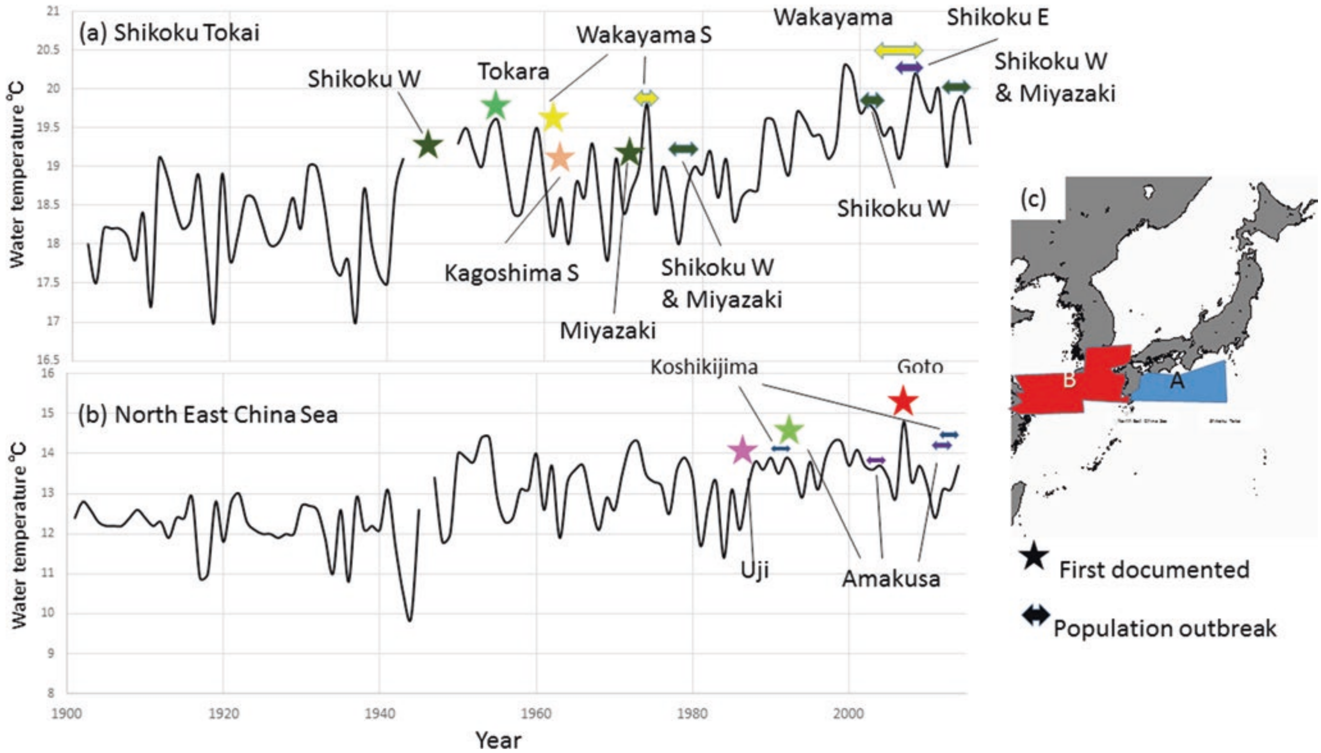

Fig. 9.7 Average water temperature during the winter months since 1904 in the (**a**) Shikoku Tokai region and (**b**) North East China Sea region (see (**c**)). The first observations of *Acanthaster planci* sensu lato occurrence (*stars*) and outbreaks (*double-headed arrows*) are shown. Temperature data are taken from the Japan Meteorological Agency (http://www.data.jma.go.jp/kaiyou/data/shindan/a_1/japan_warm/japan_warm.html)

efforts from the 1970s to 2004 in Fig. 9.8), the control effort failed, with all but a few corals in Okinawa disappearing before 1985 (Yamaguchi 1986). Chronic and successive population outbreaks were observed along the Nansei Islands and temperate areas (further north than Osumi Islands, >30.40°N). Population outbreaks in the southern parts of Kyushu (31.47°N), Shikoku (32.76°N), Wakayama (33.47°N), and even Miyake Island (34.04°N) were observed, representing the northernmost habitats for *A. planci* sensu lato.

Possible primary population outbreaks (possible origins of the secondary outbreaks) were observed after 1969 at the following locations: Onna village on western Okinawa Island (Yamaguchi 1986), Ie Island (27.44°N, 10 km west of Okinawa Island, Takemoto 2005), Kume Island (Environment Agency 1974), and Hatoma Island (Environment Agency 1974; Okinawa Prefectural Tourism and Development Public Corporation Foundation 1976). Population density peaked at Ie Island in 1972, with approximately 120,000 starfish being removed (Takemoto 2005). In 1973, roughly 1,800,000 starfish were killed along the western coast of Okinawa Island (Okinawa Prefectural Tourism Development Bureau 1976). On Kume Island, 97,500 (within 10 days) and 80,360 (within 6 days) starfish were killed in 1972 and 1973, respectively (Nature Conservation Bureau, Environment Agency 1974), and the population outbreak lasted at least until 1975 (Marine Parks Center of Japan 1987). Subsequent population outbreaks occurred in Yoron Island (23 km north of Okinawa Island), with 309,000 starfish being killed in 1973 (Natural Environmental Bureau, Ministry of the Environment 2003), and Iheya Island (27.04°N) approximately 30 km northwest of Okinawa Island, with 12,000 starfish being killed in 1973 and 260,000 starfish being removed in 1975 and 1976 (Takemoto 2005). From 1975 to early 1998, small but persistent population outbreaks were observed at Tokunoshima (27.87°N, 90 km north of Yoron 27.05°N), with about 2,000 starfish being removed each year since 1976 (Natural Environmental Bureau, Ministry of the Environment 2003, Council of Management for Coral Reef Conservation in Amami Islands 2014, Takemoto 2005). In Amami Oshima, *A. planci* sensu lato numbers peaked in 1980, with 91,602 starfish being removed (Natural Environmental Bureau, Ministry of the Environment 2003; Oki 2014; Council of Management for Coral Reef Conservation in Amami Islands 2014).

Yamaguchi (1987) pointed out that the population outbreaks in Okinawa might have also intensified in Amami Oshima during the early 1980s, when winter water temperatures were higher in the northern Ryukyu Islands.

