Reproductive Strategies of Annual and Perennial Zostera marina in Mie, Central Japan

Teruwo Morita1,*, Yasushi Tsuchihashi2, Hiroyuki Okumura2, Akira Kurashima1 and Miyuki Maegawa1

Abstract: Seed production and “rafting” of Zostera marina L. in outdoor mesocosm tanks were examined to better understand the reproductive strategies of annual- and perennial-type Z. marina populations in Ago Bay, Mie. Almost all spadices on reproductive shoots of annual-type population achieved fruit ripening. Prior to seed release from spadices, annual-type reproductive shoots emerged from bottom sediments due to rafting. In contrast, reproductive shoots of perennial-type population released seeds from spadices, after which were broken off from the leaf sheath. The maturity index of the upper branches in annual-type population was higher than that of the lower branches. In perennial-type population, the maturity index of the upper branches was lower than that of the lower branches. Spadices formation in the upper branches of perennial-type population occurred continuously in the flowering season; however, the maturity index of the upper branches rapidly increased in the second half of the flowering season. Out of the 7286 seeds/m² produced by annual-type populations, 88% disappeared from the stand and 12% became buried locally. In contrast, out of the 4100 seeds/m² produced annually by perennial-type populations, 100% were buried locally.

Key words: Zostera marina; Flowering stage; Reproductive strategies; Spadix

Zostera marina L. propagates sexually and asexually (Jacobs 1982; Van Lent and Verschuure 1995) and in any one locality generally exhibits both vegetative and sexual reproduction. Annual-type Z. marina is found in the Netherlands (Hootsmans et al. 1987; Van Lent and Verschuure 1994, 1995), the Gulf of California (Phillips and Backman 1983; Meling-Lopez and Ibarra-Obando 1999; Santamaria-Gallegos et al. 2000), and Nova Scotia (Keddy and Patriquin 1978) as well as in the southern sea shore of Japan. In the central Japan, its flowering period also occurs from March to June. Between summer and fall, almost all of the reproductive and vegetative shoots wither and disappear. Thus, the seeds in the bottom sediment, which act as a seed bank, are the most important factor in the maintenance and propagation of annual-type population (Hootsmans et al. 1987; Curiel et al. 1996; Olesen 1999; Santamaria-Gallegos et al. 2000; Morita et al. 2007).

Perennial-type populations are found in the Northern Hemisphere (Silberhorn et al. 1983; Robertson and Mann 1984; Sfriso and Ghetti 1998; Van Lent and Verschuure 1994). In the central sea shore of Japan, the flowering period occurs from March to June and is characterized by the appearance of reproductive shoots, maturation and the release of seeds (Morita et al. 2007). Rhizomes that survive in bottom sediments during the summer give rise to seedlings, which appear in December. The recruitment of lateral shoots from rhizomes plays an important role in maintaining a stable population structure in perennial-type population (Abe et al. 2004).

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There have been many studies of *Z. marina* with respect to density, biomass, vegetative and reproductive shoot production, seed production and seedling germination (Phillips et al. 1983; Silberhorn et al. 1983; Hootsmans et al. 1987; Keddy 1987; Olesen 1999). However, there are few reports on the flowering stage of *Z. marina* (Keddy and Patriquin 1978; Churchill and Riner 1978; De Cock 1980) and *Z. noltii* (Caye and Meinesz 1988), and the reproductive strategies of flowering and seed production in both annual and perennial population of *Z. marina* have not been described in the literature.

Orth et al. (1994) suggested that reproductive shoots with mature seeds float out from *Zostera* beds, with a seed dispersal distance reaching 100 km (Harwell and Orth 2002). Thus, “rafting” of reproductive shoots plays an important role in new colonization for the annual-type population. Many studies confirmed rafting of reproductive shoots were mainly in annual-type population (McMillan 1983; Phillips and Backman 1983; Thayer et al. 1984; Bodnar 1985), whereas data for perennial types have not been reported. However, the density and fate of reproductive shoots in annual- and in perennial-type population are likely to be the most important factor affecting the regeneration and propagation of these populations.

In Ago Bay, central Japan, annual- and perennial-type populations grow over an area of 102 ha, mainly in the mouth of the bay, and an area of 69 ha, in the innermost portion of the bay (Okumura and Kokubu 2006). In this study, we examined flowering, seed production and rafting of reproductive shoots in outdoor mesocosms in order to elucidate the reproductive strategies of annual- and perennial-populations of *Z. marina*.

