Rocky shore turfs dominated by *Corallina* (Corallinales, Rhodophyta) in northern Japan[†]

Hidetsugu Akioka,¹ Masasuke Baba,² Tomitaro Masaki^{3*} and H. William Johansen⁴

¹Laboratory of Biology, Hokkaido Kyoiku University, Hakodate Branch, Hakodate 040-8567, Japan, ²Marine Ecology Research Institute, 4-7-17 Arahama, Kashiwazaki, Niigata 945-0322, Japan, ³Laboratory of Marine Botany, Faculty of Fisheries, Hokkaido University, Hakodate 041-8611, Japan and ⁴Department of Biology, Clark University, Worcester, Massachusetts 01610, USA.

SUMMARY

Three intertidal sites dominated by Corallina turfs were investigated in Hokkaido, Japan. The sites (A, B and C) differed in slope, wave exposure and length of time exposed to air during tidal cycles. Monthly samples were analyzed for frond morphology and other features. Site A, the most wave-exposed site, was dominated by Corallina sp. X, an unknown species, and sites B and C by Corallina pilulifera Postels et Ruprecht. At the different sites the populations differed in conceptacle abundance, coverage by epiphytic Titanoderma corallinae (P. Crouan et H. Crouan) Woelkerling, Chamberlain et Silva, amount of contained sediment, numbers of axes per guadrat, numbers of branch fusions, branch entanglement, frond dryweight, frond length, amount of adventitious branching, numbers of epiphytes (exclusive of T. corallinae), and numbers of animal species. Ninety-one animal species were recorded from the turfs. Corallina is affected morphologically by conditions inherent in its microhabitat, including desiccation, epiphyte loading and the abundance of herbivores.

Key words: algal turfs, *Corallina*, coralline algae, intertidal ecology, Japan, Rhodophyta.

INTRODUCTION

A prominent feature of intertidal rock surfaces in northern Japan is dense, carpet-like turfs dominated by *Corallina* species (Corallinales, Rhodophyta). The turfs are usually located in wave-exposed areas and provide a habitat for many other species of algae and animals (Atobe and Saito 1974). *Corallina* turfs are also present on other rocky shores (e.g. S. California, Stewart 1982, 1989; S. Australia, Womersley and Edmonds 1958), but sometimes turfs are dominated by other taxa of articulated coralline algae [e.g. *Jania adherens* Lamouroux (Ballesteros and Afonso-Carrillo 1995) or *Lithothrix aspergillum* J. E. Gray (Tyrrell and Johansen 1995)]. Even though only 1–3 cm thick, coralline turfs may catch and hold significant quantities of sand (Stewart 1983). Stewart (1982) has called the articulated coralline algae in these turfs anchor taxa. A satisfactory definition of turf is that by Hay (1981): masses of tightly packed upright branches forming a stiff matrix more than 0.5 cm thick. Mats are entangled masses of small filamentous species where branches are oriented both vertically and horizontally; mats are less than 0.5 cm thick.

Baba *et al.* (1988) have shown that three species of *Corallina*, *C. officinalis* Linnaeus, *C. pilulifera* Postels et Ruprecht and *Corallina* sp. X, occur in intertidal and upper subtidal zones in southern Hokkaido. The identity of *Corallina* sp. X is unresolved, but it bears some resemblance to small forms of *Corallina vancouveriensis* Yendo from western North America (M. Baba, unpubl. obs., 1988). Interestingly, Taylor and Hay (1984) identified a turf-form of *Corallina* in southern California as *C. vancouveriensis*.

Our goals were to answer the following questions concerning the *Corallina* turfs in northern Japan: (i) are there different types of turfs determined by location and environmental factors? (ii) Do turf structure and turf communities vary with seasons? (iii) Are branches of *Corallina* modified structurally or reproductively by their occurrence in turfs? (iv) What algae and invertebrate animals inhabit *Corallina* turfs in northern Japan?

