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Tabularia waernii (Diatomophyceae) in the northern Baltic Sea

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Tabularia waernii Snoeijs is a common epiphyte in the Baltic Sea. We have studied its distribution in 313 samples of epiphytic diatoms collected along the SW coast of Finland. *T. waernii* is abundant in the upper sublittoral of the outer archipelago zone and the sea zone. In the most exposed localities it was present throughout the year, with maximum abundance in June–July. *T. waernii* was an epiphyte on all filamentous macroalgae examined, however, it clearly preferred *Pilayella littoralis* as a host alga. It appears to be a slow colonizer, since it was rarely found on the young thalli of any host.

Keywords: Baltic Sea, brackish water, diatom, distribution, *Tabularia waernii*

INTRODUCTION

Tabularia waernii Snoeijs was recently described from the east coast of Sweden, the Baltic Sea (Snoeijs & Kuylenstierna 1991). Its occurrence was studied in nine localities along the Swedish east coast by the Baltic Sea and the west coast by Kattegat. Samples from Nordre Älv estuary on the west coast showed that the species was common within a salinity range of 2–20‰, and it was most abundant during the cold season (October–May). On the Swedish east coast *T. waernii* appeared to become rare in salinities below 6‰.

The description of *Tabularia waernii* agrees well with a species previously found in Finnish coastal waters, which has been misidentified as *Synedra famelica* Kütz. (Mölder & Tynni 1970) and *S. barbatula* Kütz. (Leskinen & Sarvala 1988, Leskinen & Hällfors 1990, 1994). The goal of this work is to investigate the distribution of *T. waernii* in the complex archipelago at the SW coast of Finland. Our study area lies in a salinity gradient frequently bisected by the 6‰ isohaline. Other physiological and chemical gradients in this area are those of exposure, turbulence, turbidity and nutrient concentration.

STUDY AREA

Most of the samples were collected in the Tvärminne area, which is an archipelago with a complex structure. Basically, it is an old peneplain tilted towards the south, and dissected by numerous fracture zones. The main fracture zone leads from the open Gulf of Finland in a NNE direction to a fjord-like inlet, Pohja Bay (Fig. 1). Pohja Bay is also the main source of freshwater input to the area. The archipelago consists of numerous islands separated by fracture zones running in an east–west direction, with large sheltered areas close to the mainland, and a gradual decrease in

