P.S.Z.N. I: Marine Ecology, 13 (2): 175–185 (1992)

ISSN 0173-9565

Accepted: July 15, 1991

Vegetative Reproduction in *Posidonia oceanica*

II. Effects of Depth Changes on Transplanted Orthotropic Shoots

HEIKE MOLENAAR & ALEXANDRE MEINESZ

Laboratoire Environnement Marin Littoral, Université de Nice-Sophia Antipolis, Parc Valrose, F-06108 Nice Cedex 2, France.

With 1 figure and 5 tables

Key words: Transplantation, *Posidonia oceanica*, Mediterranean Sea.

Abstract. In an investigation of vegetative reproduction in *Posidonia oceanica,* carried out in Corsica, survival and development were studied in initially orthotropic rhizomes transplanted to different depths. Batches of transplants originating from 30 m depth and replanted in shallower water (3, 14, and 20 m) showed survival of 96 to 100 % after eleven months, with ramification in 42 % of the transplants and root formation in 44 %. After the same time interval, batches originating from 3 m depth and transplanted to deeper water showed lower survival – 59 % at 14 m, 41 % at 29 m, and 3 % at 36 m – complete absence of ramification, and rooting in only one batch. Transplantation to water shallower than their origin was favorable for survival, growth, and development, while transplantation to deeper water led to progressively lower survival, growth, and development of the shoots. Whatever the depth at which they were replanted horizontally, most transplants changed their growth mode from orthotropic to plagiotropic, as evidenced by both the change in leaf growth angle from horizontal to oblique and by the development of shorter, narrower leaves.

Problem

Although *Posidonia oceanica* (LINNAEUS) DELILE is the principal marine phanerogam in the Mediterranean (DEN HARTOG, 1970), understanding of its potential for vegetative reproduction remains poor. Vegetative reproduction appears to be the principal means of proliferation in this species, which can spread horizontally by slow growth, only 3 to 7 cm $\cdot$ a^{-1}, of plagiotropic rhizomes (CAYE, 1980; MEINESZ & LEFEVRE, 1984). Storm activity also detaches rhizomes, which then propagate as natural transplants. MEINESZ & LEFEVRE (1984) showed in a cartographic study that this natural transplantation could amount to only three transplants $\cdot$ ha^{-1} $\cdot$ a^{-1} on a favourable substrate.

MEINESZ *et al.* (1990) recently reviewed 100 publications involving culture and transplantation in 37 species of marine phanerogams worldwide. In *Posidonia oceanica,* MAGGI (1972, 1973), CINELLI (1980), GIACCONE & CALVO (1980), and

U. S. Copyright Clearance Center Code Statement: 0173-9565/92/1302-0175$02.50/0

COOPER (1982) have carried out transplantation experiments. However, some of the authors used pieces of rhizome found floating or cast up, and they did not give details of the size, morphology, or the state of these transplants; only partial details of the results are available. In transplant experiments carried out under aquarium conditions (OTT, 1979; MEINESZ *et al.*, 1991) the mortality rate was in excess of 50 %, but the results suggested that transplantation would prove a powerful tool for investigating the mechanisms of vegetative reproduction in *P. oceanica.* It might ultimately lead to the development of routine techniques for restoring seagrass beds. These results led to the work by MEINESZ *et al.* (1992) on orthotropic rhizomes transplanted *in situ,* which showed the effects both of rhizome size and transplantation season on growth and development of transplants.

The present investigation addresses the effect of changes in depth on similar, orthotropic transplants. Depth change is an important factor in the natural vegetative reproduction of *P. oceanica* because rhizomes are frequently broken away during storms. This process occurs mostly at shallow depths, where water movement is violent. These potential transplants are then dispersed to water of various depths. We thus investigated transplant growth and development throughout the depth range occupied by *P. oceanica* on the Corsican coast, *i. e.,* 0 to 40 m.