MATERIALS AND METHODS

Three sites supporting turfs (designated A, B and C) on a rocky intertidal shore at Toyoura, Esan Town, Kameda Gun were selected for study (Fig. 1). This shore is located 40 km east of Ohanazaki in Hakodate (41°44′N, 140°42′E; see Baba *et al.* 1988). Esan Town is influenced by the warm Tsugaru Current from September to February and the cold Oyashio Current from March to

*To whom correspondence should be addressed. Present address: Trondhjemsgade 12, 2. tv. DK-2100 Copenhagen Ø, Denmark. Dedicated to Professors Tadao Yoshida and Masakazu Tatewaki on the occasion of their academic retirement. Email: <hide@cc.hokkyodai.ac.jp> Communicating editor: I. K. Lee Received 17 September 1998; accepted 6 April 1999. August (Ohtani and Murakami 1986). Site selection, in 1985–1986, was based on the presence of *Corallina* populations in distinctive microhabitats where overall cover was extensive enough for monthly sampling (Table 1). As determined by 2-h observations during low

 Table 1.
 Descriptions of the three intertidal sites occupied by coralline turfs at Toyoura, Esan Town. See Figure 1.

Site	Description
A	Substrate a steep, south-facing slope; high wave action; moderate desiccation, no shading.
В	Substrate horizontally oriented; moderate wave action; severe desiccation at spring low tides; no shading.
С	Substrate horizontally oriented, in tide pool and never

becoming emersed; moderate wave action; turfs loosely compacted; shaded for part of each day.



Fig. 1. Map of Hokkaido and a profile of the study sites.

tide cycles and reference to tide data provided by the Hakodate Marine Observatory, the sites were approximately 100 cm above mean tidal level. The sites are described in Table 1.

At each visit the algal cover from two 5×5 cm quadrats were totally removed by scraping with a putty knife and spoon. The collections were preserved in a 10% solution of formalin in seawater.

Each sample was separated into four fractions: fronds of Corallina, non-corallinaceous algae, animals and sediment. The sediment fractions, containing sand, animals and detrital fragments, were sieved through a 0.5 mm sieve to remove larger fragments and make possible the recovery of animals as small as 50 µm. The remaining sediment fractions were dried and weighed. The number of Corallina fronds per guadrat was recorded. A frond is an articulated branching system with a single attachment to the crustose holdfast. The animals and non-corallinaceous algae were identified and enumerated. Ten fronds of Corallina were chosen randomly from each sample and measured to determine frond length, intergenicular length and width, branching frequency along the main axes and the presence or absence of conceptacles. The fronds in each 10-frond sample were photographed, dried and weighed.

RESULTS

Morphology

Corallina pilulifera and *Corallina* sp. X comprised the turfforming coralline species, the former at sites B and C and the latter at site A. Identification was based on characters of the axial intergenicula, which in *C. pilulifera* were 0.9–1.2 mm long and contained 12–16 tiers of medullary cells and in *Corallina* sp. X were 0.7–0.8 mm long and contained 7–9 tiers. At the study site and nearby areas, *Corallina* sp. X consistently occupied more wave-exposed sites than did *C. pilulifera* (H. Akioka, pers. obs.).

Table 2. Characteristics of the turf populations. Unless otherwise indicated, numbers are mean, (SD) and sample sizes of monthly means during the study period.

	Site A	Site B	Site C
	Site A	Site D	Sile C
Dominant species	Corallina sp. X	C. pilulifera	C. pilulifera
Fronds per quadrat	417 (119) 28	278 (73) 24	549 (216) 28
Frond dryweight (g/quadrat)	5.3 (1.4) 28	6.8 (1.9) 24	1.7 (0.4) 28
Frond length (mm)	33.7 (8.7) 140	27.8 (6.8) 120	14.1 (4.8) 140
Frond weight (mg)	120 (48.6) 140	68 (1.9) 120	13 (11.3) 140
Adventitious branches	None	None	Present
Branch entanglement	None	Present	None
Branch fusions	None	Common	None
Conceptacles per frond	Many	Rare	Few
Sediment dryweight (g/quadrat)	1.7 (1.4) 28	9.7 (6.9) 24	7.1 (3.6) 28
Titanoderma coverage	Low	High	High
Non-corallinaceous epiphyte abundance	Much	Much	Little
No. epiphyte species	12	8	6
No. animal species	73	75	59