**Materials and Methods**

**Sampling site**

Ago Bay is a typical enclosed coastal sea in the Shima Peninsula, which connects to the Pacific Ocean by a very narrow and shallow entrance (Fig. 1). The entrance is 1.7 km wide and 12 m deep; the maximum depth in the middle of the bay is 40 m. Annual-type population occurs at Tategami (34°17’N; 136°47’E), at the innermost area of the bay. The Tategami population forms an extensive subtidal meadow with a depth of 1–4 m (below sea level at low tide). The sea floor at Tategami consists of muddy bottom sediments.

Ise Bay is also a typical enclosed coastal sea. The entrance is 34.7 km wide and 43 m deep; the maximum depth in the middle of the bay is 49 m. Perennial-type population occurs at Matsunase (34°36’N; 136°35’E), on the west coast of the Ise Bay. The Matsunase population forms a patchy subtidal meadow with a depth of 1–3 m, and the sediments are sandy.

**Mesocosm tank culture**

Annual- and perennial-types population, together with respective bottom sediments, were collected at Tategami and Matsunase and then cultured in 30 m³ outdoor mesocosm tanks with 2 m depth (Fig. 2) at the Mie Prefectural
Science and Technology Promotion Center in Hamajima, at the mouth of Ago Bay. The outdoor tanks were supplied with a constant flow of raw seawater obtained from a depth of 5 m off the coast of Hamajima. Average seawater temperature and salinity at Tategami, Matsunase, and Hamajima from 2003 to 2007 are shown in Fig. 3. *Z. marina* shoots and their bottom sediments were obtained from Tategami and Matsunase populations on 6 and 21 December 2006 (*n* = 5), respectively. Samples with a size of 30 × 50 × 15 cm³ (length × width × depth) were collected from dense *Z. marina* beds by scuba diving, placed in containers (30 × 50 × 20 cm³) and transported to Hamajima, where they were cultured in outdoor mesocosm tanks. The Tategami population consisted only of 15 cm long seedlings, and the Matsunase population did only of vegetative shoots.

The Tategami and Matsunase populations were separately cultured in tanks under ambient conditions of light, temperature and weather. The mesocosm tank cultures were aerated with an air compressor, and seawater temperature was recorded hourly with temperature loggers (TBI32-05+37, Onset Computer Corporation, USA). The tank cultures were continued until the end of August 2007.

**Shoot density and spadices of annual- and perennial-type populations**

From 15 March to 23 August 2007, shoots annual- and perennial-type population in plastic containers were labeled and marked on a dispersion map as follows; the ends of the sheath or stem were labeled with numbered tags. All new shoots on the rhizome beyond the clipped stem were labeled and marked. The fate of shoots was distinguished according to six categories: (1) loss of the tags in vegetative and reproductive shoots, (2) expiration of maturation in reproductive shoots, (3) floating branches of reproductive shoots, (4) floating reproductive shoots, (5) production of new lateral shoots from vegetative shoots and (6) floating vegetative shoots. Shoot density was expressed as the number of shoots/m². Shoot density was measured and compared between *Z. marina* populations.

For the natural populations in Tategami and Matsunase, vegetative and reproductive shoots were monthly collected from dense population beds within three 50 × 50 cm² plots from March to August 2007.

**Flowering and seed production by annual- and perennial-types population**

To measure flowering and seed production, 25 and 24 reproductive shoots were selected from annual- and perennial-type populations, respectively. The spadix on each branch was numbered sequentially according to the order of formation. Additionally, the number of spadices in each reproductive shoot, the flowering stage, and seed development were checked until June, when reproductive shoots emerged in both types as following six maturity stages; (1) anther visible or styles erect, (2) styles bending back and abscission of stigmata, (3) pollen release, (4) fruit ripening, (5) seed release and (6) detachment from the leaf-sheath (Fig. 4).

A maturity index was defined as the sum of numbers for the maturity stages (1–6) in each branch of the reproductive shoots. The maturity index was used to compare between branches of populations in natural and the tanks. The numbers of branches per reproductive shoot and

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**Fig. 3.** Monthly mean seawater temperature and salinity at Hamajima, Tategami, and Matsunase in Mie prefecture, central Japan, for 2003–2007.
the number of spadices per branch were also recorded in both populations until the reproductive shoots emerged. The reproductive shoots of annual- and perennial-type populations were not labeled or marked.