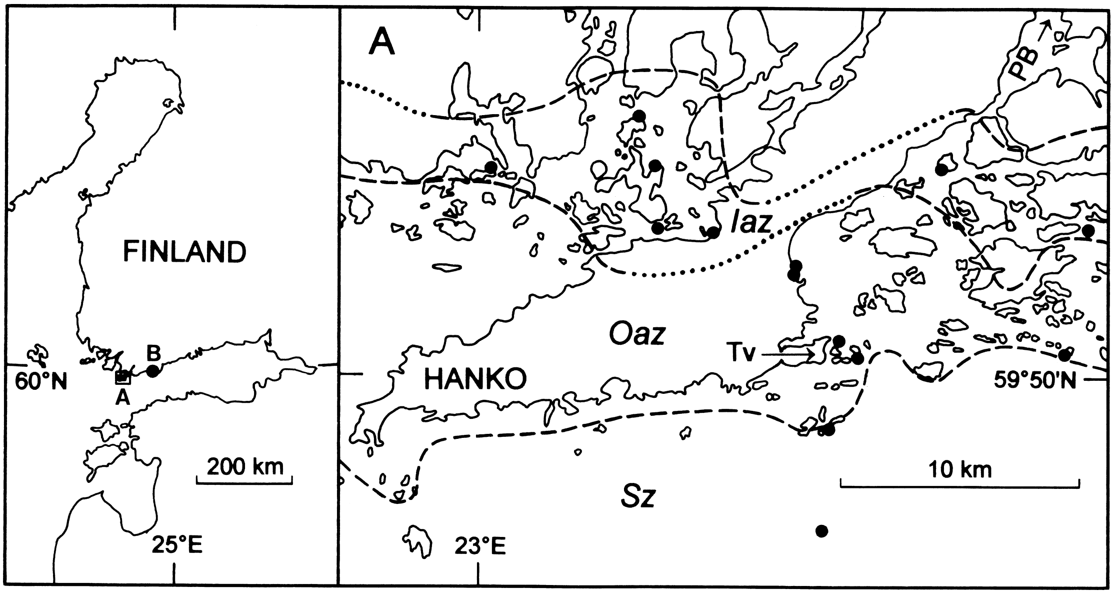

Fig. 1. Location of the sampling sites along the SW coast of Finland. — A. The 14 sampling sites and archipelago zones near the Tvärminne Zoological Station. — B. Location of the 5 sampling sites in Pikkala Bay, in the inner archipelago of Inkoo, 50 km east of Tvärminne. Tv = Tvärminne Zoological Station, PB = Pohja Bay, *Iaz = inner archipelago zone, Oaz = outer archipelago zone, Sz = sea zone.*

the size of the islands and increase of exposure towards the open sea. For a description of the archipelago zones, see Häyrén (1931).

The salinity of the surface water is about 6‰ in the sea zone and the outer archipelago, but gradually decreases to about 5‰ in the inner archipelago (Niemi 1973, 1975). In the late 1970s and early 1980s the salinity in the Baltic Sea was exceptionally high, occasionally exceeding 7‰ on the SW coast of Finland (Hällfors *et al.* 1983). In spring, outflow of freshwater from Pohja Bay gives rise to a 2–3-m-thick layer of markedly lower salinity (sometimes even below 1‰) under the ice (Niemi 1975, Hällfors *et al.* 1983, Niemi & Åström 1987).

The other sampling locality, Pikkala Bay, Inkoo, lies about 50 km east of Tvärminne. It is a relatively shallow (mostly < 10 m) bay area several kilometres wide and scattered with islands. Salinity is ca. 0.25–0.5‰ lower than in the Tvärminne archipelago. Other differences are that Pikkala Bay is not an upwelling area and there is no distinct salinity gradient, since no major rivers discharge into the bay.

The temperature of the surface water is usually below 0°C between January and March in both localities. Maximum temperatures (around 20°C) are reached in June to August. In Tvärminne, however, upwelling may occasionally lower the temperature considerably (Niemi 1975, Hällfors *et al.* 1983).

In the Gulf of Finland, nutrient concentrations are lowest in June after the planktonic spring bloom of cold-water diatoms and dinoflagellates. Nitrogen normally becomes limiting for further production (2–5 µg/l) before orthophosphate has decreased below 5 µg/l. Also silicate may become low enough to limit further growth of planktonic diatoms (Hällfors *et al.* 1983, Niemi & Åström 1987). After the diatom bloom, nutrient levels gradually rise in late summer and autumn, and the highest concentrations are reached in winter before the spring bloom. The values for nitrate and ammonium are then about 50–100 µg/l and 10 µg/l, respectively, but may exceed these amounts by an order of magnitude in the layer of low salinity under the ice. The values for phosphate are more stable, with a maximum concentration of about 20 µg/l (Niemi 1973, 1975, Hällfors *et al.* 1983).

MATERIAL AND METHODS

Samples, 313 in total, were collected at 14 sampling sites in the vicinity of the Tvärminne Zoological Station, ranging from sheltered localities in the inner archipelago to exposed rocks in the sea zone, and at 5 sampling sites in the inner archipelago zone in Pikkala Bay about 50 km to the east (Fig. 1). Sampling was done by SCUBA diving in the whole euphotic zone, from the upper hydrolittoral (Du Rietz 1932) to a depth of about 15 m in the lower sublittoral. The diatoms growing on filamentous algae were sampled from March to December in 1977–1980 in all seasons except mid winter. The host algae sampled included 20 taxa of red, brown and green algae (Table 1). During sampling, care was taken not to disturb the epiphytic diatoms, some of which were loosely attached. The filamentous host algae were therefore gently detached with forceps by a diver and put into sample jars under water.