Within turfs, the fronds of both species were approximately 30 mm long at sites A and B, but only half as long at site C (Table 2). Lateral branches tended to be restricted to upper parts of the percurrent axes (Figs 2,3). At site B, more than at sites A and C, lateral branches and adventitious branches growing from axial intergenicula were entangled and interconnected by discs that fused to various surfaces (Table 2, Figs 4,7). These fusion discs (Figs 11–13) developed when intergenicular surfaces remained in contact with branches, rock, shells or fragments of drift *Phyllospadix iwatensis* Makino for unknown periods of time. In addition to increasing turf cohesion, the fusion discs were capable of generating new fronds (Figs 12,13). At all sites the fronds were firmly attached by irregularly organized crustose holdfasts up



Figs 2–9. *Corallina* sp. X from site A and *Corallina pilulifera* from sites B and C. 2,3. *Corallina* sp. X. 4. *Corallina pilulifera* from site B dominated by adventitious branches (arrowheads). 5. Two connected (arrows) fronds of *Corallina pilulifera* from site B, one of which bears *Monostroma angicava* (arrowhead M). 6. *Titanoderma corallinae* (TC) on *Corallina pilulifera* from site B. 7. Attachment disc (arrowhead) of *Corallina pilulifera* from site B. 8. Adventitious branches arising (arrowheads, SB) from an axis of *Corallina pilulifera* from site C. 9. Excessive coverage by *Titanoderma corallinae* (TC) on *Corallina pilulifera* from site C.

to 700 μ m thick, which regenerated fronds in large numbers (Figs 14,15).

At site C, more than at sites A and B, many apical meristems had been injured by vigorous grazing, especially by the gastropods *Neritrema sitkana* (Philippi) and *Barleeir angustata* (Pilsbry). This phenomenon resulted in an excessive production of adventitious branches arising from parts of intergenicula typically lacking branches (Table 2, Figs 8,10). Damage to apical meristems also appeared to be responsible for the frequent prominence of stunted fronds at site C. In many injured fronds, axial growth had been aborted, but adventitious

branches often exhibited indeterminate growth and dominated the thalli (Figs 8,9).

Conceptacle production varied considerably between sites (Table 2). More conceptacles were produced at site A (*Corallina* sp. X) than at either of the other sites, most of them from May to September, during which period the mean number of tetrasporangial conceptacles per frond exceeded 300 per month. Although a few conceptacles were produced at sites B and C (*C. pilulifera*) during the spring (March–May) and summer (June–August), for the rest of the year conceptacles were almost non-existent at these sites.



Figs 10–15. *Corallina* sp. X from site A and *Corallina pilulifera* from sites B and C. 10. Section of two adventitious branches (arrowheads) of *Corallina pilulifera* from site C. 11. Section of secondary fusion disc produced by intergenicular apex of *Corallina pilulifera* that had been growing in contact with a fragment of *Phyllospadix*. 12. Section of secondary fusion disc bearing a new frond (arrowhead) produced by two intergenicula of *Corallina pilulifera*. 13. Section of an attachment disc (Z) of *Corallina pilulifera* from site B encircling other branches (X) and bearing a new frond (Y). 14. Fronds of *Corallina pilulifera* growing from basal crust at site C. 15. Section of overgrowing basal crusts of *Corallina* sp. X from site A.

Ecology

The most dense packing of fronds occurred in the tidepool at site C, with more than 700 fronds of *C. pilulifera* per quadrat recorded for several months in the fall (August–November) of 1985 (Table 2, Fig. 16). At the other extreme, fewer than 300 fronds per quadrat were recorded most of the year at site B and in the summer at site A. Paradoxically, in spite of more dense packing, total frond dryweight per quadrat was consistently lower at site C than at A or B (Table 2). No appreciable seasonal variation in dryweight occurred at any of the sites (Fig. 16).

A small tetraspore- and bispore-producing crustose coralline, *Titanoderma corallinae* (P. Crouan et H. Crouan) Woelkerling, Chamberlain et Silva, was a common epiphyte of *Corallina*, especially at sites B and C (Table 2, Figs 6,9). Although present all year, coverage by *T. corallinae* was greatest in winter (December–February) and spring (March–May) (H. Akioka, pers. obs.).