**Results**

**Densities of vegetative and reproductive shoot in mesocosm tank**

In the annual-type population, the density of the vegetative shoots varied from 90.7 to 125.4 shoots/m² from 28 March to 23 August (Fig. 5). The density of the reproductive shoots was initially high, 124.1 – 152.1 shoots/m², from March to May, but then decreased. Reproductive shoots accounted for 4.7 – 60% of the total shoot during March and May. In the perennial-type population, the densities of the vegetative shoots in the tanks varied from 173.4 to 249.5 shoots/m². The density of the reproductive shoots in this population was also high at the beginning of the experiment, 45.4 – 48.0 shoots/m² from March to May, but then decreased. The highest density of reproductive shoots was recorded on 15 March. By 13 June, the number of perennial-type reproductive shoots had decreased substantially, accounting for 10.1 – 17.0% of the total shoot observed during March and May, and was much lower than those of annual-type population in the same period.

**Densities of vegetative and reproductive shoot in natural population**

During 30 March to 18 July, the densities of the vegetative shoots of annual-type population ranged from 9.2 to 162.4 shoots/m² (Fig. 6). Reproductive shoots densities on 30 March were 470.4 shoots/m² but then decreased to 200 shoots/m² from April to June. Throughout the maturation season, reproductive shoots accounted...
for 37.5–96.4% of the total shoot. By 6 July, all reproductive shoots had disappeared, while the vegetative shoots disappeared by 20 August.

The densities of the vegetative shoots for perennial-type population were higher than those of the annual-type population, reaching a maximum of 513.2 shoots/m² on 27 April and decreased thereafter. The densities of perennial-type reproductive shoots were lower than those of the annual-type reproductive shoots. Throughout the maturation season, reproductive shoots accounted for 5.7–16.6% of the total shoot. By 21 August, all reproductive shoots of the perennial-type population had disappeared whereas the vegetative shoots were still alive.

**Fate of annual-type vegetative and reproductive shoots in mesocosm tank culture**

The fate of the shoots was assessed with respect to six categories (Table 1). Shoot density was expressed as the number of leaf shoots/m². The production of new lateral shoots in annual-type population was first confirmed on 2 May, with the density of new lateral shoots reaching the maximum, 28.0 shoots/m², on 31 May. The temperature range for the production of new lateral shoots in annual-type tank cultures was 17.9–25.8°C. The total production of new lateral shoots for this population was 100.0 shoots/m². The maximum number of floating annual-type vegetative shoots was obtained on 18 May, and the total density was 82.7 shoots/m². In contrast, floating reproductive shoots were firstly confirmed on 6 April, reaching the maximum density of 40.0 shoots/m² on 18 May. Floating branches of reproductive shoots firstly appeared on 28 March, and the maximum density of 22.7 shoots/m² was recorded on 18 May. Additionally, the temperature range for floating annual-type reproductive shoots and floating branches was 15.7–22.3°C and 16.5–19.7°C, respectively. The total production of floating branches and reproductive shoots was 60.0 and 88.0 shoots/m², respectively. The maturation of reproductive shoots ceased at the density of 20.0 shoots/m² (11.9%), and temperature for the whole process of opening and seed release in reproductive shoots was around 22.3°C.

**Fate of perennial-type vegetative and reproductive shoots in mesocosm tank culture**

The production of new lateral shoots in perennial-type population was firstly confirmed on 18 April (Table 1) and reached the maximum density of 29.3 shoots/m² on 11 July. The temperature range for the production of new lateral shoots was 16.8–27.4°C. Total production was 134.7 shoots/m². For the perennial-type population, the maximum density of floating vegetative shoots was 33.4 shoots/m² on 16 May, while the total production was 144.1 shoots/m². The largest cause of floating vegetative shoots in this experiment was due to grazing by Amphipoda.