In the laboratory, the organic matter was oxidized by boiling the algae in concentrated nitric acid followed by an addition of a small amount of concentrated sulphuric acid. After washing by centrifugation with at least five rinses of distilled water, the samples were diluted to a known volume. Slides for microscopic examination were prepared by pipetting 50 µl of the oxidized sample suspension onto a cover glass, which was allowed to dry under a hood followed by mounting in Clophenharpiks. The diatoms were identified and counted with a Leitz Dialux microscope fitted with a 100 × planapochromatic phase-contrast oil immersion objective (N.A. 1.32). The number of valves counted per sample varied from 477 to 2 151.

Multiple regression analysis was used to identify which environmental factor(s) are most important for the distribution of *Tabularia waernii*. Multiple regression analysis makes it possible to test for the effects of different variables acting in combination (Jongman *et al.* 1987). A significant regression coefficient implies that the variable has a definite effect, when the other variables are held constant. Multiple regression variables can be generalized to include class predictor variables as well as quantitative variables. As response variables, we used relative abundance of *T. waernii*, and as class predictor variables, season (month), substratum (host alga), and depth (depth zone).

RESULTS

Tabularia waernii in our material (Fig. 2A–J) conforms well with the material from the type locality (figs. 1–20 in Snoeijs & Kuylenstierna 1991). The valves have the same shape and the same narrow sternum, and measure 11–42 µm in length. Wider and more densely striated valves, which were included in the original description, were not observed. The single rimoportula is usually visible in LM (arrows in Fig. 2A, C, D and G). One feature which was not included in the original description is that occasional valves may be slightly sigmoid (Fig. 2E and J).

Tabularia waernii was most abundant in the sea zone and the outer archipelago zone (Fig. 3). Its mean relative abundance for the 4-year sampling period was 7.2% in the sea zone, 4.0% in

Table 1. Summary of investigated samples showing the host algae, number of samples, sampling depth and archipelago zone. i = inner archipelago zone, o = outer archipelago zone and s = sea zone.

Host algae	No. of samples	Sampling depth	Archipelago zone
Chlorophyta			
Acrosiphonia centralis (Lyngb.) Kjellm.	1	0.4	s
Capsosiphon fulvescens (C. Ag.) Setch. & Gardn.	1	0.1	o
Cladophora glomerata (L.) Kütz.	95	0.0–5.0	i, o, s
C. rupestris (L.) Kütz.	11	2.5–5.0	o, s
Enteromorpha ahlneriana Bliding	3	0.0–0.8	i
E. intestinalis (L.) Link	2	0.0–0.5	o
Enteromorpha sp.	7	0.0–1.1	i, o
Spongomorpha pallida (Kjellm.) Wille	4	0.5–1.2	s
Urospora penicilliformis (Roth) Aresch.	4	0.0–0.2	o, s
Phaeophyta			
Dictyosiphon foeniculaceus (Huds.) Grev.	6	0.5–2.5	o, s
Ectocarpus siliculosus (Dillw.) Lyngb.	3	0.1–2.5	i, o, s
Eudesme virescens (Carm. ex Harv. in Hook.) J. Ag.	1	0.6	o
Pilayella littoralis (L.) Kjellm.	79	0.0–9.0	i, o, s
Sphacelaria arctica Harv.	7	2.5–8.5	o, s
S. radicans (Dillw.) C. Ag.	2	0.7–1.2	o
Sphacelaria sp.	2	2.5	o
Stictyosiphon tortilis (Rupr.) Reinke	10	0.5–1.0	o
Rhodophyta			
Ceramium rubrum (Huds.) C. Ag.	2	5.0–10.0	s
C. tenuicorne (Kütz.) Wærn [incl. *C. gobii* Wærn]	70	0.4–15.0	i, o, s
Rhodomela confervoides (Huds.) Silva	3	9.0–15.0	s