Several non-corallinaceous algal epiphytes grew on the *Corallina* turfs, most prominently in the spring (March–May) at site A and, to a lesser extent, site B. The most abundant epiphyte was *Monostroma angicava* Kjellman and during the spring this species covered large portions of the turfs, especially at sites A and B (Fig. 5). Other prominent epiphytes were *Dictyota dichotoma* (Hudson) Lamouroux, *Leathesia difformis* (Linnaeus) Areschoug, *Alaria crassifolia* Kjellman, *Lomentaria hakodatensis* Yendo, *Acrosorium yendoi* Yamada, *Symphyocladia latiuscula* (Harvey) Yamada and juveniles of *Laminaria* spp. (*L. japonica* Areschoug or *L. angustata* Kjellman).

Large numbers of small animals lived in the turfs; 91 taxa were recorded at sites A, B and C. Turfs at sites A (300–3000 animals per quadrat) and B (800–7500) contained more animals than those at C (400–1500; Fig. 17). The categorization 'abundant' was assigned to species at site A, 17 times, site B, 27 times and site C, 10 times. Thus, site B clearly dominated in numbers of animals. Moreover, species diversity at site A was 73, site B, 75 and site C, 59. Some animal species were prominent at all three sites, but others differed widely in abundance between the sites. Particularly noteworthy were molluscs, such as the gastropod *Barleeia angus*-



Fig. 16. Mean number of fronds per quadrat (\bigcirc), dryweight of total fronds per quadrat (\blacksquare) and sediment weight (\square) for three sites at Toyoura Esan Town, Japan. No data were collected for site B in June and July of 1986. (a) Site A; (b) site B; (c) site C.



Fig. 17. Abundance of animal groups in the turfs at sites (a) A, (b) B and (c) C. No data were collected for site B in June and July of 1986. (□) Foraminifera; (□) Annelida, including Nemertinea & Nematoda; (□) Gastropoda; (□) Pelecypoda; (■) Arthropoda.

tata and the bivalve *Turtonia minuta* (Fabricius) at site B. The former species formed an epifaunal assemblage of egg and adult stages in August 1985, and appeared to spend its entire life in the turfs. The latter species was mostly absent after attaining a high density of juveniles in July 1985. A colonial bryozoan, *Celleporina costazii* (Audouin), was prominent on turf *Corallina*, especially at site A in summer. The foraminiferan *Quinqueloculina seminila* (Linnaeus) and the gastropods *Neritrema sitkana* (Philippi) and *B. angustata* consumed coralline epithallial cells (H. Akioka, pers. obs.). A listing of the animal species and indications of their abundances at sites A, B and C are given in Appendix I.

The sediment weight per quadrat varied through the year at all sites (Fig. 16) and there was no discernible pattern. The sloping shore at site A $(30-60^\circ)$ held less sand than the flatter shores at sites B and C (Table 2).

DISCUSSION

In low intertidal and upper subtidal zones on many rocky shores in northern Japan and elsewhere (e.g. southern California; Stewart 1982, 1989) turfs dominated by articulated coralline algae are common substrate covers, although non-corallinaceous algae, such as species of *Gelidium* and *Pterocladia*, can also form turfs (Womersley and Edmonds 1958; Stewart 1968). Turfs often trap considerable quantities of sediment (Stewart, 1983, 1989).

As has been shown in southern California (Taylor and Littler 1982) and in Alaska (Johansen 1971; Lebednik 1973), coralline algae are extremely sensitive to desiccation. The ability of *Corallina* to grow in turfs allows the clustered branches to retain water and extend their coverage into areas of greater aerial exposure (Padilla 1984; Taylor 1985).

As has been documented for articulated coralline algae and certain non-corallinaceous turf-forming algae, species in turfs differ morphologically from the same species outside turfs, even though they are unquestionably the same species [e.g. *Pterocladia capillacea* (Gmelin) Bornet et Thuret, Stewart 1968; *Padina jamaicensis* (Collins) Papenfuss, Lewis *et al.* 1987]. In southern California, Taylor and Hay (1984) found that *Corallina vancouveriensis* exhibited a turf morphology in intertidal habitats and a non-turf morphology in submerged conditions. They found that the turf form had two to three-fold more mass and thallus area per volume than did the nonturf form and that net photosynthetic capacity was approximately half of that in non-turf fronds.