### Table 1. Fate of shoots in annual- and perennial-type *Z. marina*

<table>
<thead>
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<th>Date</th>
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<td>A</td>
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</tr>
<tr>
<td>6 April</td>
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</tr>
<tr>
<td>19 April</td>
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<td>5.3</td>
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<tr>
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<td>16.0</td>
<td>8.0</td>
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<tr>
<td>31 May</td>
<td>10.7</td>
<td>28.0</td>
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<td>29 June</td>
<td>14.7</td>
<td>6.7</td>
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<tr>
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<td>10.7</td>
<td>10.7</td>
</tr>
<tr>
<td>23 August</td>
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<td>0</td>
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A; floating Vegetative shoots, B; production of new lateral shoots from vegetative shoots, C; floating reproductive shoots, D; floating branches of reproductive shoots, E; expiration of maturation in reproductive shoots, F; loss of the tags in vegetative and reproductive shoots.
Floating reproductive shoots and branches were not confirmed in perennial-type population. The complete process of opening and seed release was carried out in perennial-type population. The temperature at which the maturation of reproductive shoots ceased was 22.3°C.

Branches and spadices in mesocosm tank culture and natural population

During the maturation period, 2.6 spadices and 1.3 branches of an annual-type shoot were recorded in mesocosm tank cultures on 19 April and 2 May, respectively (Table 2). In a perennial-type shoots, the highest number of 20.5 spadices and 5.2 branches was recorded on 18 April and 5 April, respectively. The number of branches and spadices was higher in the perennial-type shoot than the annual-type shoot. The average number of seeds per spadix in annual- and perennial-type plants of natural populations was 3.6 ± 2.0 (n=25) and 4.4 ± 2.0 (n=20), respectively. So, 7286 and 4100 seeds/m² produced by annual- and perennial-type natural populations, respectively.

As for the natural population, the highest number of 10 spadices and 2.9 branches of an annual-type shoot was recorded on 19 April, respectively. In a perennial-type shoot, 12.5 spadices and 4.5 branches were recorded on 17 May and 30 June, respectively (Table 3). In the maturity season, from March to June, 1–4 spadices per branch were observed in both tank culture and natural population. The average number of seeds per spadix in annual- and perennial-type plants of natural populations was 3.6 ± 2.0 (n=25) and 4.4 ± 2.0 (n=20), respectively.

Maturity stage of spadix in mesocosm tank culture

The typical flowering and seed development processes of spadices in annual and reproductive shoots are shown in Fig. 7. The maturity stage of the spadices tended to decrease acropetally along each branch and on the terminal branch. From 3 April to 12 April, the spadices of annual-type shoots were in maturity stage 1. For almost all the spadices, maturation was not reached stage 5 until 24 May, when the seawater temperature was 19.6°C. On 31 May, floating reproductive shoots with immature seeds were observed in annual-type population. A large proportion of the spadices of annual-type

<table>
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<td>1.0 ± 0.1</td>
<td>1.9</td>
<td>15 March</td>
<td>8.6 ± 3.6</td>
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<td>2.4 ± 0.3</td>
<td>1.2 ± 0.2</td>
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<td>4.6 ± 0.7</td>
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<td>1.3 ± 0.1</td>
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<td>5 April</td>
<td>19.0 ± 2.6</td>
<td>5.2 ± 0.6</td>
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<td>2 May</td>
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<td>1.3 ± 0.1</td>
<td>2.0</td>
<td>18 April</td>
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<td>5.1 ± 0.6</td>
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<tr>
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<td>1.0 ± 0.1</td>
<td>2.1</td>
<td>1 May</td>
<td>15.1 ± 5.3</td>
<td>4.9 ± 0.6</td>
</tr>
<tr>
<td>31 May</td>
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<td>0.8 ± 0.4</td>
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<td>16 May</td>
<td>7.3 ± 4.8</td>
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<td>1.7 ± 1.7</td>
<td>0.5 ± 0.4</td>
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<td>1.5 ± 0.4</td>
<td>1.3</td>
<td>27 April1</td>
<td>9.1 ± 0.6</td>
<td>3.2 ± 0.2</td>
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<td>19 April</td>
<td>10.0 ± 1.6</td>
<td>2.9 ± 0.3</td>
<td>3.4</td>
<td>17 May</td>
<td>12.5 ± 3.9</td>
<td>3.5 ± 1.0</td>
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<tr>
<td>21 May</td>
<td>5.8 ± 1.1</td>
<td>1.8 ± 0.2</td>
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<td>30 June</td>
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<td>4.5 ± 1.3</td>
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<td>8 June</td>
<td>3.4 ± 0.6</td>
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<tr>
<td>18 June</td>
<td>1.9 ± 0.8</td>
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<td>21 August</td>
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<tr>
<td>27 June</td>
<td>0.4 ± 0.5</td>
<td>1.1 ± 0.1</td>
<td>0.1</td>
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<tr>
<td>6 July</td>
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Reproductive strategies of *Zostera marina*