During the 1970s, population outbreaks in temperate waters were observed for the first time. Around Ashizuri-Uwakai (33.10°N, see Fig. 9.5), in the southern part of

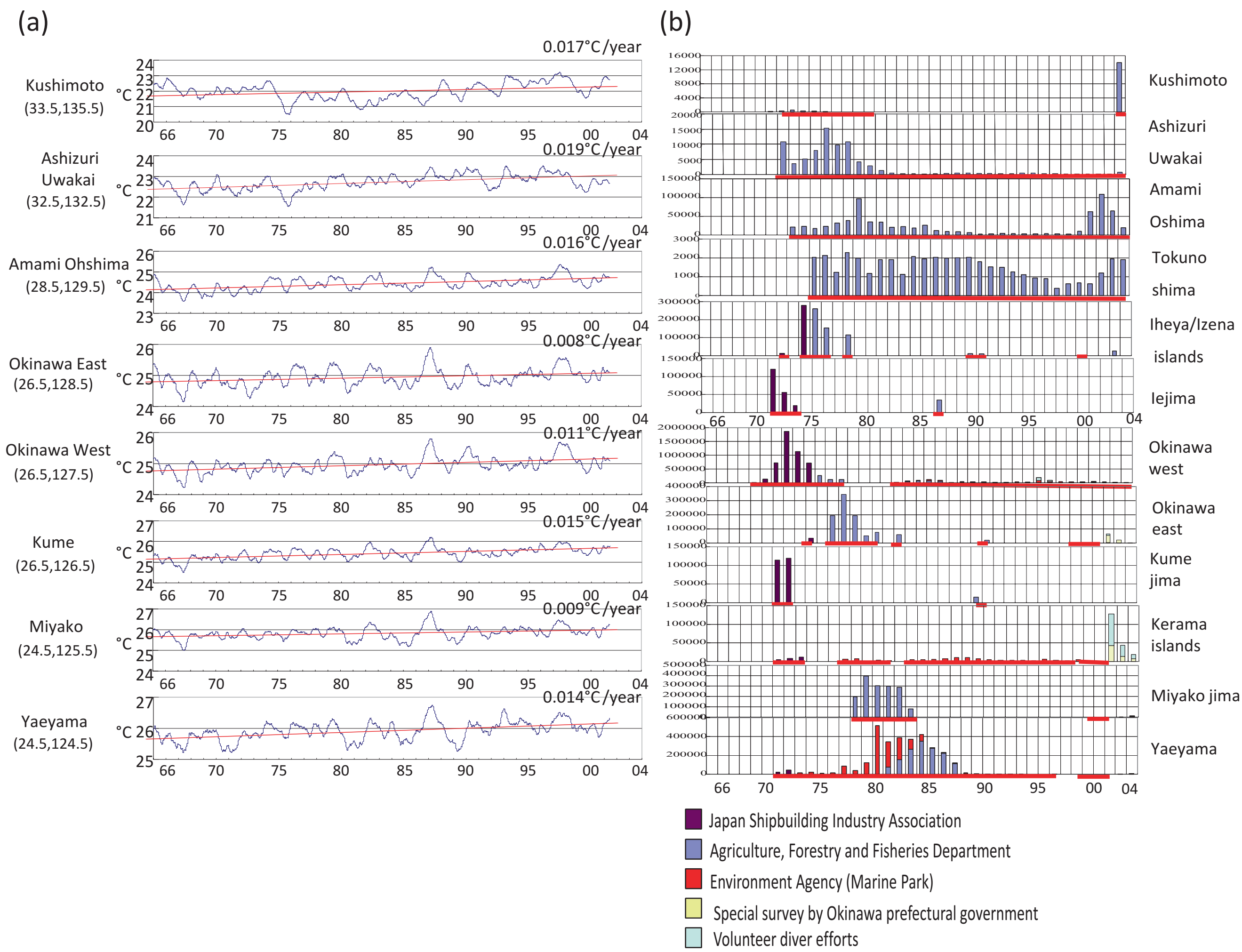

Fig. 9.8 One-year moving average of water temperature from the Japan Meteorological Agency (**a**) and *Acanthaster planci* sensu lato control efforts in Japan (**b**) from 1970 to 2004. Years of reported control efforts are shown as red underbars (Modified from Takemoto 2005)

Shikoku, more than 10,000 starfish were killed in 1973 (Natural Environmental Bureau, Ministry of the Environment 2003). At this time, local people found ten times more starfish in the area of southern Kochi (32.41°N) than in the northern Ehime area (33.10°N). The Kuroshio Current directly approaches the southern Kochi Prefecture, while only a small branch of the current intrudes into the northern Ehime area. Similarly, a small-scale population outbreak was observed at Kushimoto (33.48°N, south Wakayama, Honshu) for the first time in 1973, with 370 starfish being removed in 1974 (Natural Environmental Bureau, Ministry of the Environment 2003). Interestingly, corals were not much damaged by the small outbreak in 1974 because most of the starfish appeared at the southern part of Cape Shionomisaki (33.25°N) and Cape Sumisaki (33.26°N, western side of Shionomisaki Cape) where small numbers of tabular corals were present at the time (Nature Conservation Bureau, Environment Agency 1974). Some corals were present in neighboring areas, including the tabular *Acropora* spp., which is a preferred food resource of *A. planci* sensu lato; however, *A. planci* sensu lato individuals were not found initially. Because *A. planci* was never found on the eastern side of the Kii Peninsula (or even the eastern side of Cape Shionomisaki), which faces the opposite side of the Kuroshio Current and is colder, *A. planci* sensu lato distribution in Kushimoto is primarily determined by where the Kuroshio Current brings larvae, followed by settlement (Nature Conservation Bureau, Environment Agency 1974). The *A. planci* sensu lato removed at Kushimoto in 1973 ranged from juveniles (6 cm) to adults of over 3 years of age (39 cm), implying that successive recruitment may have occurred (either self-seeding in Kushimoto and/or continuous larval supply from the south) (Nature Conservation Bureau, Environment Agency 1974).