Material and Methods

1. Study areas

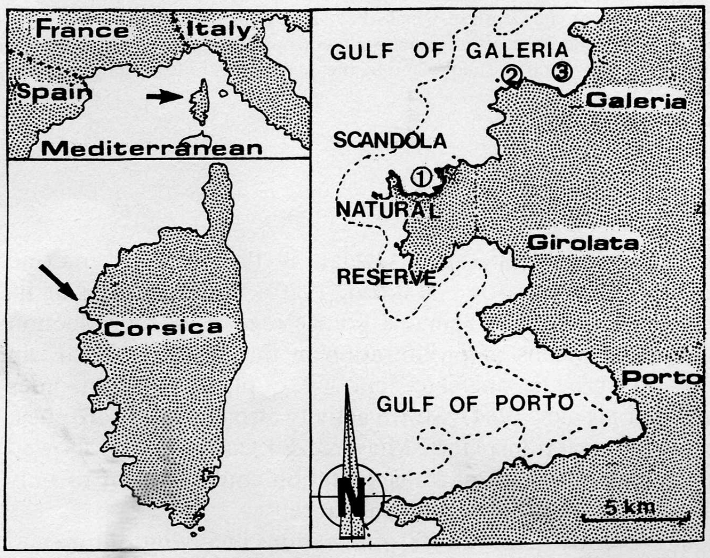

Fig. 1. Study area. 1: station in the marine reserve of Scandola (3 m depth). 2: station in the Gulf of Galeria (20, 29, 36 m). 3: station in the Gulf of Galeria (14 m).

The investigation was conducted in the waters of the Parc Naturel Régional de la Corse (French Department of Haute-Corse), on the west coast of the island (42°25′ N, 8°35′ E). One of the stations was in the marine reserve of Scandola, while the other two were in the Gulf of Galéria (Fig. 1).

2. Collection, preparation, and fixation of experimental transplants

Orthotropic rhizomes were collected by SCUBA diving in *P. oceanica* meadows. One set of batches was obtained in 3 m of water where the meadow density was 640 leaf bundles · m^{-2}, and a second set was taken in 30 m where the density was 168 bundles · m^{-2}.

Transplants were carefully selected on the basis of their size, state, and general appearance. They consisted of non-ramified orthotropic rhizomes. Any roots or epiphytes were removed. These experimental transplants were fixed horizontally to rectangles of plastic meshing 60 cm long by 17 cm wide (1 cm square mesh; see Fig. 3 in Meinesz *et al.*, 1992). Before transplantation, all rhizomes were sectioned transversely so that they were of the same apparent length, 12 cm. The apparent length is the distance from the transverse section to the extremity of the first dead petiole remaining on the rhizome, while the real length is that from the transverse section to the terminal caulinary meristem (see Fig. 2: Lr in Meinesz *et al.*, 1992). The real length, measured on 100 rhizomes before transplantation, was 7.3 (sd = 0.9) cm.

The horizontal position of the experimental transplants corresponds to that typically found in nature, when portions of rhizome torn away by water movement come to rest horizontally on the sea bed before attachment.

Similar attempts using shoots fixed to grids have already been made in *Posidonia australis* (Brown) Hook (Larkum, 1976), *Posidonia oceanica* (Cinelli, 1980; Cooper, 1982; Meinesz *et al.*, 1992), and by Fonseca *et al.* (1979) and Kenworthy *et al.* (1980) for both *Halodule wrightii* Ascherson and *Zostera marina* Linnaeus.

Transplants obtained at 3 m depth were replanted in batches of 72 at 3 m (control), 14 m, 20 m, 29 m, and 36 m. Transplants obtained at 30 m were replanted in similar batches at the same depths. Each batch was divided among four meshing supports. A total of 720 shoots were thus replanted. The substrates used for transplantation were portions of natural *P. oceanica* meadows which had been cleared by hand. They thus constituted favourable substrates.

3. Monitoring the development of transplants

The rhizomes were transplanted in August 1988. They were examined for the first time after six months, in February 1989, when half of each batch was removed by SCUBA diving. The following parameters were noted for each transplant: state (live or dead), change in orientation (orthotropy-plagiotropy), presence of ramification, presence of new roots, remains of flowers (some flowering occurred in autumn 1988).

After detailed examination, these transplants were replaced by SCUBA diving; we also noted the *in situ* state of those transplants left undisturbed.

A second examination was made in July 1989, eleven months after transplantation; all the batches were removed. The parameters noted were the same as above. Additionally, however, the number of leaves in terminal leaf bundles as well as their lengths and widths were recorded, both in the harvested batches and in 50 control rhizomes taken from wild plants in adjacent *P. oceanica* meadows. These parameters were determined for each of three categories of leaves defined by Giraud (1977): adult, intermediate, and juvenile.