Reproductive shoots were in maturity stage 4. On 11 April, the spadices of perennial-type branche had reached maturity stages 1–4. Almost all the spadices had reached maturity stage 4, and stages 5 and 6 by 25 April and 9 May, respectively. At the latter date, the temperature of seawater was 19.2°C. After one month, at the end of the flowering season, all of the spadices had reached maturity stage 6. In perennial-type population, floating reproductive shoots and floating branches were not observed.

**Maturity index of branch in tank cultures and natural population**

In the mesocosm tank culture, the highest maturity index was obtained (Fig. 8) in the 3rd branch of annual-type reproductive shoots on 3 April. Reproductive shoots with 3rd branch were rare in annual-type population. Additionally, the spadices of 3rd branch almost reached maturity stage 6, with the maximum maturity index 18 on 14 June. In June, reproductive shoots of 1st and 2nd branches were emerged. In perennial-type reproductive shoots, the maturity index of 1st branch was highest on 30 March. On that day, the maturity index of the branches varied and tended to decrease acropetally along the shoot. At the end of the flowering season, the maturity index had increased in 5th and 7th branches, and the maximum maturity index of 7th branch was recorded on 6 and 13 June.

![Fig. 7. Maturation stages of spadices in annual- and perennial-type Z. marina. (P) show Amphipod predation.](image)

![Fig. 8. Seasonal variation of maturity in each branch of reproductive shoots in mesocosm tank.](image)

![Fig. 9. Seasonal variation in the maturity of each branch of reproductive shoots in *Zostera* beds.](image)
In annual-type reproductive shoots of natural population, the maturity index of 3rd branch was lower than other branches on 30 March (Fig. 9). However, the maturity index of the branches tended to increase acropetally along the shoot. The maximum maturity index of 2nd branch occurred on 18 June. In perennial-type reproductive shoots of natural population, the maturity index of 1st branch on 27 April was highest among the branches, and that of branches varied and tended to decrease acropetally along the shoot. At the end of the flowering season, it was difficult to distinguish the maturation stages of the spadices due to grazing by Amphipoda.

**Discussion**

In this study, we examined the reproductive strategies of annual and perennial type populations of *Z. marina* in mesocosm tank cultures. The shoots were labeled and marked according to a distribution map, as it is difficult to investigate the behavior of a single spadix and shoot in natural *Z. marina* populations due to grazing.

In this study, the ratio of reproductive shoots to vegetative shoots was similar in tank and in natural population, and both annual- and perennial-type population, suggesting normal growth and maturation under mesocosm tank conditions. Several studies have reported that reproductive shoots accounted for 100% of the shoots in annual-type populations in Nova Scotia (Keddy and Patriquin 1978), the Midriff Islands (Meling-López and Ibarra-Obando 1999) and Bahía Concepción (Santamaria-Gallegos et al. 2000). In our mesocosm tanks, the ratio of reproductive shoots to vegetative shoots in annual-type population was accounted for 60% of all shoots. This result was consistent with 40–80% reported for annual-type population in Tategami (Abe et al. 2005). However, in other countries, the ratio of reproductive shoots in perennial-type population was reported to be 10–60% (Rigollet et al. 1998; Olesen 1999; Guidetti 2000), while it was 17% in the mesocosm tanks. Our result was consistent with 10–30% reported for perennial-type population in Japan (Umebayashi 1989; Kawasaki et al. 1988; Douke et al. 2000; Hayashida 2000).