In 1973, several individuals of *A. planci* sensu lato were collected for the first time at both Miyazaki and south Oita,

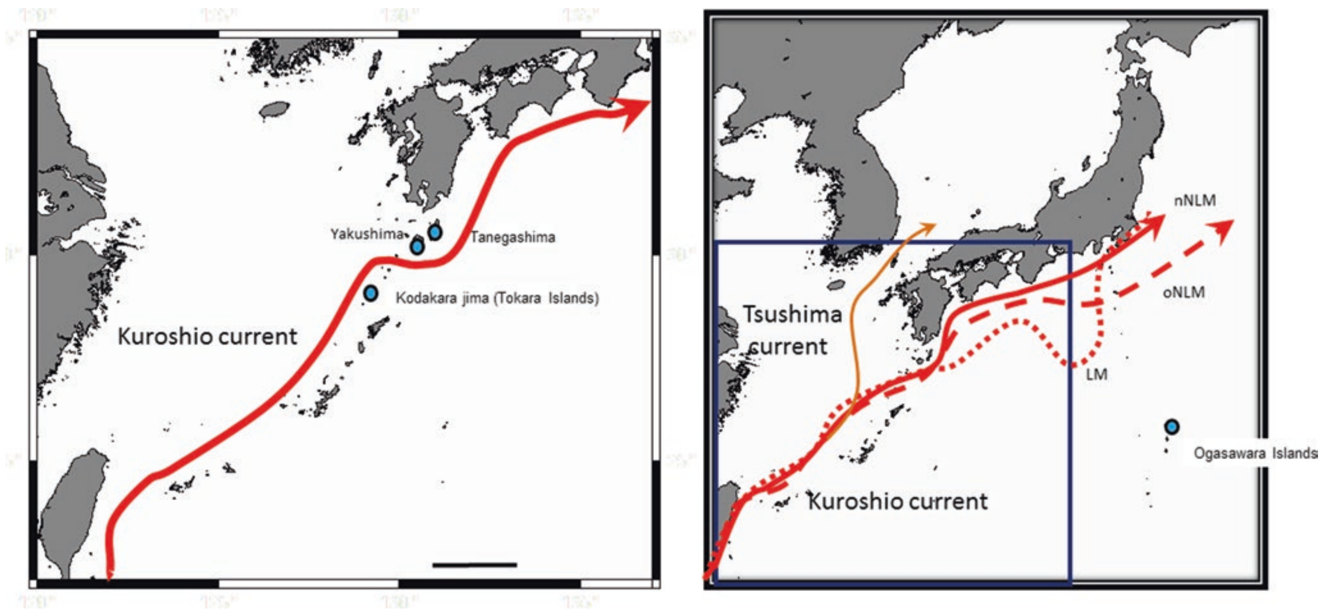

Fig. 9.9 Typical Kuroshio Current paths (*right*). *LM* large meander path far from the temperate shore, except for Miyake Island, *oNLM* offshore non-large meander path far from the shore, *nNLM* nearshore non-large meander path (Modified from Miyazawa 2004; Yasuda et al. 2009)

eastern Kyushu (Ministry of the Environment and Japanese Coral Reef Society 2004). In early 1978, the first population outbreaks of possibly 1- to 2-year-old *A. planci* sensu lato (9–10 cm in length) were also observed further north, at Miyake Island (Moyer and Tanaka 1978). Moyer and Tanaka (1978) suggested that the variety in size of *A. planci* sensu lato found in 1978 implies that larvae transported from the south reproduced in Miyake Island, increasing their numbers by self-seeding. Yamaguchi (1986) suggested that these population outbreaks were caused by larval transportation via the warm tropical Kuroshio Current after it changed its path to pass along the coasts of Shikoku and Miyake Island. Yamaguchi (1987) also noted that the first *A. planci* sensu lato was recorded at Miyake Island (34.05°N) in 1977, coinciding with a period of warmer years associated with the large Kuroshio Current's meandering approach toward Miyake Island (see Fig. 9.9).

The spread of *A. planci* sensu lato outbreaks was detected along both northward and southward population migratory paths. For example, population outbreaks were observed at Ikema Island (24.94°N) and Yabiji (24.94°N) in 1973 (Okinawa Prefectural Tourism Development Bureau 1976) and then from 1979 to 1984, with almost 400,000 starfish being killed at Miyako (24.75°N) in 1981 (Yamaguchi 1984; Takemoto 2005). The Yaeyama area, located further south of Okinawa Island, had an outbreak in 1981, with approximately 500,000 starfish being removed (Kamezaki et al. 1987). However, the density of *A. planci* sensu lato remained relatively high in this region until 1989 (Yaeyama Environmental Network by Yaeyama Fishermen's Cooperative *Web site 2). Hateruma Island (24.07°N), located to the southwest of Sekisei Lagoon, was also infested in 1984 (Ministry of the Environment and Japanese Coral Reef Society 2004). This outbreak could have been a secondary outbreak following the primary outbreak at Sekisei Lagoon (24.32°N).

Notably, almost all corals along Okinawa Island, Kume Island, and other adjacent small islands disappeared during these outbreaks (Yamaguchi 1984; Nature Conservation Division, Department of Cultural and Environmental Affairs, Okinawa Prefectural Government 2006; Yamaguchi 1986). Yamaguchi (1984) suggested the delineation of regular monitoring sites for the early detection of *A. planci* sensu lato population outbreaks to save important reefs, which is critical for tourism, biodiversity, and research.

9.2.4 The 1990s: Few *A. planci* sensu lato Outbreaks but Further Northward Migration

Few intensive population outbreaks newly began in the 1990s (Table 9.3, Nomura 2004; Oki 2014; Takemoto 2005; Natural Conservation Division Okinawa Prefectural Government 2006; Ministry of the Environment and Japanese Coral Reef Society 2004). Instead, chronic outbreaks with origins from the 1970s were observed on Yaeyama, Okinawa Island, Chibishi in Kerama (west of Okinawa Island), Yoron, and Tokunoshima. Notably, coral reefs in Japan were severely damaged by coral bleaching in

1998 (Ministry of the Environment and Japanese Coral Reef Society 2004).

According to an issue of a local newspaper, the Okinawa Times, published on November 7, 1996, approximately 81,000 starfish were killed at Onna Village (the western part of Okinawa Island) in 1996, and high densities have been continually detected around the village until the present (Nakamura et al. 2014, Yasuda personal observation). A huge starfish population was observed at Atta, on the eastern part of Okinawa Island (an average of 367.5 starfish per 10-min swim), and at Chibishi in Kerama in 1997 (Nature Conservation Division, Department of Cultural and Environmental Affairs, Okinawa Prefectural Government 2006; Shimoike 2000). In the Yaeyama area, 1000–2000 starfish per year were continuously removed from 1990 to 1994 (Yaeyama Environmental Network by Yaeyama Fishermen's Cooperative, *Web site 2, Takemoto 2005), but these numbers were much lower than those documented in the 1980s (e.g., 270,000 in 1982, Yaeyama Fishermen's Cooperative *Web site 2).