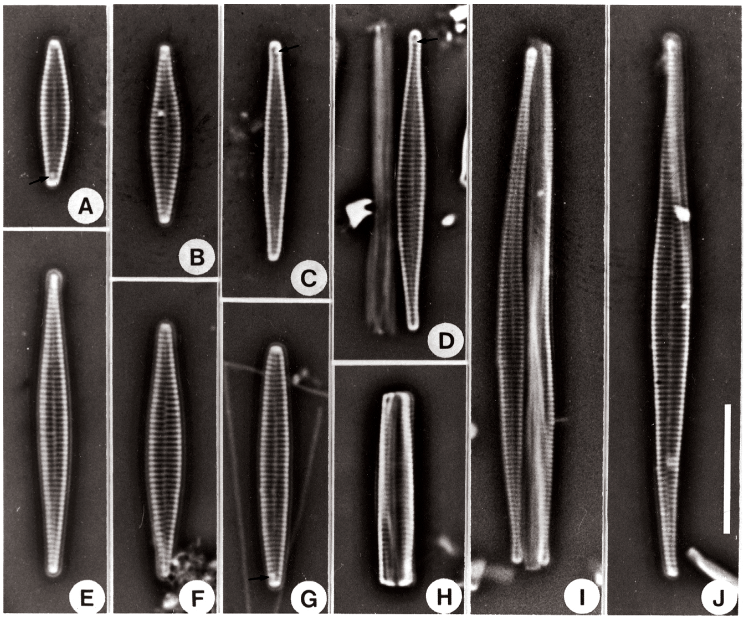

Fig. 2. Light micrographs of *Tabularia waernii*. — A–C: Small valves. — D: Medium-sized valve with strongly protracted ends and girdle bands. — E: Medium-sized valve with slightly sigmoid ends. — F, G: Medium-sized valves with ends only little or not protracted. — H: Frustule in girdle view. — I: Large frustule with separated valves, the bent shape probably being a preparation artefact. — J: Large valve with sigmoid ends. The rimoportula is indicated with an arrow in Figs. A, C and G. Scale bar = 10 µm.

the outer archipelago zone and 0.4% in the inner archipelago zone. The highest recorded abundances were 50.3% in the sea zone and 61.4% in the outer archipelago zone. Both records were from the phaeophyte *Pilayella littoralis* collected at depths of 9 and 5 m, respectively, in July 1979 and 1980. In the outer archipelago, *Tabularia waernii* was most common in June and July (Fig. 3), when it amounted to mean relative abundances of 8.7% and 10.7%, respectively, of all epiphytic diatoms. In August, its relative abundance suddenly dropped to less than 1%, and remained so until the following spring. In the sea zone, its peak abundance of 13.0% occurred in June, decreasing to 10.8% in July. The decrease here in late summer was even more striking than in the outer archipelago zone, as the species was not found at all in autumn and winter samples.

Tabularia waernii was present throughout the euphotic zone, but it was usually most abundant in the upper sublittoral at the depth of 2.5 to 5 m (Table 2). Its average abundance for the 4-year sampling period was 1.8% in the hydrolittoral and 6.5–13.4% in the sublittoral, being highest at 5 m depth. The highest monthly means were recorded in June–July. During prolonged periods of calm

Table 2. Monthly mean relative abundances (1977–1980) of *Tabularia waernii* (*x*), standard error of the mean (*S.E.*) and number of samples studied (*n*) in the different depth zones; – = not sampled.

