

Article

Seasonal Algal Host Shifts of the Symbiotic Amphipod *Ceinina japonica* Stephensen, 1933 (Amphipoda: Eophliantidae) in the Sea of Japan (East Sea)

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Abstract: The phenology of the alga-dwelling amphipod *Ceinina japonica* Stephensen, 1933 (Amphipoda: Eophliantidae) was studied at Rishiri Island, Hokkaido, Japan, from May 2016 to March 2017. Seasonal shifting between the host algal species was confirmed through observations at a coastal field site and a nearby aquaculture facility for kelp. Amphipods mainly occurred in the farmed biennial kelp *Saccharina japonica* var. *ochotensis* and wild algae *Undaria pinnatifida*, with *Agarum clathratum*, *Costaria costata*, *Saccharina cichorioides*, and *Sargassum boreale* as new host algal records. Amphipods occurred in sporophytes of *U. pinnatifida* at the field site from February to March and from May to July, but they were found in the kelp of *S. j.* var. *ochotensis* during the rest of the year, from August to the following January. Individuals of *C. japonica* infected sporophytes of the large brown alga *Undaria pinnatifida* from February to July, and *C. japonica* reproduced from July to September, a period during which the amphipods switch to a different host in July, the sporophytes of the saccharinan kelp *S. j.* var. *ochotensis*, where they stay until January. The amphipods then switched back to *U. pinnatifida* in January or February. Experimental evidence from a kelp-culturing facility also confirmed the timing of this host shift. The removal of *U. pinnatifida* from algal culture ropes in such facilities is suggested as a method to prevent amphipod damage, which is important for commercially farmed *S. j.* var. *ochotensis*.

Keywords: aquaculture pest control; *Costaria costata*; Hokkaido; Rishiri Island; symbiotic domiciles; *Saccharina japonica* var. *ochotensis*; *Undaria pinnatifida*



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1. Introduction

Various species of brown macroalgae dominate the coasts of East Asia from northern Japan to the Kamchatka Peninsula [1,2], where several species are commercially harvested as food or sources of various other algal products. Among them, many species of saccharinan kelps are economically important. *Saccharina japonica* var. *ochotensis* (Miyabe) Yotsukura, Kawashima, Kawai, and Abe & Druehl, is one of the most important algal resources in northern Hokkaido, Japan; they were artificially cultured on ropes and caught from the natural coast [3,4]. The kelp industry contributes approximately JPY 200 million (USD 2 million to the Japanese market, with production in the Hokkaido region dominating this contribution, accounting for over 90% of total kelp production [3]. Kelp is primarily used to make ‘Dashi’, a Japanese soup; its distinct flavor serves as the base for many traditional Japanese foods. Additionally, kelp is used in popular Japanese dishes such as ‘Oboro Kombu’ and ‘Tororo Kombu’. Thalli of this species are harvested from natural kelp beds in the sea or are grown in aquaculture facilities that produce both this species and *Undaria pinnatifida* (Harvey) Suringar [5–7]. The latter species is another brown macroalga that is widely explored along the coast of Honshu, Japan [6].

There are multiple crustacean species associated with kelp that can have negative impacts on their growth or reproduction. For example, the copepod *Amenophia orientalis* is known to injure the blades of sporophytes such as *U. pinnatifida* in aquaculture facilities

by burrowing into them, but their life cycles are still poorly understood [8–12]. Among amphipods, the nest-building species *Pseudopleonexes lessoniae* [13] has a negative impact on its host giant kelp *Macrocystis pyrifera* [14], whereas the small burrowing amphipod *Sunamphitoe lesoniophila* [15] can cause damage in a large kelp *Lessonia berteriana* [16].

Many species of burrowing crustaceans cohabit in heterosexual pairs that mate and reproduce within the safety of their burrow [17–19]. Macroalga-dwelling crustaceans consume algal tissue [20], *Sunamphitoe stypotruripes* excavate chambers in kelp stipes [21], and *S. femorata* makes nests on blades [22].