From longitudinal sections made of the rhizomes (Meinesz *et al.*, 1991, 1992), the living and necrosed portions were drawn on tracing paper. This permitted the necrosed part of the longitudinal section to be quantified and expressed as a percentage of the whole area.

4. Statistics

Confidence limits at 95 % were calculated for the following parameters: survival, ramification, rooting, change in orientation, measured area of necrosis. The significance of comparisons in number, length, and width made between different categories of leaves was determined using Students's t-tests.

Results

1. Success rate of fixation method

The method of fixation to the substrate was fairly successful, although some losses occurred during winter gales. The following batches were lost: the controls replanted at 3 m and 30 m depth; and the transplants obtained at 3 m and replanted at 20 m.

2. Survival of transplants

As shown in Table 1, the rhizomes obtained at 30 m and transplanted to shallow depths – 3 m, 14 m, and 20 m – showed 96 % to 100 % survival after six months, and 93 % to 100 % after eleven months. Those transplanted in deeper water, 36 m, were significantly less successful, with only 88 % surviving after six months and 72 % after eleven months.

The rhizomes obtained at 3 m and planted in deep water (see Table 2) showed much lower survival rates than their counterparts obtained in deep water, with six-months survival rates of only 14 % at 36 m, 74 % at 29 m, and 81 % for those grown at 14 m. The corresponding survival figures after eleven months were

Table 1. Survival and changes in surviving orthotropic rhizomes, originating at 30 m depth, transplanted to 3 14, 20, and 36 m after 6 and 11 months transplantation. *: significantly different from the transplants at 20 m **: significantly different from all other batches; ***: significantly different from the transplants at 36 m; n number of shoots.

transplant depths (m)	date of monitoring	survival (%)	confidence limits (n) 95 %	ramification (%)	confidence limits (n) 95 %	changes in orientation (%)	confidence limits (n) 95 %	root formation (%)	confidence limits (n) 95 %
3 m	2/89	96	91–100 (72)	6	0–13 (70)	/	/	11	0–22 (70)
	7/89	93	86–100 (72)	22	10–34 (67)	77	65–89 (67)	43	29–57 (67)
14 m	2/89	98	94–100 (72)	15	5–25 (71)	/	/	11	1–21 (71)
	7/89	96	91–100 (72)	42	28–56 (70)	91***	83–99 (70)	44	30–58 (70)
20 m	2/89	100	/ (72)	0	0 (72)	/	/	28	13–43 (72)
	7/89	100	/ (72)	22	3–41 (72)	58	35–86 (72)	28	7–49 (72)
36 m	2/89	88*	80–96 (72)	0	0 (63)	/	/	3*	0–9 (63)
	7/89	72**	61–83 (72)	11	3–19 (52)	63	51–75 (52)	0	0 (52)

Table 2. Survival and changes in surviving orthotropic rhizomes, originating at 3 m depth, transplanted to 14, 29, and 36 m after 6 and 11 months transplantation. * : significantly different from all other batches; n: number of shoots.

transplant depths (m)	date of monitoring	survival (%)	confidence limits (n) 95 %	ramification (%)	changes in orientation (%)	confidence limits (n) 95 %	root formation (%)	confidence limits (n) 95 %
14 m	2/89	74	62–86 (72)	0	/	/	11	0–23 (53)
	7/89	5	46–72 (72)	0	/	/	/	/
29 m	2/89	81	68–94 (72)	0	/	/	0	/ (58)
	7/89	41	24–58 (72)	0	0	/ (30)	0	/ (30)
36 m	2/89	14*	6–22 (72)	0	/	/	0	/ (10)
	7/89	3*	0–7 (72)	0	/	/	0	/

3 %, 41 %, and 59 %. Those transplanted at 36 m showed a significantly lower survival rate than those transplanted at the other depths.

Transplantation to deeper water thus progressively reduced the survival rate of transplants, while transplantation to shallower conditions tended to increase survival.

3. Development and growth of transplants

Mode of growth. In all batches originating from 30 m, change from orthotropic (leaf bundles horizontal) to plagiotropic (leaf bundles sub-vertical) growth had occurred in 58 % to 91 % of the transplants still living after eleven months. The transplants at 14 m, originating at 30 m, showed a significantly higher rate of change in orientation then those transplanted to 36 m depth (Table 1).

In material originating at 3 m, however, only 44 % of transplants of one batch (14 m) had changed to plagiotropic growth after eleven months (Table 2).