	Hydrolittoral			Sublittoral								
	0.0–1.0 m			2.5 m			5.0 m			> 5.0 m		
Month	*x*	*S.E.*	*n*	*x*	*S.E.*	*n*	*x*	*S.E.*	*n*	*x*	*S.E.*	*n*
March	0.30	± 0.10	(3)	0.41	± 0.15	(4)	–	–	–	–	–	–
May	0.77	± 0.20	(16)	1.98	± 1.05	(12)	–	–	–	–	–	–
June	5.47	± 1.84	(19)	16.68	± 3.42	(13)	10.27	± 3.43	(6)	8.71	± 7.88	(2)
July	3.53	± 0.71	(48)	8.69	± 1.96	(29)	22.68	± 5.32	(12)	9.60	± 4.53	(11)
August	0.64	± 0.18	(55)	1.01	± 0.75	(6)	–	–	–	–	–	–
September	0.07	± 0.04	(11)	0.51	± 0.36	(7)	0.00	± 0.00	(5)	0.00	± 0.00	(3)
October	0.82	± 0.18	(27)	0.37	± 0.37	(3)	0.19	± 0.19	(2)	–	–	–
November	0.10	± 0.05	(11)	0.00	± 0.00	(2)	–	–	–	–	–	–
December	0.22	± 0.11	(4)	0.00	± 0.00	(2)	–	–	–	–	–	–
Grand mean	1.79	± 0.29	(194)	6.47	± 1.13	(78)	13.37	± 3.27	(25)	7.69	± 3.29	(16)

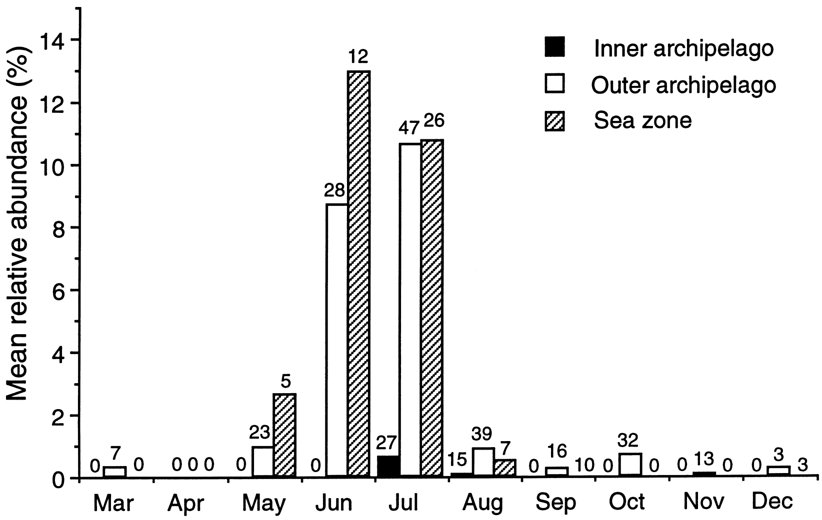

Fig. 3. Monthly mean relative abundances (1977–1980) of *Tabularia waernii* in the different archipelago zones. The number of samples studied is indicated above each column.

weather *T. waernii* also increased in the hydrolittoral reaching maximum abundances of 19.6% in the outer archipelago zone and 16.0% in the sea zone. On exposed shores, however, heavy wave action usually reduced its numbers in the hydrolittoral so that the highest monthly mean was only 5.5% (Table 2). Below 10 m *T. waernii* was seldom abundant, suggesting that low light intensity may have been a limiting factor.

As host algae, *Tabularia waernii* preferred brown algae to red and green algae (Table 3), but it was found as an epiphyte on all filamentous macroalgal species examined in this study (Table 1). Its average abundance was 7.0% on brown algae, 3.1% on red algae and 2.2% on green algae. Among the brown algae *T. waernii* clearly favoured the uniseriate filaments of *Pilayella littoralis* (Table 3). Furthermore, it was more abundant on *Ceramium tenuicorne* than on *Cladophora glomerata*, and other red or green algae.