The alga-dwelling amphipod *Ceinina japonica* Stephensen, 1933 has been reported to penetrate the stipe of saccharinan kelps [23], inflicting damage to *U. pinnatifida*, *Saccharina angustata* Lane, Mayes, Druehl & Saunders, *S. japonica* (var. *japonica* Yotsukura, Kawashima, Kawai, Abe, & Druehl, and var. *religiosa* var. *ochotensis* Yotsukura, Kawashima, Kawai, Abe, & Druehl), and *Saccharina sculpera* Lane, Mayes, Druehl and Saunders in coastal areas from southwestern Hokkaido and the Pacific coast of northern Honshu to South Korea [23–26]. Burrowing amphipods like *C. japonica* can have a detrimental economic impact as the damaged algae are not suitable for human consumption due to the decay of the affected thalli [27–29]. In order to minimize economic losses caused by this parasite, *U. pinnatifida* are harvested earlier in algae aquaculture farms than harvested from the wild in Hokkaido. Despite their economic importance, information on the life cycles and ecology of alga-dwelling aquatic organisms is still scarce, and there is no information available at all concerning the phenology of *C. japonica*. Here, we present the results of a field study and an experiment in a kelp culture facility that revealed a host shift in the amphipod *C. japonica* during its breeding season, its life cycle, and its lifetime, including the timing of the host swap. This provides our first understanding of the life cycles of symbiotic amphipods on saccharinan kelp in Asia, a finding that may contribute to the improved management of aquacultural facilities for marine algae.

2. Materials and Methods

2.1. Study Site

This field study was conducted in the Oniwaki region of Rishiri Island, off the coast of Hokkaido in the Sea of Japan (East Sea) ($45^{\circ}7'29''$ N, $141^{\circ}17'42''$ E) (Figure 1A). The marine flora of this area is representative of northern Hokkaido [4]. The surface water temperature there is recorded daily, and the compiled temperature data are publicly available on the website of the Hokkaido Aquaculture Promotion Corporation (https://www.saibai.or.jp/water_temperature, accessed on 28 November 2023). For the present study, the monthly mean temperatures were calculated for the period of investigation based on these data.

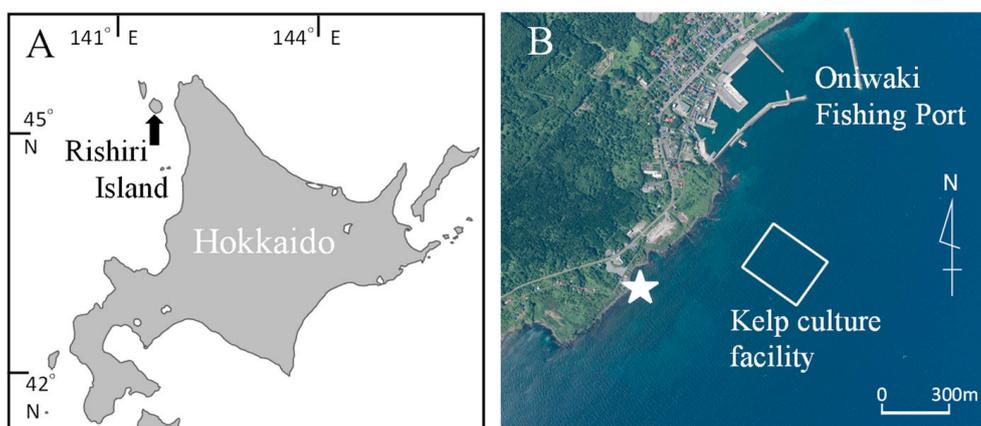


Figure 1. Cont.