Ramification. Table 2 shows that none of the material originating from 3 m ramified at all. Material originating from 30 m, however, ramified, with 22 % to 42 % of batches having developed new ramifications after eleven months in shallow depths, but only 11 % at 36 m (Table 1).

Transplantation to greater depths was thus detrimental to ramification, while transplantation to shallower water increased ramification.

Root development. Table 2 shows that in the material originating from 3 m, only the batch transplanted to 14 m developed roots. In material originating from 30 m (Table 1), root formation after eleven months had occurred in 28 % to 44 % of plants transferred to shallow water. In the batch transferred to 36 m, the small percentage (3 %) of plants which exhibited roots after six months were no longer alive after eleven months.

Transplantation to greater depths thus reduced root development, while transplantation to shallower water increased it.

Table 3. Mean number of leaves per foliar bundle for the different types of leaves. Control rhizomes represent those growing undisturbed in the meadow.

original depth	trans-plant depth	adult leaves	sd	inter-mediate leaves	sd	juvenile leaves	sd	n	total leaves	sd
control	30 m	4.2	0.7	1.3	0.6	2.6	0.5	9	8.1	1.2
30 m	3 m	3.6	1.2	1.7	0.6	3.1	1.1	12	8.4	1.7
30 m	14 m	3.8	0.9	1.4	0.7	2.6	0.5	10	7.8	1.2
30 m	20 m	4.6	0.8	1.9	0.7	3.7	0.9	14	10.2	1.4
30 m	36 m	3.2	1.1	1.2	0.6	2.9	0.7	18	7.3	1.4
control	3 m	4.7	0.6	0.9	0.3	2.7	1.2	10	8.3	1.4
3 m	14 m	3.9	0.9	1.7	0.5	2.4	0.8	10	8.0	1.3
3 m	29 m	2.4	0.5	0.1	0.5	0.2	0.5	9	5.4	0.9
control	14 m	3.8	0.7	1.3	0.6	2.5	0.6	16	7.6	1.5

Leaves. The mean numbers of adult, intermediate, juvenile, and total leaves per plant are shown in Table 3. For the material originating at 30 m, the number of leaves per transplant showed a maximum at 20 m and decreased significantly at both smaller and greater depths. This 20 m maximum was also shown by all three leaf categories, but the differences were not always statistically significant.

For the material originating at 3 m, there was no difference in total leaf number between transplants at 14 m and undisturbed controls at 3 m. The number of adult leaves decreased progressively with depth, but the number of intermediate leaves showed a significant maximum at 14 m. Grown at 14 m, transplants from 30 m and 3 m showed no difference in leaf number. Controls and transplants grown at similar depths had similar numbers of total leaves, although some significant differences did occur for adult and intermediate leaves.

In all batches, adult leaves in the transplants – growing horizontally – were significantly shorter and narrower than in undisturbed rhizomes growing vertically, both at the site of origin and at the transplantation site (Table 4). The

Table 4. Mean length and width of the different types of leaves (mm). Control rhizomes represent those growing undisturbed in the meadow.

original depth	trans-plant depth	adult leaf length	sd	adult leaf width	sd	n	inter-mediate leaf length	sd	inter-mediate leaf width	sd	n
control	30 m	427.9	117.7	10.0	0.6	12	263.5	171.4	9.5	0.5	13
30 m	3 m	214.2	53.8	8.7	0.5	18	103.7	42.5	8.4	0.6	19
30 m	14 m	229.3	53.2	8.6	1.2	34	105.0	41.9	8.5	0.6	14
30 m	20 m	294.4	97.0	8.9	1.0	26	100.3	40.5	8.9	0.8	20
30 m	36 m	319.5	111.9	8.9	0.9	30	168.8	91.7	8.7	0.8	17
control	3 m	563.5	145.7	10.6	0.5	10	147.9	48.9	10.7	0.5	7
3 m	14 m	289.8	71.3	9.6	0.7	31	106.5	47.4	9.2	0.7	17
3 m	29 m	340.0	119.5	8.9	0.8	9	108.9	58.8	8.3	0.7	9
control	14 m	427.3	111.9	9.1	0.6	48	242.3	148.0	8.5	0.9	20

Table 3. Mean number of leaves per foliar bundle for the different types of leaves. Control rhizomes represent those growing undisturbed in the meadow.