The paucity of conceptacles produced by *C. pilulifera* at sites B and C suggests that a turf environment suppresses conceptacle production in this species. Our observations on other populations of this species in Hokkaido and the findings of Chihara (1973) 800 km farther south on the Izu Peninsula, reveal that conceptacle production peaks in winter (October–April). In Hokkaido, however, conceptacle production is not as vigorous in *C. pilulifera* as in *Corallina* sp. X, which peaks in summer (June–August). The paucity of conceptacles at sites B and C suggests that regeneration from holdfasts is the principal method of replacing lost fronds and maintaining the turfs, an ability previously recorded for *Corallina* sp. in the eastern Pacific (Littler and Murray 1978; Littler and Kauker 1984).

Stewart (1989) and others have suggested several adaptations allowing species of Corallina to successfully form desiccation-resistant turfs: (i) extensive and longlived basal crusts; (ii) strong adherence of basal crusts to underlying rock; (iii) crusts that regrow readily after being buried (Littler and Kauker 1984); (iv) thalli that are calcified and resist abrasion well; (v) apical meristems projecting above turfs; (vi) low calorific values (Littler and Murray 1978; Littler and Littler 1980); (vii) long periods during the year when spores are being released; (viii) ready generation of new axes from basal crusts (Littler and Kauker 1984); (ix) branching patterns that result in densely compacted fronds; (x) slow growth rates (Masaki et al. 1981); (xi) dispersal by spores augmenting vegetative propagation. To these we add (i) the tendency to form branch-to-branch attachment discs; (ii) the provision of shelter for many animals; and (iii) a tendency for epiphytic algae to grow on Corallina.

Because turf algae can readily be identified as belonging to species also present outside turfs, there is no reason to recognize new species simply on the basis of their morphology in a turf. For example, *Corallina compacta* Crouan et Crouan is probably the turf form of a previously described species of *Corallina*. The excessive number of taxa of articulated coralline algae described during the last two centuries (> 400) is probably due to ignoring morphological variation that fronds exhibit in different habitats (Johansen 1981; Johansen and Colthart 1975).

The prominence of Corallina in intertidal turfs and the reports of many animals associated with Corallina in Norway (Dommasnes 1968, 1969; Hagerman 1968), southern California (Stewart 1982) and England (Grahame and Hanna 1989), support the observation that many epifaunal species are present in Japan. Coull and Wells (1983) and Hicks (1986) found that the structurally complex matrices provided by fronds of Corallina officinalis offer invertebrate animals important refuges from predation. The 91 animal species recorded in this study suggest that Corallina turfs are diverse and thriving communities that vary in their suitability as animal habitats. Approximately as many species were recorded at the most surf-exposed turf (site A) as at the moderately-exposed turf (site B), with the continually submerged turf at site C harboring the fewest species.

The *Corallina* turf in northern Japan is a successful reaction of two species that outcompete other species in a stressful intertidal environment. The stresses are strong wave action, periodic desiccation, severe epi-

phytism and herbivorous animals. *Corallina* meets the challenge by producing adventitious branches, lateral fusions and complex interstices by compaction.

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APPENDIX I

Animal taxa in $\ensuremath{\textit{Corallina}}$ turfs and their abundances at sites A, B and C

Таха	А	В	С
Protozoa: Class Foraminifera Quinqueloculina seminila (L.)	2+	3+	3+
Baggina sp.	+	+	+
Asterigerina carinata (d'Orbigny)	+	+	+
Elphidium poeyanum (d'Orbigny)	+	3+	+
Elphidium sp.	+	2+	+
<i>Cymbaroporetta bradyi</i> (Cushman)	+	+	+
<i>Hoeglundina elegans</i> (d'Orbigny)	+	+	+
Hoeglundina sp.	+	+	+
One other unidentified species	+	+	+
Porifera * <i>Sycon</i> sp.	2+	_	+
Coelenterata			
* <i>Coryne pusilla</i> (Gaertner)	+	_	_
*Obelia sp.	+	_	_
Nemertinea: Several unidentified species			
(juveniles)	+	2+	+
Nematoda: One unidentified species	3+	3+	2+
Mollusca: Class Polyplacophora			
Acanthochiton rubrolineata (Lischke)	+	+	_
Mollusca: Class Gastropoda			
Acmaea sybaritica (Dall)	-	+	+
Littorina squalida (Brodirep & Sowerby)	-	-	+
Littorina mandschurica (Schrenck)	-	+	+
<i>Neritrema sitkana</i> (Philippi)	+	3+	3+
<i>Barleeia angustata</i> (Pilsbry) (adults)	3+	3+	3+
* <i>Barleeia angustata</i> (Pilsbry) (eggs)	+	3+	2+
Pellamora trochlearis (Gould)	-	-	+
<i>Brochina glabella</i> (A. Adams)	-	+	-
Stenotis cariniferus (A. Adams)	+	+	+
Reticunassa fraterculus hypolius (Pilsbry)	+	-	-
Odostomia sp.	-	+	+
Cingulina laticingulata (Dall & Bartsch)	-	-	+
Haloa japonica (Pilsbry)	-	+	-
Fossarina picta A. Adams	-	+	-
Several taxa in the order Nudibranchia			
(Juvernies)	+	+	+
Mollusca: Class Pelecypoda			
Mytilus coruscus (Gould)	+	+	-
Hormomya mutabilis (Gould)	+	+	+
Modiolus modiolus difficilis (Kuroda & Habe)	+	+	+
Lasaea undulata (Gould)	+	+	+
^ IURTONIA MINUTA (FADRICIUS)	3+	2+	+
	-	+	+
Annelida: Class Polychaeta	~		
Pholoë parva Johnston	3+	3+	+
Anaitides maculata (L.)	+	+	+
<i>Eteone longa</i> (Fabricius)	+	+	+