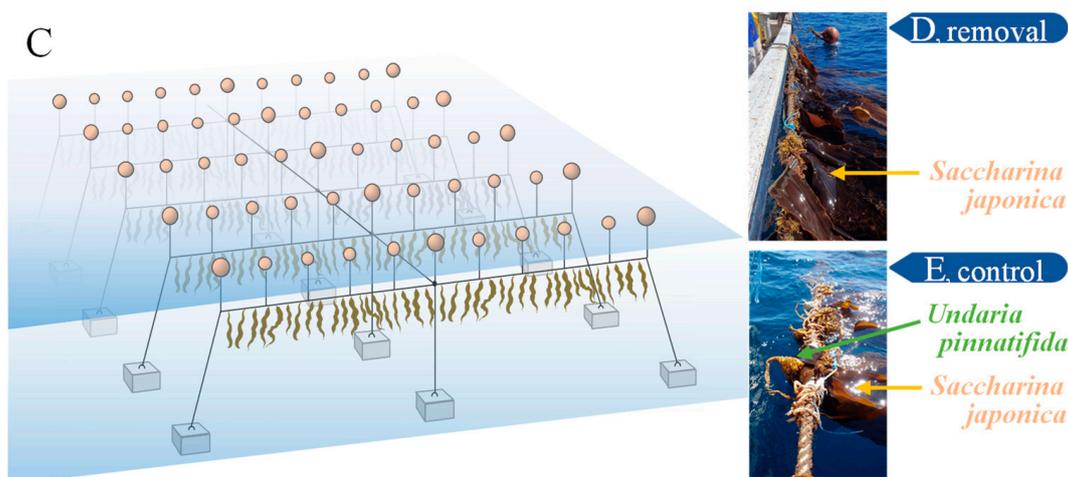


Figure 1. Sites of field sampling and experiment. Location of Rishiri Island off Hokkaido, Japan (A). Location of the nearshore monthly sampling site (white star) and offshore experimental site in the kelp aquaculture facility (white box) near Oniwaki Fishing Port, Rishiri Island (satellite photo from <https://www.gsi.go.jp/tizu-kutyu.html>, accessed on 28 November 2023) (B). Diagram of culture rope deployment in the kelp aquaculture facility; horizontal ropes are ca 300 m long and arranged in parallel at 25 m intervals, suspended approximately 5 m from floating buoys and fixed by anchor ropes to concrete blocks on the sea's bottom (C). "removal" treatment: all *Undaria pinnatifida* sporophytes were removed from the rope in April 2017 (D). "control" treatment: *U. pinnatifida* sporophytes were allowed to remain on the rope (E).

2.2. Host Algae

In order to assess the host algae species of *Ceinina japonica*, a nearshore area of ca 2500 m² and up to 2 m deep at the study site was investigated via snorkeling. A total of 110 large brown algal thalli (sporophytes of >1 m in maximum length) in that area were collected by hand on 24 May and 20 June 2016; then, these large algae were dissected and checked for the presence or absence of *C. japonica* under a stereomicroscope (Olympus SHZ10, Olympus, Tokyo, Japan).

2.3. Phenology

The host use and host shifts of *Ceinina japonica*, as well as the amphipod's breeding season in the field, were monitored at a fixed sampling site in the natural kelp forest of Oniwaki (Figure 1B). Samples were collected monthly from May 2016 to March 2017 while snorkeling at a 1–2 m water depth. On each sampling date, 100 cm × 100 cm were randomly placed on the sea's bottom in the field; then, the three most dominant kelp species, the two annuals *Undaria pinnatifida* and *Costaria costata* (C. Agardh) De Saunders, and the biennial *Saccharina japonica* var. *ochotensis*, in the quadrat were sampled. In order to collect all the *C. japonica* specimens infecting a given thallus, a knife was used to pry off the holdfast (the alga's benthic adhesion organ) along with the stipe and blade from the underlying substratum. All collected thalli were placed individually in plastic bags underwater so as to avoid the escape of *C. japonica* from them. The bagged thalli were then transported to the laboratory, where the blade lengths of all the thalli were measured, and the age of each thallus of *S. j.* var. *ochotensis* was determined based on the method of Yotsukura et al. [2]. The blade length is defined from the terminal tip of the thallus to the proximal end of the blade; the age of the thallus was discriminated from the shape of the holdfast; the collected thalli had holdfasts that were initially shaped like a single plate due to the spreading roots on the substratum. Then, the following year, due to the new plate's spreading and roots overlaying the old single plate, the layers of roots formed a conical holdfast and the type of these two layers was defined as a biennial (second year) and the type with only a new layer was defined as an annual thallus (first year). For each of the three most dominant