The Tsushima Current is a smaller branch of the Kuroshio Current that flows along the western side of Kyushu (Fig. 9.9). This current might have brought *A. planci* sensu lato larvae to this temperate area in the 1990s. An increased *A. planci* sensu lato population around the Uji Island (31.21°N), located at the west of southern Kyushu, was first observed in 1987 (Nature Conservation Bureau, Environment Agency and Marine Parks Center of Japan 1994). A population outbreak was also detected at Koshiki Island (31.85°N), located at slightly further north of Uji Island, in 1990 (Nature Conservation Bureau, Environment Agency and Marine Parks Center of Japan 1994). In 1994, *A. planci* sensu lato was first observed in Amamkusa (32.19°N), located at further north of Koshiki Island (Ministry of the Environment, Japanese Coral Reef Society 2004). In 2007, *A. planci* sensu lato was first observed by a local diver at Fukue Island in the Goto Islands (32.75°N, Local diver's website *Web site 3). Although annual data on the path of the Tsushima Current and its associated currents along the west side of Kyushu are not available, it is possible that *A. planci* sensu lato larvae dispersed along these currents, facilitated by the increase in water temperature (Fig. 9.7). A comparison of the fish species at Wakasa Bay, on the western side of Kyushu along the Tsushima Current, between the early 1970s and middle 2000s, suggested that southern fish species such as the rockfish, *Sebastiscus marmoratus*, have significantly increased, while those indigenous to northern waters have decreased, highlighting the effect of global warming around this region (Masuda 2007). Kobayashi et al. (2006) also reported that subtropical species such as slipper lobster *Scyllarides haanii*, brown-tipped sea star *Thromidia catalai*, and blue-lipped sea krait *Laticauda laticaudata* have been recently observed in the area due to global warming.

9.2.5 The 2000s: Further Intensive, Persistent *A. planci* sensu lato Population Outbreaks Throughout Southern Japan

In the 2000s, *A. planci* sensu lato population outbreaks in the northern temperate area of Japan seemed more chronic and occurred at comparable or greater intensity than in the 1970s (Table 9.3). Consequently, it was difficult to differentiate between primary and secondary outbreaks. Furthermore, *A. planci* sensu lato population outbreaks were observed for the first time in several new areas.

9.2.5.1 Areas Between Kume Island and Okinawa Island (Around 26°N)

Population outbreaks occurred in the Kerama Islands from 2001 until 2006, peaking in 2002 (Taniguchi 2012). Over 120,000 starfish were killed around the Kerama Islands, with volunteers removing almost two-thirds of the individuals in 2002 (Takemoto 2005, Fig. 9.8). A persistent population outbreak was also observed at Onna village in western Okinawa. Over 20,000 starfish were removed in 2001 and 2002, but the outbreak gradually subsided from 2003 to 2008 (Nakamura et al. 2014).

A population outbreak occurred around Kume Island in 2003 and peaked in 2004, after the population outbreaks in western Okinawa and the Yaeyama region, including the Sekisei Lagoon (Ministry of the Environment and Japanese Coral Reef Society 2004; Natural Conservation Division Okinawa Prefecture 2011; Nature Conservation Division, Department of Cultural and Environmental Affairs, Okinawa Prefectural Government 2006).

9.2.5.2 From Okinawa Island to Amami Oshima

In 2000, a starfish population in the southern part of Amami Oshima (Setouchi-cho and Uken-mura) began to increase, peaking in 2002, when over 100,000 starfish were removed and corals disappeared (Oki 2014; Council of Management for Coral Reef Conservation in Amami Islands [H16-H25, H represents Heisei, Japanese Era name, 2004–2013] 2014). The population outbreak in Amami Oshima lasted until 2007 (Oki 2014; Council of Management for Coral Reef Conservation in Amami Islands [H16-H25] 2014), with the *A. planci* sensu lato population almost disappearing by 2015. Fortunately, corals are now recovering in this area (Fig. 9.10). A starfish population in Tokunoshima (situated between Okinawa Island and Amami Oshima) also began to increase in 2002, doubling in 2003 (Oki 2014; Council of Management for Coral Reef Conservation in Amami Islands [H16-H25] 2014).

9.2.5.3 Yaeyama Region

In the Yaeyama region, which is in the upstream area of the Kuroshio Current, signs of a population increase were

Fig. 9.10 Changes in coral cover observed at Saneku Point, Amami, through a devastating population outbreak of *Acanthaster planci* sensu lato from 2002 to 2007 and its recovery in 2015 (The 2002 and 2007 images are courtesy of Katsuki Oki)

observed in 2002, and nearly 3000 individuals of *A. planci* sensu lato were removed from Yaeyama in 2003 (Yaeyama Environmental Network by Yaeyama Fishermen's Cooperative *Web site 2). The population size suddenly increased in 2008 and remained at the high density until 2012, when 287,421 individuals were removed (Yaeyama Environmental Network by Yaeyama Fishermen's Cooperative *Web site 2). The population seemed to decrease from 2013 to 2015.

A population outbreak was observed around Miyako Island in 2004, and starfish remained at relatively high density until 2012 (Biodiversity Center of Japan, Natural Environmental Bureau Ministry of the Environment 2015). Intensive population outbreaks were observed in 2004, 2007, and 2011 around Miyako Island, with a persistent population outbreak observed from 2005 to 2008 at Yabiji, 5 km north of Miyako Island.

9.2.5.4 Temperate Areas

A population outbreak in Kinko Bay (south of Kyushu) began in 2004, and 300–500 starfish were removed (Minaminihon Shinbun Newspaper 2004). A moderate population outbreak was observed from 2007 to 2008, and an intensive population outbreak began in 2011 (Biodiversity Center of Japan, Natural Environmental Bureau, Ministry of the Environment 2015). A population outbreak started in Kushima (south of Miyazaki) at the end of 2011 and peaked in 2013. Subsequently, possible secondary outbreaks were observed approximately 25 km north at Tsuki Island and Nichinan in 2014 and 2015, possibly via a branch current of the Kuroshio flowing northward from Kushima to Nichinan. In summer 2016, three divers still found 45 individuals (mostly >30 cm) per day around Nichinan, where almost no hard corals were left uneaten (Yasuda personal observation).