Genetyllis castanea (Marenzeller) Eumida sanguinea (Oersted) Eulalia viridis (L.) Sphaerosyllis hirsuta Ehlers Typosyllis fasciata (Malmgren) Typosyllis hyalina Grube Typosyllis aciculata orientalis Imajoma and	+ + 3+ 3+ +	- + 3+ 2+ -	- - + +
Hartman <i>Typosyllis</i> sp. <i>Langerhansia</i> sp. <i>Onuphis</i> sp. <i>Sphaerodoridium minutum</i> (Webster &	+ + +	- + +	+ + - +
Benedict) <i>Lumbrineris japonica</i> (Marenzeller) <i>Lumbrineris latreilli</i> (A. & M. Edwards) <i>Arabella iricolor</i> (Montagu) <i>Nainereis laevigata</i> Grube	- 3+ + 3+	+ 3+ + - 3+	- + + +
One unidentified spinoid taxon (juveniles) <i>Cirratulus cirratus</i> (O. F. Müller) <i>Cirriformia tentaculata</i> (Montagu) <i>Timarete</i> sp. <i>Capitella capitata</i> (Fabricius)	+ + - +	3+ + + +	+ - - -
Branchiomaldone sp. Chone teres (Bush) Chone sp. (juveniles) *Dexiospira foraminosus (Bush) *Dexiospira nipponica Okuda *Circeis spirillum (L)	- + + 2+ +	+ + 3+ 3+ +	- + 2+ 2+ +
One species in the family Maldanidae Annelida: Class Oligochaeta Pachydrilus nipponicus (Yamaguchi)	- 2+	+ 3+	- +
Arthropoda: Class Arachnida Agauopsis sp. Copidognathus sp. Halacarus sp. Rhombognathus dissociatus Abe Rhombognathus atuy Abe Pontarachna sp. Family Oribate: one unidentified specimen	+ + + + -	3+ + 3+ 3+ + +	+ - - -
Arthropoda: Class Pycnogonida Achelia ohshimai Uchinomi	2+	+	+
Arthropoda: Class Crustacea Leptochelia dubia (Kröyor) Dynoides dentisinus shen Parametopella sp. Pontogeneia sp. Merita sp. Hyle spp.	+ 3+ + 2+ +	+ 2+ + 2+ - 3+	- + + + +
Amphithoe sp. Two other unidentified gammarid species One taxon in the family Idoteidae Two taxa in the family Caprellidae Two or more taxa in the subclass Ostracoda Two or three taxa in the order Copepoda	+ + + + +	- + + 3+ 3+	- + + 2+ +
Arthropoda: Class Insecta Telmatogeton japonicus Tokunaga (larvae) One taxon in the order Trichoptera (larvae)	3+ -	3+ +	3+ -
Bryozoa *Tricellaria erecta (Robertson) *Celleporina costazii (Audouin)	+ 3+	-	- +

*Taxa are attached to branches of Corallina. +, rare; 2+, common; 3+, abundant; –, absent