kelp species, the mean blade length was calculated using the largest 10 thalli, and a total of 30 sampled kelp were also checked for the presence or absence of *C. japonica* using a stereomicroscope. Herein, we considered in each of the three dominant kelp species the number of individuals of host alga infected with *C. japonica*/the number of host individuals examined as “Prevalence”, as suggested by Margolis et al. [30]. Finally, *C. japonica* was extracted from each kelp sample using the formalin-wash method; they were collected, their body length was measured, and their sex was differentiated (see below). For the measurements of the body length, the samples were carefully stretched out using forceps; then, the total length was measured from the anterior end of the cephalon segment to the posterior end of the telson with a measurement ocular in the stereomicroscope. The occurrence of ovigerous females was assessed. Males were identified based on the presence of penis appendages, and adult females were recognized from the oostegites. In preliminary observations, it was found that ovigerous females were larger than 2 mm in total length, and the number of ovigerous females among the 10 selected large females (more than 2 mm in total length) were counted to calculate the occurrence frequency of ovigerous females. Although the formalin-wash method [31,32] can enable the sampling of *C. japonica*, it was confirmed that several individuals of *C. japonica* remained in nest-like burrows in the thalli of *S. j. var. ochotensis*. Thus, the present study was not able to count the absolute number of *C. japonica* within the thalli of *S. j. var. ochotensis*, and subsequent prevalence was used comparatively. All samples were stored at Hokkaido Research Organization, Central Fisheries Research Institute, Japan.

2.4. Field Experiment

In order to examine for host shifts in the field, an experiment was conducted within a kelp aquaculture facility for *S. j. var. ochotensis*, which was situated ca 400 m from both the shore and the fixed sampling site described above (Figure 1B). There, based on the experience of kelp culture fishermen in Rishiri Island, the thalli of *S. j. var. ochotensis* were artificially attached to kelp culture ropes in December every year, but *U. pinnatifida* naturally recruited the ropes as well; this resulted in the co-occurrence of the two kelp species on the same rope within the culture facility. And under these circumstances, when only *S. j. var. ochotensis* occurred on the rope kelp, individuals usually did not become infected with *C. japonica*, whereas when the thalli of *U. pinnatifida* co-occurred on the same ropes, individuals showed a near 100% prevalence of infection by *C. japonica*.

Saccharina j. var. ochotensis sporophytes were reared in one aquaculture tank in Oniwaki Fishing Port (Figure 1B); large (more than 30–40 cm blade length) artificially reared sporophytes were selected and attached to kelp culture ropes (Figure 1C) in September 2016. By the end of April 2017, small (less than 50 cm blade length) and large (more than 100 cm) sporophytes were removed from kelp culture ropes so that the blade length of the sporophytes in the kelp culture rope was similar in April 2017.

In the experiment, three kelp culture ropes were cleaned of all *U. pinnatifida* sporophytes in April 2017, thus creating a monoculture of *S. j. var. ochotensis* on these ropes (Figure 1C, “removal” treatment). On another three kelp culture ropes, *U. pinnatifida* sporophytes were left untouched, thus resulting in a mixed culture of *S. j. var. ochotensis* and *U. pinnatifida* (Figure 1C, “control” treatment). The six culture ropes (three “removal” and three “control”) were situated at distances of 25 m from each other and were, thus, assumed not to influence either each other or other ropes’ resident amphipods. In September 2017, after 5 months of exposure, 30 sporophytes of *S. j. var. ochotensis* were collected from each of the monoculture (“removal”) and mixed culture (“control”) ropes; i.e., 90 “removal” treatment and 90 “control” sporophyte thalli were collected for observation. In the laboratory, these sporophytes were checked individually for the presence of *C. japonica*. The blade lengths of 30 collected sporophytes of *S. j. var. ochotensis* in “removal” and 30 sporophytes in the “control” were measured in September 2017.

3. Results

3.1. Host Algae

Along the shoreline of Rishiri Island and in the nearshore field site, algal communities were dominated by *Saccharina japonica* var. *ochotensis*, *Undaria pinnatifida*, and *Costaria costata*. The amphipod *Ceinina japonica* was associated with a broad spectrum of hosts as follows: *Agarum clathratum* Dumortier, *C. costata*, *Saccharina cichorioides* (Miyabe) C. E. Lane, C. Mayes, Druehl & G. W. Saunders, *S. j.* var. *ochotensis*, *U. pinnatifida*, and *Sargassum boreale* Yoshida & Horiguchi. The amphipods bored cavities (“domiciles” sensu in Mejaes et al. [33]) in the blades of the five saccharinan species (*A. clathratum*, *C. costata*, *S. cichorioides*, *S. j.* var. *ochotensis*, and *U. pinnatifida*), but were only found in the holdfasts of *S. boreale*.