original depth	trans-plant depth	adult leaves	sd	inter-mediate leaves	sd	juvenile leaves	sd	n	total leaves	sd
control	30 m	4.2	0.7	1.3	0.6	2.6	0.5	9	8.1	1.2
30 m	3 m	3.6	1.2	1.7	0.6	3.1	1.1	12	8.4	1.7
30 m	14 m	3.8	0.9	1.4	0.7	2.6	0.5	10	7.8	1.2
30 m	20 m	4.6	0.8	1.9	0.7	3.7	0.9	14	10.2	1.4
30 m	36 m	3.2	1.1	1.2	0.6	2.9	0.7	18	7.3	1.4
control	3 m	4.7	0.6	0.9	0.3	2.7	1.2	10	8.3	1.4
3 m	14 m	3.9	0.9	1.7	0.5	2.4	0.8	10	8.0	1.3
3 m	29 m	2.4	0.5	0.1	0.5	0.2	0.5	9	5.4	0.9
control	14 m	3.8	0.7	1.3	0.6	2.5	0.6	16	7.6	1.5

Leaves. The mean numbers of adult, intermediate, juvenile, and total leaves per plant are shown in Table 3. For the material originating at 30 m, the number of leaves per transplant showed a maximum at 20 m and decreased significantly at both smaller and greater depths. This 20 m maximum was also shown by all three leaf categories, but the differences were not always statistically significant.

For the material originating at 3 m, there was no difference in total leaf number between transplants at 14 m and undisturbed controls at 3 m. The number of adult leaves decreased progressively with depth, but the number of intermediate leaves showed a significant maximum at 14 m. Grown at 14 m, transplants from 30 m and 3 m showed no difference in leaf number. Controls and transplants grown at similar depths had similar numbers of total leaves, although some significant differences did occur for adult and intermediate leaves.

In all batches, adult leaves in the transplants – growing horizontally – were significantly shorter and narrower than in undisturbed rhizomes growing vertically, both at the site of origin and at the transplantation site (Table 4). The

Table 4. Mean length and width of the different types of leaves (mm). Control rhizomes represent those growing undisturbed in the meadow.

original depth	trans-plant depth	adult leaf length	sd	adult leaf width	sd	n	inter-mediate leaf length	sd	inter-mediate leaf width	sd	n
control	30 m	427.9	117.7	10.0	0.6	12	263.5	171.4	9.5	0.5	13
30 m	3 m	214.2	53.8	8.7	0.5	18	103.7	42.5	8.4	0.6	19
30 m	14 m	229.3	53.2	8.6	1.2	34	105.0	41.9	8.5	0.6	14
30 m	20 m	294.4	97.0	8.9	1.0	26	100.3	40.5	8.9	0.8	20
30 m	36 m	319.5	111.9	8.9	0.9	30	168.8	91.7	8.7	0.8	17
control	3 m	563.5	145.7	10.6	0.5	10	147.9	48.9	10.7	0.5	7
3 m	14 m	289.8	71.3	9.6	0.7	31	106.5	47.4	9.2	0.7	17
3 m	29 m	340.0	119.5	8.9	0.8	9	108.9	58.8	8.3	0.7	9
control	14 m	427.3	111.9	9.1	0.6	48	242.3	148.0	8.5	0.9	20

same relationship held for intermediate leaves, except for two cases in which the differences were not statistically significant. This modification in leaf size likely reflects the change in growth mode from orthotropic to plagiotropic.

Rhizomes. After eleven months, increase in real length ranged from 0.8 to 2.8 cm (Table 5). This increase is significant (at 99 %) in all batches. The change in apparent length ranged from a reduction of 1.0 cm to an increase of 1.2 cm. That apparent length remained largely unchanged is due to the sum of two opposing factors: growth by the terminal meristem versus loss at the basal part of the rhizome as a result of necrosis.

Two zones were present in longitudinal rhizome sections, a pinkish zone towards the meristematic end (living tissue), and a brownish zone towards the sectioned end (necrosed tissue). Light microscopy using Congo red, which stains cellulose, and iodine green, which stains lignin, showed that in the scar zone the parenchyma cells are lignified. After eleven months, the mean length of the living part of the rhizome varied in different batches from 4. 2 to 6.9 cm between the terminal caulinary meristem and the scar of lignified cells. As shown in Table 5, transplants originating at 30 m depth and replanted at shallow depths (3 to 20 m) showed necrosed tissue representing 13 % to 28 % of the longitudinal section, while in those replanted at 36 m, necrosed tissue represented 35 %; the differences between these percentages are not significant.