In Koshiki Island, a population outbreak suddenly started in 2010, with 13 fishermen collecting more than 1000 starfish in a day (a blog by a local person in Koshiki Island, *Web site 4) in 2011. However, according to a local fisherman, Mr. Gensui Shimono, the number of *A. planci* sensu lato dramatically decreased from 2012 onward, with just 15 individuals being found by eight divers per year in 2014. Along the western side of Kyushu, a population outbreak was observed for the first time around Amakusa from 2002 to 2003. This outbreak occurred 8 years after the first *A. planci* sensu lato was found in the Amakusa area (Yomiuri Shinbun Oct. 3, 2010). The population density between 2002 and 2003 was not very high (only hundreds of starfish were removed), and the individuals of starfish were of similar size to each other, suggesting a single mass recruitment from the south (Natural Environmental Bureau, Ministry of the Environment 2003). However, the second population outbreak in Amakusa, from 2009 to 2010, was approximately ten times larger than the previous one (over 2000 starfish were removed). At the time, different age classes of starfish were detected (including juveniles), implying a degree of local self-seeding and/or successive migration from the south (Yomiuri Shinbun Oct. 3, 2010).

Population outbreaks more intense than those observed in the 1970s (almost 50 times as many starfish removed) began around the southern part of Kushimoto (Wakayama) in 2004 and continued until 2008 (Biodiversity Center of Japan, Natural Environmental Bureau, Ministry of the Environment 2015). However, signs of potential outbreaks were detected starting in 1999 (Nomura 2004). Like the outbreaks in the 1970s, the 2004 outbreak started on the western side of Cape Shionomisaki, which is very close to the path of the Kuroshio Current. However, because of higher water temperatures (Fig. 9.8), a local researcher speculated that the large population in 2004 might have been promoted by the self-seeding of the local population. Specifically, the population was the offspring of a smaller population in 2002 that had already increased in size since 1999 (Natural Environmental Bureau, Ministry of the Environment 2005). The populations observed in 1999 and 2002 were likely formed by larval clouds transported from southern population outbreaks.

9.2.5.5 Daito Islands

The first known population outbreak at Minami Daito Island (located approximately 360 km east of Okinawa Island) was recorded in 2007, and the outbreak had ended by 2011 (Biodiversity Center of Japan, Natural Environmental Bureau, Ministry of Environment 2015). A local who has dived around Minami Daito Island for the last 30 years, Mr. Hisao Kohama, claimed he had not observed or heard *A. planci* sensu lato occurring around Minami Daito Island before the outbreak in the 2000s but said that *A. planci* sensu lato may have occurred at very low density in the past. However, a few years after major successive population outbreaks around the Okinawa Islands (although he could not remember the actual year), the number of *A. planci* sensu lato increased near the Minami Daito Island (especially around its northern part) to the extent that they were piling up on top of each other for a 3-year period (probably from 2004 to 2007). Although this island is located 360 km from Okinawa Island and is far from the main Kuroshio path, a GPS-equipped buoy released from western Okinawa Island reached Minami Daito Island within a month (Nakamura et al. 2015), implying that larval dispersal from western Okinawa Island to Minami Daito Island is possible.

9.2.6 Possible Source Origins of Secondary Population Outbreaks in Japan

Successive outbreaks (category >4 in Table 9.2) were not observed for from 1992 to 1994 in Japan (Table 9.3). Therefore, at least two prolonged successive population outbreaks have occurred in Japan: one from 1969 to 1991, beginning in western Okinawa and Kume Islands, and another from 1995 to 2015 (possibly ongoing at 2016), beginning in western Okinawa. The patterns of these two successive population outbreaks are similar: both started in the region around western Okinawa and progressed to populations in the south (Yaeyama) and north (Amami and temperate areas). The timing of the population outbreaks in Ashizuri-Uwakai and Kushimoto was also similar in both successive outbreaks. Nevertheless, it is not easy to differentiate between primary and secondary outbreaks in Japan because prolonged successive outbreaks also imply self-seeding, which obscures the primary or secondary nature of the outbreak. Thus, I have summarized the possible source populations for each new population outbreak (≥2 in Table 9.3) based on the timing of documented outbreaks in Japan, on the assumption that new outbreaks were caused by larval recruits from other outbreak populations (Table 9.4). Because a period of almost 2 years is required for *A. planci* sensu lato to reach maturity if corals are abundant, larval dispersal from a source population would need at least 2 years before a secondary outbreak. While the counter-Kuroshio Current occurs along the Ryukyu Islands, currents running from temperate to tropical areas have not been documented. Therefore, I have listed all *A. planci* sensu lato populations that have been documented at upstream of the Kuroshio and counter–Kuroshio Currents for each possible secondary outbreak. In addition, I have counted how many times the population of a particular Japanese site (>3) became the possible source origin for another outbreak (>2) that occurred 2 years after the original outbreak (Table 9.4). The areas with the highest likelihood of providing source populations were west Okinawa (44 times) and Yaeyama (40 times) (Table 9.4). If I selected the population geographically closest to the area of a new population outbreak as the most likely source origin (i.e., those shaded in Table 9.4), the highest frequency was detected for west Okinawa (22 times), followed by Amami Oshima (11 times) (Table 9.4). Therefore, one plausible source origin of secondary outbreaks in Japan is west Okinawa. The Amami Oshima population also plays an important role as a “hub population” that may connect population outbreaks from tropical to temperate areas, and it is likely critical for successive population outbreaks in temperate areas. However, more sophisticated methods (such as biophysical modeling) are required to estimate larval dispersal distances from west Okinawa to other places.

9.2.7 Places Where Population Outbreaks Have Not Been Observed in Japan

After examining the records of population outbreaks throughout Japan, I identified at least two regions (the Osumi Islands and Ogasawara) where *A. planci* sensu lato population outbreaks have not been observed (or at least recognized), although the starfish has been confirmed to be distributed at these sites (Fig. 9.5). These locations appeared to have been colonized by *A. planci* sensu lato or experienced an increase in population size after WWII (Kurata 1984; Tokioka 1953; Uchinomi 1962).