3.2. Phenology

The mean water temperature was higher than 15 °C from July to September and was lower than 5 °C from January to March (Figure 2A). The occurrence of *Undaria pinnatifida* and *Costaria costata* were limited to the period at the beginning of the study in May (mean water temperature 8.7 °C), June (12.0) and again occurred in the following year from January (3.4 °C) until study’s end in March (3.5 °C) but did not occur during the summer and fall months (Figure 2B). Second-year *Saccharina japonica* var. *ochotensis* were found throughout the year, but the first-year *S. j.* var. *ochotensis* occurred from May to December (5.1 °C) and March of the next year (Figure 2B).

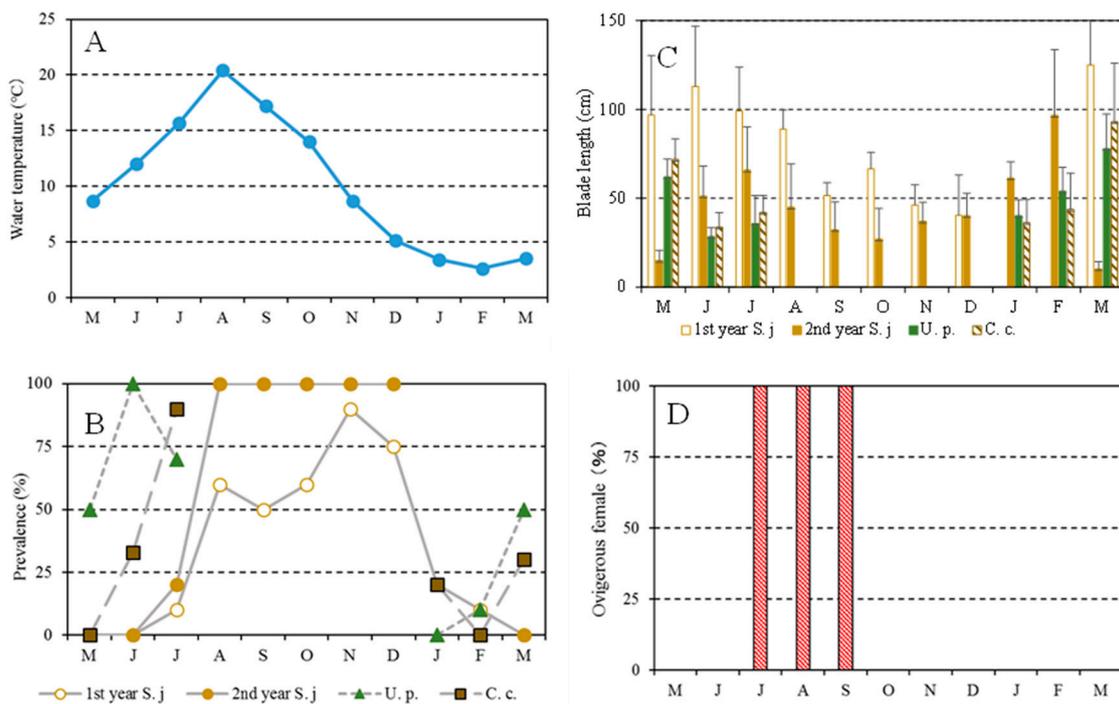


Figure 2. The phenology of host brown macroalgae and the alga-dwelling symbiotic amphipod crustacean *Ceinina japonica* at Oniwaki, Rishiri Island, Hokkaido, Japan, with monthly seawater temperature data. The monthly mean seawater temperature at Rishiri Island in 2016–2017 (A). The monthly prevalence data of *C. japonica* on each kelp species: *S. j.* = *Saccharina japonica* var. *ochotensis* (divided into two years of classes); *U. p.* = *Undaria pinnatifida*; *C. c.* = *Costaria costata* (B). The monthly changes in mean blade length distribution for each kelp species; the vertical bar is the standard deviation (C). Monthly changes in the occurrence of ovigerous females; the proportion was calculated as the number of ovigerous females of *C. japonica*/selected 10 adults (more than 2 mm in total length) and females, X 100, % (D).