In transplants originating at 3 m, necrosed tissue represented 19 % in those replanted at 14 m and 48 % in those replanted at 29 m. Displacement to greater depths thus resulted in progressively greater proportions of necrosed tissue in rhizomes.

Flowering. In the meadow from which the transplants at 30 m were taken, 14 % of rhizomes (sampled haphazardly) bore a flower stalk in August 1988 (flowering occurred in autumn 1987). Of the rhizomes transplanted (any bearing floral spikes at the time were rejected), the percentage having flowered two months

Table 5. Percentage of necrosed area of rhizome after 11 months, apparent and real length of the rhizomes (cm). * : significantly different from the transplants at 36 m; ** : significantly different from all other batches originating from the same depth; n: number of shoots examined.

original depth	transplant depth	percentage of necrosed area (%)	confidence limits −95 %	mean apparent length of rhizomes (cm)	sd	mean real length of rhizomes (cm)	sd	n
at transplantation:		0	/	12.0	0	7.3	0.9	50
after 11 months:								
30 m	3 m	13.3	3–23	11.0	0.9	8.1**	0.9	12
	14 m	28.1	14–42	11.9	0.8	9.6*	0.6	10
	20 m	21.5	9–35	12.2	0.5	9.2	0.8	10
	36 m	35.3	23–47	12.2	0.5	8.8	0.5	15
3 m	14 m	18.9	7–31	13.2	0.7	10.1**	0.6	10
	29 m	47.5**	31–65	12.5	0.7	8.7	0.5	9

later in October was 33 % of those planted at 3 m, 21 % of those at 14 m, and 0 % of those at both 20 m and 36 m. Transplantation to shallower water thus increased flowering.

Discussion

Orthotropic transplants of *Posidonia oceanica* selected at 30 m depth survived and developed well when replanted in shallower water. By contrast, transplants selected from a shallow-water (3 m) meadow survived and developed progressively less well the deeper the water in which they were replanted. This investigation permits the comparative efficacity of vegetative reproduction to be estimated for natural transplants torn away by water movement. These natural transplants are generally orthotropic rhizomes and are most likely to be torn away in shallow water (0 to 10 m), where wave action is greatest. Rhizomes originating from such depths are probably mostly cast up on beaches or carried to greater depths. Our results suggest that the greater part of naturally torn away rhizomes would not survive.

Unlike on most coasts of Corsica, retreat of the lower limit of *P. oceanica* meadows has been widely documented on the coasts of the Provence-Alpes-Côte-d'Azur region (South of France), where it frequently attains some tens of meters. This retreat has been ascribed to increased water turbidity due to coastal development and pollution (MEINESZ & LAURENT, 1978). With recent and ongoing construction of numerous wastewater treatment plants, improvement in water quality and transparency is awaited. Our results suggest that *P. oceanica* will be slow to recolonize the deeper waters once these are rendered more suitable, because natural transplants originate mostly in shallow water and are less likely to survive, grow, and develop at greater depths. The only significant natural method of recolonization may be slow, horizontal growth of the nearest surviving rhizomes.

WEST *et al.* (1990) investigated the effects of transplanting *Posidonia australis,* originating at 1 m depth, to 1, 2, and 3 m using different fixation methods. Three months after transplantation using the best fixation method (steel pegs), survival was found to decrease with increasing depth, as in the present study.

Previous work under aquarium conditions has yielded relatively low survival rates: 50 % after 22 months (OTT, 1979); 41 % after one year (MEINESZ *et al.,* 1991). Higher survival after one year (up to 97 %) has recently been obtained *in situ* at 4 m depth by MEINESZ *et al.* (1992). The present work shows that by selecting material originating from deep water (30 m) and transplanting to 3–20 m, even greater survival can be obtained (93 % to 100 %).

MEINESZ *et al.* (1992), working entirely at 4 m, found that summer was the least favourable season for transplantation, apparently because high water temperatures favour necrosis, which spreads in from the cut end of the rhizome: they obtained 67 % to 88 % survival after one year for transplants made in June, and 92 % to 97 % for transplants made in September. Our transplants, made in August, gave survival rates after eleven months of 93 % to 100 % for rhizomes originating at 30 m and transplanted to 3 to 20 m, but only 59 % survival for rhizomes originating at 3 m and transplanted to 14 m. Rhizomes from 30 m are thus more resistant to transplantation than those from 3 m.