The Ogasawara Islands are isolated volcanic islands in the Pacific that formed approximately 50 million years ago and are situated roughly 1000 km south of Tokyo, Honshu. No records of *A. planci* sensu lato exist from the Ogasawara Islands before WWII, and it was first officially recorded in 1968 (Kurata 1984). A maximum of 23 individuals were found by local divers in 1979, after the large meandering Kuroshio path (LM in Fig. 9.9) approached the islands (Kurata 1984). In 1994, Tachikawa found a few individuals (Ministry of the Environment and Japanese Coral Reef Society 2004). Subsequently, *A. planci* sensu lato was rarely observed until 2011, when a single individual was observed at Chichi Island in Ogasawara (Biodiversity Center of Japan,

Table 9.4 Possible sources of secondary outbreaks and its frequency in Japan

Possible Source		Seconday Sink	Outbreak Year
Yoron	→	Okinawa W	1942
Iheya/Izena	→	Amami	1955
Yaeyama	→	Amami	1955
Amami	→	Okinawa W	1957
Amami	→	Miyako	1957
Okinawa W	→	Yoron	1972
Kume	→	Yoron	
Yaeyama	→	Yoron	
Okinawa W	→	Kerama	1972
Kume	→	Kerama	
Yaeyama	→	Kerama	
Yaeyama	→	Miyako	1973
Okinawa W	→	Miyako	
Kume	→	Miyako	
Okinawa W	→	Iheya/Izena	1973
Yaeyama	→	Iheya/Izena	
Kume	→	Iheya/Izena	
Okinawa W	→	Yoron	1973
Kume	→	Yoron	
Yaeyama	→	Yoron	
Okinawa W	→	Amami	1973
Yaeyama	→	Amami	
Kume	→	Amami	
Okinawa W	→	Miyazaki	1973
Yaeyama	→	Miyazaki	
Kume	→	Miyazaki	
Okinawa W	→	Ashizuri-Uwakai	1973
Yaeyama	→	Ashizuri-Uwakai	
Kume	→	Ashizuri-Uwakai	
Okinawa W	→	Kushimoto	1973
Yaeyama	→	Kushimoto	
Kume	→	Kushimoto	
Okinawa W	→	Yoron	1973
Yaeyama	→	Yoron	
Kume	→	Yoron	
Okinawa W	→	Iheya/Izena	1973
Yaeyama	→	Iheya/Izena	
Kume	→	Iheya/Izena	
Amami	→	Okinawa E	1975
Yoron	→	Okinawa E	
Iheya/Izena	→	Okinawa E	
Okinawa W	→	Okinawa E	
Kerama	→	Okinawa E	
Kume	→	Okinawa E	
Miyako	→	Okinawa E	
Yaeyama	→	Okinawa E	
Hateruma	→	Okinawa E	
Amami	→	Miyazaki	1976
Yoron	→	Miyazaki	
Iheya/Izena	→	Miyazaki	
Okinawa W	→	Miyazaki	
Kerama	→	Miyazaki	
Kume	→	Miyazaki	
Yaeyama	→	Miyazaki	
Amami	→	Kagoshima S	1976
Yoron	→	Kagoshima S	
Iheya/Izena	→	Kagoshima S	
Okinawa W	→	Kagoshima S	
Kerama	→	Kagoshima S	
Kume	→	Kagoshima S	
Yaeyama	→	Kagoshima S	

Possible Source		Seconday Sink	Outbreak Year
Ashizuri-Uwakai	→	Miyake	1978
Amami	→	Miyake	
Tokunoshima	→	Miyake	
Yoron	→	Miyake	
Iheya/Izena	→	Miyake	
Okinawa W	→	Miyake	
Kerama	→	Miyake	
Yaeyama	→	Miyake	
Yaeyama	→	Miyako	1979
Okinawa W	→	Miyako	
Okinawa E	→	Miyako	
Tokunoshima	→	Miyako	
Yoron	→	Miyako	
Iheya/Izena	→	Miyako	
Tokunoshima	→	Okinoerabu	1982
Amami	→	Okinoerabu	
Yoron	→	Okinoerabu	
Okinawa E	→	Okinoerabu	
Kerama	→	Okinoerabu	
Miyako	→	Okinoerabu	
Yaeyama	→	Okinoerabu	
Miyako	→	Okinawa W	1983
Yaeyama	→	Okinawa W	
Kerama	→	Okinawa W	
Okinawa E	→	Okinawa W	
Yoron	→	Okinawa W	
Tokunoshima	→	Okinawa W	
Yaeyama	→	Hateruma	1984
Miyako	→	Hateruma	
Kerama	→	Hateruma	
Tokunoshima	→	Uji	1987
Amami	→	Uji	
Kerama	→	Uji	
Okinawa W	→	Uji	
Yoron	→	Uji	
Yaeyama	→	Uji	
Hateruma	→	Uji	
Amami	→	Koshiki	1990
Tokunoshima	→	Koshiki	
Kerama	→	Koshiki	
Yaeyama	→	Koshiki	
Kerama	→	Iheya/Izena	1990
Amami	→	Iheya/Izena	
Tokunoshima	→	Iheya/Izena	
Yaeyama	→	Iheya/Izena	
Kerama	→	Kume	1990
Amami	→	Kume	
Tokunoshima	→	Kume	
Yaeyama	→	Kume	
Kerama	→	Okinawa E	1991
Yaeyama	→	Okinawa E	
Amami	→	Okinawa E	
Tokunoshima	→	Okinawa E	
Kerama	→	Okinawa W	1996
Tokunoshima	→	Okinawa W	
Amami	→	Okinawa W	
Kerama	→	Okinawa E	1997
Amami	→	Okinawa E	
Amami	→	Ashizuri-Uwakai	2000
Okinawa W	→	Ashizuri-Uwakai	
Kerama	→	Ashizuri-Uwakai	