Multiple regression analysis gave significant values ($p < 0.0001$, $n = 313$, $R^2 = 0.40$) for the correlation of the relative abundance of *Tabularia waernii* with archipelago zone ($p < 0.001$, $n = 3$), season (month; $p < 0.0001$, $n = 9$), depth (depth zone; $p < 0.0001$, $n = 4$) and substratum (host alga; $p < 0.0001$, $n = 6$). Reanalysing the data according to archipelago zones revealed that in the inner archipelago the relative abundance of *T. waernii* was weakly correlated with substratum ($p < 0.05$) and depth ($p < 0.05$), and not with season (Table 4). The number of macroalgal species sampled and the sampling depths were limited in the inner archipelago in comparison with the other archi-

Table 3. Monthly mean relative abundances (1977–1980) of *Tabularia waernii* (*x*), number of samples studied (*n*) and standard error of the mean (*S.E.*) on the different host algae; – = not sampled.

	Cladophora glomerata			Other green algae			*Pilayella littoralis*			Other brown algae			*Ceramium tenuicorne*			Other red algae		
Month	*x*	*S.E.*	*n*	*x*	*S.E.*	*n*	*x*	*S.E.*	*n*	*x*	*S.E.*	*n*	*x*	*S.E.*	*n*	x	s.e.	n
March	–	–	–	0.68	± 0.00	(1)	0.10	± 0.00	(1)	0.11	± 0.00	(1)	0.41	± 0.09	(4)	–	–	–
May	0.72	± 0.11	(2)	0.16	± 0.04	(4)	2.75	± 1.50	(8)	0.91	± 0.54	(5)	0.83	± 0.31	(9)	–	–	–
June	2.89	± 1.07	(5)	6.28	± 1.33	(5)	11.66	± 2.94	(18)	11.97	± 6.56	(5)	12.04	± 3.23	(7)	–	–	–
July	4.35	± 1.02	(37)	4.50	± 2.66	(6)	18.16	± 4.13	(22)	4.79	± 1.35	(17)	8.23	± 1.92	(15)	2.26	± 0.57	(3)
August	0.86	± 0.36	(25)	0.26	± 0.22	(8)	0.98	± 0.34	(16)	0.30	± 0.13	(5)	0.10	± 0.06	(7)	–	–	–
September	0.12	± 0.09	(5)	0.06	± 0.06	(3)	0.67	± 0.63	(4)	0.00	± 0.00	(3)	0.10	± 0.10	(9)	0.00	± 0.00	(2)
October	0.77	± 0.27	(13)	0.19	± 0.00	(1)	1.26	± 0.45	(7)	–	–	–	0.42	± 0.16	(11)	–	–	–
November	0.04	± 0.04	(6)	–	–	–	0.15	± 0.15	(3)	–	–	–	0.11	± 0.07	(4)	–	–	–
December	0.05	± 0.05	(2)	–	–	–	–	–	–	–	–	–	0.19	± 0.12	(4)	–	–	–
Grand mean	2.20	± 2.22	(95)	2.22	± 0.76	(28)	8.34	± 1.56	(79)	4.09	± 1.22	(36)	3.20	± 0.73	(70)	1.35	± 0.64	(5)

pelago zones (Table 1). The sampling season could not attain significance, as samples from the inner archipelago were collected only in July and August (Fig. 3). In the outer archipelago both season, with a distinct peak in abundance in the midsummer (Fig. 3), and depth, with an abundance peak in the upper sublittoral (Table 2), were highly significant ($p < 0.001$). Also, the substratum was significant ($p < 0.01$), as the filamentous brown algae and *Ceramium tenuicorne* offered *T. waernii* a very suitable substrate (Table 3). In the sea zone, the most significant factor was season ($p < 0.01$), followed by depth ($p < 0.05$), whereas substratum was not significant.