PIRC (1984) showed that the chlorophyll level in *Posidonia oceanica* was higher in plants growing at 30 m than in those at 5 m throughout the year (except in September). Levels of soluble carbohydrates and starch in the rhizomes and leaves were also higher in these deeper growing plants. The relatively high mortality and poor development in material replanted at greater depths, where illumination is poorer, could thus be due to difficulty in adaptation due to insufficient energy reserves and chlorophyll levels.

The living part of the rhizomes measured 4.2 to 6.9 cm mean length in the present study involving rhizomes with an apparent length of 12 cm; this is comparable with the length of living tissue – 5.5 to 7.5 cm – found in rhizomes with an apparent length of 10 to 20 cm after one year by MEINESZ *et al.* (1992). Their conclusion that callus formation is induced by proximity to the apical part of the rhizome, where levels of mineral and organic substances are higher (CALMET *et al.,* 1988), is consistent with our results. High levels of these substances appear to be associated with bacteriocidal activity (BERNARD & PESANDO, 1989); this may ultimately control necrosis.

Comparison of the previous descriptions of the orthotropic and plagiotropic growth modes (CAYE, 1980; BOUDOURESQUE & BIANCONI, 1986) with the way in which leaf bundles change orientation during the present study indicates that our transplanted rhizomes changed progressively from orthotropic to plagiotropic growth. The progressive development of roots also corresponds to this change in growth mode, root development occurring seldomly in orthotropic rhizomes (PERGENT, 1987).

The amount of flowering in transplants originating at 30 m and replanted at 3 m and 14 m was greater than that observed the previous year at 30 m. Increase in illumination, temperature, or both may have thus stimulated development in the floral meristems. This possible effect could be tested in future investigation of flowering.

Summary

Investigation of *Posidonia oceanica* rhizomes eleven months after transplantation has led to the following conclusions:

1) Transplants taken from a depth of 30 m survive and develop well when transplanted to shallower water.

2) Transplants taken from a depth of 3 m survive progressively less well as transplantation depth is increased.

3) Modifications in number, length, and width of the leaves in the transplants are due to a change from an orthotropic to a plagiotropic mode of growth.

Acknowledgements

We are indebted to the following colleagues for their indispensable help in diving and in the preparation of rhizomes: ERIC BELLONE, CHARLES-HENRI BIANCONI, ANGELA CALTAGIRONE, GILBERTE CAYE, FRANK FINELLI, FLORENCE GAUMET, FRANÇOISE LOQUES, CARLO MORUCCI, VALÉRIE RICO, JEAN-MICHEL SIMONIAN, and MICHEL SIMONIAN. We thank Dr. IAN JENKINSON for the English translation. We are obliged to the Parc Naturel Régional de la Corse and to the marine reserve of Scandola for financial and logistic support.

References

BERNARD, P. & D. PESANDO, 1989: Antibacterial and Antifungal Activity of Extracts from the Rhizomes of the Mediterranean Seagrass *Posidonia oceanica* (L.) DELILE. Bot. Mar., **32:** 85–88.

BOUDOURESQUE, C. F. & C. H. BIANCONI, 1986: Posidonies profondes dans le coralligène de Sulana. Trav. Sci. Parc Natl. rég. Res. Nat. Corse, France, **2:** 36–39.

CALMET, D., C. F. BOUDOURESQUE & A. MEINESZ, 1988: Memorization of nuclear atmospheric tests by rhizomes and scales of the Mediterranean seagrass *Posidonia oceanica* (L.) DELILE. Aquat. Bot., **30:** 279–294.

CAYE, G., 1980: Analyse du polymorphisme caulinaire de *Posidonia oceanica* (L.) DELILE. Bull. Soc. Bot. Fr., **127** (3): 257–262.

CINELLI, F., 1980: Le fanerogame marine: problemi di trapianto e di riforestazione. Mem. Biol. Mar. Oceanogr., Suppl., **10:** 17–25.

COOPER, G., 1982: Reimplantation de *Posidonia oceanica* protection des implants. Bull. Ecol., **13** (1): 65–73.

DEN HARTOG, C., 1970: The sea-grasses of the world. North-Holland Publ. Co., Amsterdam; 275 pp., 31 pl. h. t.