Amphipod prevalence exceeded 50% in *U. pinnatifida* and was 30% in *C. costata* in June when the prevalence in *S. j.* var. *ochotensis* was less than 20% (Figure 2B). When more than

50% of amphipod prevalence was observed in *S. j.* var. *ochotensis* from August (20.4 °C) to December, the prevalence in *U. pinnatifida* and *C. costata* was reduced to zero (Figure 2B) due to senescence (Figure 2C). From January to March, the prevalence of *C. japonica* in *S. j.* var. *ochotensis* decreased to below 20%, but the prevalence in *U. pinnatifida* and *C. costata* increased from January to March (Figure 2C). Ovigerous females of the symbiotic amphipod *Ceinina japonica* were only found from July to September (17.2 °C) when the occurrence of ovigerous females reached 100% (Figure 2D).

3.3. Removal Experiment

Although blade lengths of the thalli of *Saccharina japonica* var. *ochotensis* did not differ significantly between the “control” (mean 132.9 ± 47.3 SD, mm) and “removal” (152.5 ± 36.7 SD, mm) treatments in the kelp aquaculture facility (t-statistic and $p > 0.05$) in September, there were significant differences between the treatments in the prevalence of infection with the amphipod *Ceinina japonica* (Mann–Whitney U test and $p < 0.001$) in September. On the culture ropes from which the thalli of *Undaria pinnatifida* was removed in April, the prevalence of infection in *S. j.* var. *ochotensis* in September was much lower (6.7%) than on the “control” ropes on which the two algal species co-occurred with a prevalence of 100%.

4. Discussion

Until now, only saccharinan kelp species [20,23] and *Undaria pinnatifida* [24,25] had been known as host algae of the amphipod *Ceinina japonica*. In the present study, three additional kelp species *Agarum clathratum*, *Costaria costata*, and *Saccharina cichorioides*, along with *Sargassum boreale*, were recorded as new hosts for *C. japonica* at Rishiri Island. It is possible that *C. japonica* prefers to infect the dominant kelp species, while also being able to live on *Sargassum*. The ecology of amphipod, isopod, and copepod crustaceans that inhabit domiciles and bore into brown macroalgae has been well studied [14,16,34], and the results of the present study are consistent with this previous work.

The results from the monthly field sampling at Rishiri Island and from the field experiment at an aquaculture site indicated that *Ceinina japonica* infected *Undaria pinnatifida* and *Costaria costata* from February to July, then gradually moved onto *Saccharina japonica* var. *ochotensis* from July to August, and finally reinfected the former two host species in January and February. This implies the migration of *C. japonica* between other saccharinan kelp species and *S. j.* var. *ochotensis* (Figure 3). Although at Rishiri Island, *C. japonica* principally occurred in whichever kelp species was dominant throughout most of the year, ovigerous females occurred from July to September, prevalence reached 100% from August to December, and 1st year and 2nd year *S. j.* var. *ochotensis* only occurred from August to December (Figure 2). In contrast, Kim and Kim [25] found *C. japonica* to swell in the stipe of *U. pinnatifida* during the summer on Ulreung Island, South Korea, when it is the dominant kelp species.

The present study shows that the breeding season for *Ceinina japonica* occurs in summer, which is in agreement with previous reports of ovigerous females from southwestern Hokkaido, Japan, in June 1933 [24] and Ulreung Island, South Korea, on 15 July 1989 [25]. Kodama et al. [26] reported that ovigerous females of this species were abundant during summer on the Pacific side of northernmost Honshu, Japan.

In the present study, *Ceinina japonica* could complete its life cycle in one host sporophyte, but this species has a need to shift from its old algal host species to a new host when the former host of sporophytes withers away due to senescence (Figure 2). For example, the host *U. pinnatifida* dies off in summer, and then *C. japonica* undertakes a shift in its host from *U. pinnatifida* to *S. j.* var. *ochotensis*. Kawai [34] observed under laboratory conditions that *C. japonica* has two methods to migrate from the old host to a new host: by crawling or swimming to the new host.