DISCUSSION

Snoeijs and Kuylenstierna (1991) reported *Tabularia waernii* in salinities ranging from 2 to 20‰ on the Swedish west coast. Optimum salinity appeared to be 7‰, and the species was still common in 6‰. However, its abundance dropped drastically in salinities of less than 5‰. The salinity range in the present study area is from about 5 to over 6‰, being lower in the inner archipelago and increasing towards the outer archipelago zone and sea zone (Fig. 1). Our finding that *T. waernii* was more abundant in the archipelago zones with higher salinities (Fig. 3) agrees with the observations of Snoeijs and Kuylenstierna (1991).

Salinity is, however, not the only environmental factor that differs among the archipelago zones. The water is clearest in the sea zone, while in the shallow and eutrophied inner archipelago zone it is mostly turbid because of suspended clay particles and planktonic algae (Niemi 1975), which may indicate that also light might be a limiting factor for the growth of *Tabularia waernii*. The regression analysis revealed that the depth of the sampling site was less significant in the sea zone than in the outer archipelago zone (Table 4), which may be explained by the fact that the water is clearer in the sea zone (Table 2). Moreover, even in the sea zone, *T. waernii* was never numerous in the lower sublittoral (10–15 m). This suggests that the optimum light intensity for the growth of *T. waernii* may be fairly high, which is further supported by its seasonal abundance maximum (Fig. 3).

In our research area the peak occurrence of *Tabularia waernii* was in June and July, when the daily irradiance and water temperature were at their highest. In Snoeijs' (1994) study site on the Swedish east coast (Forsmark), the ice cover that blocks the free passage of light into the water disappeared earlier than in our research area, and the peak occurrence of *T. waernii* was as early as in May when the water temperature was as low as 10°C, and solar irradiance was about 90% of its midsummer maximum. This indicates that the growth of *T. waernii* responds more to light than to temperature. In general, at the SW coast of Finland *T. waernii* appears to be most abundant at the time when water is clearest and nutrient concentrations are lowest. Spatially, its abundance is highest in the sea zone and outer archipelago zone with their clearer waters and lower nutrient levels when compared with inner archipelago zone (Fig. 3; Niemi 1973, 1975). *T. waernii* can thus be tentatively regarded as a species associated with good water quality.

On exposed shores with strong wave action, *Tabularia waernii* was usually not abundant in the hydrolittoral. Only after periods of very calm weather, it was found in greater numbers in shallow water even in the sea zone. Apparently, it is not inhibited by high light levels close to the sur-

Table 4. Significance levels for the multiple regression analysis with relative abundance of *Tabularia waernii* as response variable, and season, substratum and depth as predictor variables in the three archipelago zones. n = number of class variables represented in the data. *N.S.* = not significant ($p > 0.05$).

Archipelago zone	Number of samples	R^2	Predictor variables: Season n	(Month)	Substratum n	(Host alga)	Depth n	(Depth zone)
Inner archipelago	42	0.49	2	*N.S.*	5	$p < 0.0307$	3	$p < 0.0127$
Outer archipelago	208	0.38	9	$p < 0.0001$	5	$p < 0.0018$	4	$p < 0.0006$
Sea zone	63	0.53	6	$p < 0.0021$	6	*N.S.*	4	$p < 0.0135$

face, but rather by occasional strong wave action, which tends to detach the cells. The effects of wave action can also be seen in plankton samples, as *T. waernii* is a common pseudoplanktonic component in near-coastal waters during summer.

Tabularia waernii was rarely found on young plants of the host algae. Other studies carried out in the Tvärminne archipelago suggest that *T. waernii* is a slow colonizer. In a colonization experiment it was not observed until six weeks after the substrata had been exposed in the water (Leskinen & Sarvala 1988). Thus, the lower abundance of *T. waernii* on *Cladophora glomerata* as compared with other common macroalgae (Table 4) can be explained by the dynamic growth of *C. glomerata* (Wallentinus 1978, Leskinen *et al.* 1992), which is due to both high growth rate and high grazing pressure (Jansson 1974). As a result, the thalli of *C. glomerata* are generally younger than those of the other macroalgae and thus to a lesser degree available for colonization.

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