FONSECA, M. S., W. J. KENWORTHY, J. HOMZIAK & G. W. TAYER, 1979: Transplanting of eelgrass and shoalgrass as a potential means of economically mitigating a recent loss of habitat. In: D. P. COLE (Ed.), Proc. 6th ann. conf. Wetlands restoration and creation. Hillsborough Community College, Environmental Studies: 279–326.

GIACCONE, G. & S. CALVO, 1980: Restaurazione del manto vegetale mediante trapianto di *Posidonia oceanica* (LINNEO) DELILE. Risultati preliminari. Mem. Biol. Mar. Oceanogr., Suppl., **10:** 207–211.

GIRAUD, G., 1977: Contribution à la description et à la phénologie quantitative des herbiers à *Posidonia oceanica* (L.) DELILE. Thèse Doctorat 3° cycle, Univ. Aix-Marseille II, France; 150 pp.

KENWORTHY, W. J., M. S. FONSECA, J. HOMZIAK & G. W. THAYER, 1980: Development of a transplanted seagrass (*Zostera marina* L.) meadow in Back Sound, Carteret County, North Carolina. In: D. P. COLE (Ed.), Proc. 7th ann. conf. Wetlands restoration and creation. Center & Tampa Port Authority Publ.; Tampa, Florida: 175–193.

LARKUM, A. W., 1976: Ecology of Botany Bay. 1) Growth of *Posidonia australis* (BROWN) HOOK. f. in Botany Bay and other Bays of the Sydney Basin. Aust. J. Mar. Freshwater Res., **27:** 117–127.

MAGGI, P., 1972: Les herbiers à Posidonies et la pollution urbaine dans le Golfe de Giens (Var). Ann. Inst. Michel Pacha, **5** (1): 1–11.

– –, 1973: Le problème de la disparition des herbiers à Posidonies dans le golfe de Giens (Var). Sci. Pêche (Bull. Inst. Sci. techn. pêches marit.), **221:** 7–20.

MEINESZ, A., C. GAYE, F. LOQUES & S. MACAUX, 1990: Analyse bibliographique sur la culture de phanérogames marines. Posidonia Newsletter, **3** (1): 3–57.

– –, G. CAYE, F. LOQUES & H. MOLENAAR, 1991: Growth and development in culture of orthotropic rhizomes of *Posidonia oceanica.* Aquat. Bot., **39:** 367–377.

– –, H. MOLENAAR, E. BELLONE & F. LOQUES, 1992: Vegetative reproduction in *Posidonia oceanica* (L.) DELILE. I. Effects of rhizome length and time of year on development in orthotropic transplants. P.S.Z.N.I: Marine Ecology, **13** (2): 163–174.

– – & R. Laurent, 1978: Cartographie et état de la limite inférieure de l'herbier de *Posidonia oceanica* dans les Alpes Maritimes (France). Campagne Poseidon 1976. Bot. Mar. **21** (8): 513–526.

– – & J. R. Lefevre, 1984: Regénération d'un herbier de *Posidonia oceanica* quarante ans après sa destruction par une bombe dans la rade de Villefranche sur mer (Alpes Maritimes-France). In: C. F. Boudouresque, A. Jeudy de Grissac & J. Olivier (Eds.), International workshop on *Posidonia oceanica* beds. GIS Posidonie Publ., Marseille, France, **1:** 39–44.

Ott, J. A., 1979: Persistence of a seasonal growth rhythm in *Posidonia oceanica* (L.) Delile under constant conditions of temperature and illumination. Mar. Biol. Letters, **1:** 99–104.

Pergent, G., 1987: Recherches lépidochronologiques chez *Posidonia oceanica* (Potamogetonaceae). Fluctuations des paramètres anatomiques et morphologiques des écailles des rhizomes. Thèse Doctorat Océanographie, Univ. Aix-Marseille II, France; 853 pp.

Pirc, H., 1984: Depth-adaptation in *Posidonia oceanica* (L.) Delile. In: C. F. Boudouresque, A. Jeudy de Grissac & J. Olivier (Eds.), International workshop on *Posidonia oceanica* beds. GIS Posidonie Publ., Marseille, France, **1:** 227–234.

West, R. J., N. E. Jacobs & D. E. Roberts, 1990: Experimental Transplanting of Seagrass in Botany Bay, Australia. Mar. Pollut. Bull., **21** (4): 197–203.