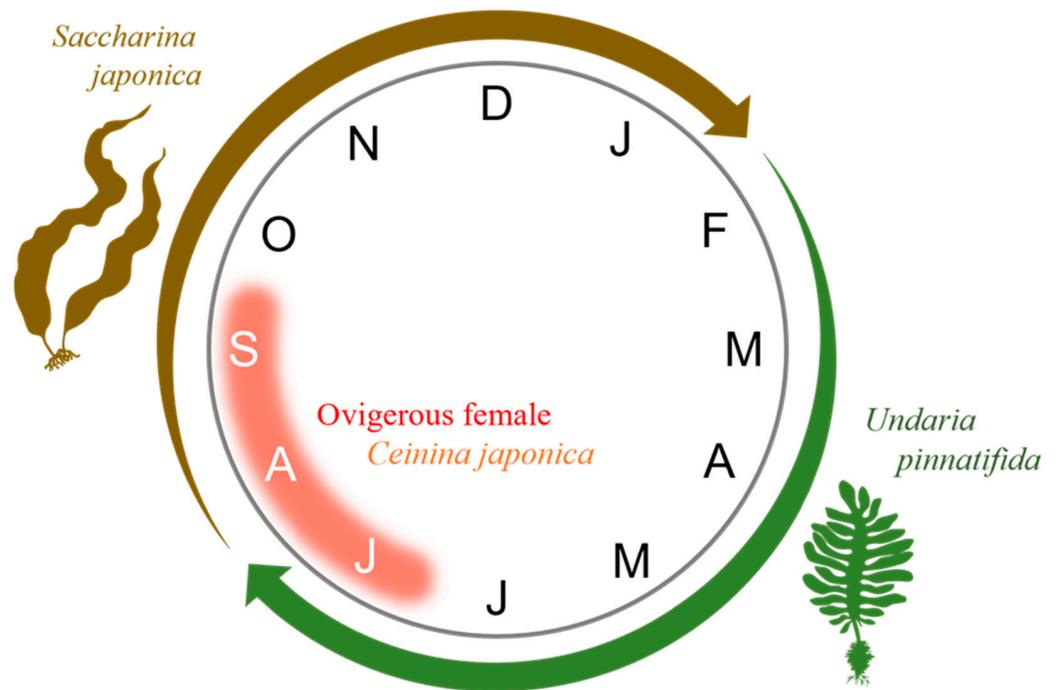


Figure 3. Schematic diagram of the life cycle and seasonal host alga shifts of the kelp-dwelling symbiotic amphipod *Ceinina japonica* at Oniwaki, Rishiri Island, Hokkaido, Japan over one year (reconstructed from data gathered over 11 months from May to March). Individuals of *C. japonica* infected sporophytes of the large brown alga *Undaria pinnatifida* from February to July. Ovigerous females occurred from July to September, a period during which the amphipods switched to a different host, the sporophytes of the saccharinan kelp *Saccharina japonica* var. *ochotensis*, where they stayed until January. The amphipods then switched back to *U. pinnatifida* in January or February.

In rope-culture aquaculture facilities in northern Hokkaido, the occurrence of *Ceinina japonica* infecting artificially cultured sporophytes of *Saccharina japonica* var. *ochotensis* occasionally becomes a serious problem [23]. The present experimental results suggest that the removal of *U. pinnatifida* from the culture ropes in such kelp-culture facilities before the breeding season of *C. japonica* could be a simple means to prevent the infection of *S. j.* var. *ochotensis* by these amphipods. These findings may, therefore, be of great significance to the kelp industry of Hokkaido, Japan.

5. Conclusions

The symbiotic and harmful amphipod *Ceinina japonica* dwells on economically important sea algae *Saccharina japonica* var. *ochotensis* as well as other less significant algae, including *Undaria pinnatifida*, *Agarum clathratum*, *Costaria costata*, *Saccharina cichorioides*, and *Sargassum boreale* along rocky shores. The individuals of *C. japonica* infect sporophytes of the large brown alga *Undaria pinnatifida* from February to July, *C. japonica* reproduces from July to September, a period during which the amphipods switch to a different host in July, and the sporophytes of the saccharinan kelp *S. j.* var. *ochotensis*, where they stay until January. The amphipods then switch back to *U. pinnatifida* in January or February. The edible and highly expensive biennial kelp *S. j.* var. *ochotensis* are cultured on aquaculture ropes along the coast of northern Hokkaido, Japan, the Sea of Japan (East Sea). *U. pinnatifida* always co-occurs on aquaculture ropes, and both species have been frequently infected by *C. japonica*. To prevent the infection of a harmful amphipod for expensive kelp *S. j.* var. *ochotensis* on the aquaculture rope of the aquaculture facility, it is effective to remove *U. pinnatifida* from aquaculture ropes that are more for an aquaculture facility, as its presence induces a higher frequency of algae infected by *C. japonica*. The best time to remove *U. pinnatifida* from aquaculture ropes is before the breeding season of an amphipod species.

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