Possible Source		Seconday Sink	Outbreak Year
Okinawa W	→	Iheya/Izena	2002
Amami	→	Iheya/Izena	
Amami	→	Kushimoto	2002
Okinawa W	→	Kushimoto	
Okinawa W	→	Okinawa E	2002
Amami	→	Okinawa E	
Amami	→	Amakusa	2002
Okinawa W	→	Amakusa	
Okinawa W	→	Yaeyama	2003
Kerama	→	Yaeyama	
Amami	→	Yaeyama	
Amami	→	Kagoshima S	2003
Okinawa W	→	Kagoshima S	
Kerama	→	Kagoshima S	
Okinawa W	→	Yaeyama	2003
Kerama	→	Yaeyama	
Amami	→	Yaeyama	
Okinawa E	→	Daoito-jima	2004
Okinawa W	→	Daoito-jima	
Kerama	→	Daoito-jima	
Amami	→	Daoito-jima	
Tokunoshima	→	Daoito-jima	
Izena/Iheya	→	Daoito-jima	
Okinawa E	→	Kume	2004
Okinawa W	→	Kume	
Kerama	→	Kume	
Amami	→	Kume	
Tokunoshima	→	Kume	
Izena/Iheya	→	Kume	
Okinawa W	→	Miyako	2004
Kerama	→	Miyako	
Okinawa E	→	Miyako	
Iheya/Izena	→	Miyako	
Ashizuri-Uwakai	→	Kushimoto	2004
Amami	→	Kushimoto	
Tokunoshima	→	Kushimoto	
Iheya/Izena	→	Kushimoto	
Okinawa E	→	Kushimoto	
Okinawa W	→	Kushimoto	
Kerama	→	Kushimoto	
Amami	→	Okinoerabu	2005
Tokunoshima	→	Okinoerabu	
Okinawa W	→	Okinoerabu	
Okinawa E	→	Okinoerabu	
Iheya/Izena	→	Okinoerabu	
Kerama	→	Okinoerabu	
Yaeyama	→	Okinoerabu	
Yaeyama	→	Muroto	2006
Miyako	→	Muroto	
Kume	→	Muroto	
Okinawa W	→	Muroto	
Okinawa E	→	Muroto	
Kerama	→	Muroto	
Tokunoshima	→	Muroto	
Ashizuri-Uwakai	→	Muroto	
Amami	→	Kagoshima S	2007
Okinawa W	→	Kagoshima S	
Okinawa E	→	Kagoshima S	
Kerama	→	Kagoshima S	
Kume	→	Kagoshima S	
Miyako	→	Kagoshima S	
Yaeyama	→	Kagoshima S	

Possible Source		Seconday Sink	Outbreak Year
Yaeyama	→	Hateruma	2008
Miyako	→	Hateruma	
Kerama	→	Hateruma	
Okinawa W	→	Hateruma	
Kushimoto	→	Miyake	2008
Ashizuri-Uwakai	→	Miyake	
Amami	→	Miyake	
Tokunoshima	→	Miyake	
Okinawa W	→	Miyake	
Kerama	→	Miyake	
Miyako	→	Miyake	
Yaeyama	→	Miyake	
Amami	→	Amakusa	2008
Tokunoshima	→	Amakusa	
Okinawa W	→	Amakusa	
Kerama	→	Amakusa	
Miyako	→	Amakusa	
Yaeyama	→	Amakusa	
Okinawa W	→	Yoron	2009
Miyako	→	Yoron	
Yaeyama	→	Yoron	
Hateruma	→	Yoron	
Kagoshima S	→	Koshiki	2010
Tokunoshima	→	Koshiki	
Okinawa W	→	Koshiki	
Miyako	→	Koshiki	
Yaeyama	→	Koshiki	
Hateruma	→	Koshiki	
Tokunoshima	→	Kagoshima S	2010
Okinawa W	→	Kagoshima S	
Miyako	→	Kagoshima S	
Yaeyama	→	Kagoshima S	
Hateruma	→	Kagoshima S	
Ashizuri-Uwakai	→	Kushimoto	2011
Yoron	→	Kushimoto	
Okinawa W	→	Kushimoto	
Miyako	→	Kushimoto	
Yaeyama	→	Kushimoto	
Amakusa	→	Goto	2011
Okinawa W	→	Goto	
Miyako	→	Goto	
Yaeyama	→	Goto	
Hateruma	→	Goto	
Ashizuri-Uwakai	→	Kushimoto	2011
Okinawa W	→	Kushimoto	
Miyako	→	Kushimoto	
Yaeyama	→	Kushimoto	
Ashizuri-Uwakai	→	Miyazaki	2011
Okinawa W	→	Miyazaki	
Miyako	→	Miyazaki	
Yaeyama	→	Miyazaki	
Hateruma	→	Miyazaki	
Okinawa W	→	Kerama	2011
Hateruma	→	Kerama	
Miyako	→	Kerama	
Yaeyama	→	Kerama	
Okinawa W	→	Yoron	2011
Miyako	→	Yoron	
Yaeyama	→	Yoron	
Hateruma	→	Yoron	

Possible source for secondary outbreak	Frequency
Okinawa W	44
Yaeyama	40
Amami	29
Kerama	28
Izena/Iheya	22
Tokunoshima	19
Miyako	18
Kume	16
Okinawa E	10
Yoron	10
Hateruma	9
Ashizuri^Uwakai	7
Amakusa	1
Kagoshima S	1
Kushimoto	1

Geographically closest source populations	Frequency
Okinawa W	22
Amami	11
Kerama	8
Ashizuri^Uwakai	6
Yaeyama	4
Tokunoshima	3
Izena/Iheya	2
Okinawa E	2
Yoron	1
Amakusa	1
Kagoshima S	1
Kushimoto	1

All possible source locations where population outbreak took place two years before the initiation of other location were listed unless it is physically impossible. Geographically nearest populations are highlighted in yellow

Natural Environmental Bureau Ministry of Environment 2015). The Ogasawara Islands are geographically isolated from the Ryukyu Islands and are not usually in the path of the main Kuroshio Current; however, the regional and local hydrodynamic patterns are largely unknown (The Ministry of the Environment and Japanese Coral Reef Society 2004). In the case of broadcast spawner coral species, Nakajima et al. (2012) found significant population differentiation between Okinawan and Ogasawara populations, indicating limited larval dispersal between the two regions. Population outbreaks have been reported in the North Mariana Islands, approximately 1000 km south of the Ogasawara Islands. Although no study has directly compared populations in Ogasawara and other Pacific Islands, previous studies using microsatellites (Yasuda et al. 2009) and mitochondrial DNA (Houk et al. 2007; Vogler et al. 2013) have indicated genetic isolation between Pacific Islands, suggesting limited larval dispersal between them. Therefore, larval dispersal from the Mariana Islands to the Ogasawara Islands is likely also limited. Kayanne et al. (2012) reported that the number of coral species is much smaller in the Ogasawara Islands than in the Mariana and Okinawan Islands, implying that the larval supply of coral species from the Mariana Islands to the Ogasawara Islands is limited.