In annual-type population, there were 168.1 reproductive shoots/m²; 88.0 (52.3%) as floating reproductive shoots and 60 (35.7%) as floating branches. Rafting of reproductive shoots with immature seeds with maturity stage 4 was observed in annual-type population. Only 20.0 shoots (11.9%) with spadices progressed to maturity stage 6. The production of new lateral shoots increased with increasing floating reproductive shoots and floating branches at the end of the flowering season. In annual-type *Z. marina*, floating reproductive shoots with immature seeds extend from the parent *Zostera* bed. These processes may be very useful for seed dispersal in annual *Z. marina*. Rafting of the reproductive shoots begins at a temperature of 15.7°C, which is below the critical temperature for growth of the plant. In general, about 20% of total seed production in the parent *Zostera* bed is lost due to rafting (Orth et al. 1994; Morita et al. 2007). Nevertheless, as observed in our detailed experiment in mesocosm tanks, the fate of the reproductive shoots is mainly rafting (88%).

In perennial-type population, neither floating reproductive shoots nor floating branches were present among the 45.4 reproductive shoots/m². However, all perennial reproductive shoot with spadices progressed to maturity stage 6. The production of new lateral shoots in perennial-type population started 2 weeks earlier than in plants of the annual-type. As for perennial-type population in mesocosm tanks, all reproductive shoots formed from rhizomes and not from seeds. Additionally, rafting of perennial-type reproductive shoots was not observed in tank cultures. So, the role of perennial reproductive shoots may maintain the population.

Churchill and Riner (1978) reported that the maturity stages of spadices tended to increase acropetally along the shoot. In this study, the opposite was found; i.e., decreasing acropetally along the branches and the terminal branch. Floating reproductive shoots with mature seeds have been confirmed in *Z. marina* populations (McMillan 1983; Phillips and Backman 1983; Thayer et al. 1984; Bodnar 1985; Morita et al. 2007). Additionally, the fate of rafting reproductive shoots was described in several studies (Setchell 1929;
Churchill et al. 1978; De Cock 1980; Robertson and Mann 1984; Olesen and Sand-Jensen 1994; Christensen et al. 1995; Harwell and Orth 2001). De Cock (1980) carefully observed the morphology and development of spadices and fertile shoots of Z. marina. Keddy and Patriquin (1978) classified the maturation stages of reproductive shoots in annual- and perennial-type Z. marina, dividing them into 10 groups. Those authors reported that the reproductive shoots of both types of Z. marina progressed to maturity stage 10. In this study, while many annual-type reproductive shoots in the mesocosm tanks exhibited immature seeds, only perennial-type reproductive shoots released seeds from spadices. Churchill and Riner (1978) first observed seed release on June 17, when the seawater temperature had reached 21°C. In this study, the temperature for seed release from spadices in annual- and perennial-type population was 19.7–22.3°C and 19.2–22.3, respectively. However, in annual-type population, floating reproductive shoots and branches were first detected at temperatures of 15.7 and 16.5°C, respectively, indicating a wider temperature range for seed dispersal in annual-type population than in perennial-type population.

A comparison of the maturity index of branches in mesocosm tank cultures of annual- vs. perennial-type population showed that the maturity index of the branches varied and tended to increase acropetally along the shoot in annual-type population. However, the observation of reproductive shoots with immature seeds in annual-type population evidenced that the maturity index decreased after 1st and 2nd branches. In contrast, in perennial-type population, the maturity index of branches varied and tended to decrease acropetally along the shoot during the early flowering season. Furthermore, spadices formed in the upper branches at the end of the flowering season. Thus, maturation of the upper branches rose sharply and confirmed the large discrepancy between annual- and perennial-type population regarding the maturity index.

Acknowledgment

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References


三重県における一年生および多年生アマモの繁殖戦略

森田晃央・土橋靖史・奥村宏征・倉島 彰・前川行幸

本研究では、屋外のメガソスム水槽にて一年生および多年生アマモの種子形成とラフティングを調査し、英虞湾におけるアマモ群落の繁殖戦略を検討した。一年生アマモのほとんどの花穂で種子形成が認められたが、多くの植株で種子放出までにラフティングが観察された。一方の多年生アマモでは、全ての花穂から種子が放出し花穂基部から花穂が脱落した。さらに、一年生アマモの成熟指数は、上部のユニットで高く下部ユニットで低い傾向となった。一方で多年生アマモの成熟指数は、上部のユニットで高く下部ユニットで低い傾向を示した。また、メガソスム水槽で得られたデータから、一年生アマモ群落の種子形成数は786粒/㎡であり、群落外へ88%流出し群落内に12%落下し、多年生アマモ群落の種子形成数は4100粒/㎡で、全ての種子が群落内に落下した。