The water temperature range of these islands is optimal (19–28 °C) for both larval and adult *A. planci* sensu lato (Ministry of the Environment and Japanese Coral Reef Society 2004). A few rivers steadily discharge into the sea from these islands; thus, the nutrient level is similar to that of other subtropical areas in Japan, such as north Okinawa Island as a whole (The Ministry of the Environment and Japanese Coral Reef Society 2004), although the nutrient concentration from the land is higher in the winter than in the summer due to limited precipitation during the summer season in the Ogasawara Islands (Nohara et al. 2009). The lower nutrient concentration due to limited precipitation during the spawning period of *A. planci* sensu lato may help prevent outbreaks in Ogasawara Islands. Another difference between the Ogasawara Islands and other coral reef areas in Japan that have experienced *A. planci* sensu lato population outbreaks is the absence of secondary population outbreaks originating from Okinawa and other areas, such as Mariana Islands. Therefore, in addition to *A. planci* sensu lato occurring at low density on the islands, secondary larval recruitment is much less than in other regions, preventing population outbreaks.

In contrast, Tanegashima and Yaku Island (Osumi Islands) are volcanic islands situated between Kyushu and the Amami Islands along the Kuroshio Current. The main stream of the Kuroshio Current flows from the East China Sea to the Pacific through these islands. The hard coral cover and number of coral species in the Osumi Islands are slightly lower than in the Ryukyu Islands, but there is higher soft coral coverage (WWF Japan 2008). Yaku Island is famous for its world heritage old cedar forest, which is supported by the highest annual precipitation in Japan, and is visited by 300,000–700,000 tourists annually, with at least 13 diving shops. An *A. planci* sensu lato was officially recorded on Yaku Island in 2003 (Nature Conservation Division, Okinawa Prefectural Government 2003). A local diver for the diving boat service Katsushinmaru, Mr. Masaru Takeishi, stated that just two individuals of *A. planci* sensu lato were observed over the last 8 years: one in 2010 and another in 2011 at Isso, in the north of Yaku Island. While basic information is more limited in Tanegashima, population outbreaks have definitely not occurred between 2003 and 2015 (Biodiversity Center of Japan, Natural Environmental Bureau, and Ministry of Environment 2015). A local diver for the Sea-Mail diving service in Tanegashima, Mr. Tetsuro Hayashi, only found one to two *A. planci* sensu lato individuals per year when the water temperature was high, although he has dived at several coral-rich places around Tanegashima almost daily since 1997.

Population outbreaks in Kyushu, Shikoku, Honshu, and even Miyake Island have been partly attributed to larval dispersal by the Kuroshio Current. The strong flow of the Kuroshio Current is believed to directly pass these islands, while the strong ocean currents around the Osumi Islands lead to the presence of few benthic species, including corals, around these islands (Hirata 1967). Juvenile *A. planci* sensu lato has a high mortality rate in the field (Keesing and Halford 1992). The growth rate of juvenile *A. planci* sensu lato dramatically increases when its food is changed from coral algae to corals (Birkeland and Lucas 1990). Therefore, without enough corals for juvenile *A. planci* sensu lato to grow quickly, mortality will be high, preventing population outbreaks. Alternatively, despite some larval transport, the survival rates of *A. planci* sensu lato juveniles that settle around these islands may be low. For instance, Mr. Tetsuro Hayashi in Tanegashima once found many small *A. planci* sensu lato juveniles (<1 cm length, probably settled that year) beneath the table corals at Nakase in 2012; however, no subsequent adult population outbreak occurred. The coral reef communities in Tanegashima are in relatively good condition; thus, predators of juvenile or adult *A. planci* sensu lato may be abundant, preventing population outbreaks. In an inquiry survey in the Okinawa Islands, a fisherman on Kume Island mentioned that, in years when the trumpet shell is abundant, the number of *A. planci* sensu lato is reported to be small (Marine Parks Center of Japan 1987). Similarly, Shirai (1956) noted that a local specialist in the collection of great green turbans (*Turbo marmoratus*) on Amami Oshima mentioned whenever he found a trumpet shell, *A. planci* sensu lato were always nearby. He also often found *A. planci* sensu lato inside the stomachs of trumpet shells (8–9 of 10 trumpet shells). These stories show that local people in Okinawa and

Amami Oshima thought the trumpet shell to be an important predator for suppressing the population density of *A. planci* sensu lato. However, it is also possible that trumpet shells vigorously ate *A. planci* sensu lato because the population density of the starfish was very high at that time.

Whatever the case, questions remain about why population outbreaks are rarely observed on other islands. Thus, the mechanisms/processes leading to population outbreaks need to be identified, and comparative analyses of these non-outbreak regions may provide answers.

9.3 Conclusions

The answers for the questions are the following:

1. Is *A. planci* sensu lato migrating toward the north like other coral species?

   I considered it is highly possible. While there is no record of *A. planci* sensu lato in temperate area between 100 and 60 years ago, now it is quite common and conspicuous. Given the increasing water temperature, it is also possible that such poleward migration is at least partly related to global warming. Further careful observations including fluctuation of the Kuroshio Current are needed.
2. Has the intensity of population outbreaks increased in recent years?

   Yes for temperate areas but not obvious for tropical ones. It was expected that intensity of population outbreaks in temperate areas such as Kushimoto, Ashizuri-Uwakai, and western side of Kyushu regions has increased based on Table 9.3. Reason for this is unclear though the sizes of population seem to be increasing even during non-outbreak periods which would be also related to the abundance of corals and less mortality of *A. planci* sensu lato during winter.
3. Is the western Okinawa population really the source of other population outbreaks in Japan?

   Considering the historical patterns (Table 9.4), yes. It is still unclear, however, how much distance large numbers of larvae can normally spread between islands causing secondary outbreaks. Population genetic methods that clarify relatively long-term migration patterns showed genetic homogeneity along *A. planci* sensu lato populations in Japan though the methods for the moment cannot distinguish secondary outbreak phenomena from a small number of migration that often occurred for evolutionally time scale.

   As a whole, it is highly possible that the impact of coral predation by *A. planci* sensu lato especially in temperate area in Japan has been increasing for several decades. Further studies regarding the balance between frequency of population outbreak of *A. planci* sensu lato and increase of corals in temperate area are critical for considering coastal conservation strategy. As the Kuroshio Current plays an important role for the transport of larvae, future examination between past ocean current pathways and the timing and spread of secondary outbreak using numerical simulation would improve our understanding of the patterns of secondary outbreaks. Furthermore, developing some methods for quantifying local self-recruitment would be important to prevent local chronicle outbreak. Direct estimation of larval identification and density in the field during spawning periods have become possible recently (Yasuda et al. 2015; Suzuki et al. 2016; Uthicke et al. 2015). Further improvement of such technique would help to gain more quantitative information about self-recruitment and make early detection of population outbreak possible in the future.

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