REPORT

Aschwin H. Engelen · Anneke M. Breeman Jeanine L. Olsen · Wytze T. Stam · Per Åberg

Life history flexibility allows *Sargassum polyceratium* to persist in different environments subjected to stochastic disturbance events

Received: 27 October 2004 / Accepted: 31 August 2005 / Published online: 8 November 2005 © Springer-Verlag 2005

Abstract Stochastic, stage-based matrix models were used to investigate the life history strategy of the seaweed Sargassum polyceratium in shallow intertidal and deep-water (18 m) populations. Matrix models were parameterized with 3 years of yearly transitions among four plant stages quantified from three bays on Curaçao (Netherlands Antilles). There were years without a storm, with a moderate (winter) storm and with a strong storm (Hurricane Lenny). The stochastic population growth rate varied among populations (λ_s : 0.54–1.03) but was not related to depth. The most important stages for population growth were reproductive adults (shallow) and non-reproductive adults (deep). With the occurrence of storms, vegetative growth (mainly deep) and fertility (mainly shallow) became the most important processes. Recruitment (shallow) and regeneration from holdfasts (deep) only contributed to population persistence after the hurricane. It is concluded that S. *polyceratium* has a flexible, depth-dependent, life history strategy that is adjusted to disturbance events.

Keywords Sargassum polyceratium · Stochastic matrix model · Life history strategy · Wave-disturbance events · Depth

Communicated by Ecological Editor P. Sale A. H. Engelen · A. M. Breeman · J. L. Olsen · W. T. Stam Department of Marine Biology, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, P.O. Box 14, 9750 AA, Haren, The Netherlands P. Åberg Department of Marine Ecology, Marine Botany, University of Göteborg, Box 461, 40530 Göteborg, Sweden *Present address*: A. H. Engelen (⊠) Centre for Marine Sciences (CCMAR), CIIMAR, Universidade do Algarve, FCMA, Campus de Gambelas, Participal Sciences (CCMAR), CIIMAR,

8005-139 Faro, Portugal E-mail: aengelen@ualg.pt Tel.: + 351-934977238

Fax: +351-289818353

Introduction

Sargassum species are among the largest and the most abundant macrophytes on rocky shores and coral reefs (Wanders 1976; McCook and Price 1997). Large patches, belts or meadows provide important spawning, nursery and feeding grounds for fish and invertebrates (Tsukidate 1992; Coston-Clements et al. 1991). Sargassum beds trap nutrients and contribute to high rates of primary production (e.g. Wanders 1976). Although Sargassum beds can be ecologically important in the maintenance of a healthy coastal ecosystem, coral reef degradation often involves growth of these algae at the expense of reef-building corals (e.g. McCook 1999). To increase the understanding of processes affecting the population dynamics of this macroalga, a greater insight is needed in the life history strategies of Sargassum in response to different environmental conditions.

Sargassum polyceratium Montagne is widely distributed in the Caribbean. Along American coasts it extends from southern Florida to northern Brazil (Diaz-Piferrer 1969). On the island of Curaçao (Netherlands Antilles) it inhabits different habitats, ranging from shallow- to deep-water (0-60 m depth) on both the leeward and windward coast. Windward coral reefs are dominated by S. polyceratium between 12 and 22 m depths. In contrast, abundances on leeward reefs are low. Population structure (in terms of biomass, density and stage distribution), the allocation of energy to the holdfast structure, and the timing of reproduction differ with wave exposure and depth (De Ruyter van Steveninck and Breeman 1987; Engelen et al. 2005). Furthermore, shallow- and deep-water populations (separated by 150 m) were shown to be genetically differentiated within bays (Engelen et al. 2001). Apart from the overall wave disturbance regime, stochastic wave disturbance events such as winter storms and hurricanes have strong effects on S. polyceratium populations (De Ruyter van Steveninck and Breeman 1987; Engelen 2004).

In this paper, alternative life history strategies of S. polyceratium in shallow- and deep-water using a modelling approach are compared. Matrix population models integrate population dynamics and population structure, and can easily be applied to organisms with different life histories (Caswell 2001). A matrix model describes the stage-specific survival and reproduction. For linear deterministic models, which assume timeinvariant vital rates, there are many analytical tools available for calculating, for example, the asymptotic population growth rate, stable stage structure, reproductive values and elasticity of the population growth rate to changes in the vital rates (Caswell 2001). However, vital rates in populations will vary with stochastic, temporal variation in the environment. Theoretical studies have shown that environmental stochasticity affects not only population dynamics (May 1975; Roughgarden 1975) but also the evolution of life histories in general (Tuljapurkar 1990a; Yoshimura and Clark 1991). This could also be the case for S. poly*ceratium*, where the relative abundances of stages vary through space and time (Engelen 2004).

Stochastic matrix models include variation in the vital rates due to random fluctuations in the environment (Caswell 2001; Tuljapurkar 1990b). For stochastic matrix models, analytical analyses are difficult (or not possible) but many analyses similar to the deterministic case can be achieved using model simulations (Åberg 1992a; Caswell 2001). The possibility of combining environmental variability with analytical rigor makes stochastic matrix models a powerful tool in research on population dynamics. For example, stochastic matrix models are now widely used in conservation biology to design or evaluate management programs that help to protect endangered species (e.g. Inchausti and Weimerskirch 2001; Hilderbrand 2002).

In this study, a stochastic, stage-based matrix model is used to investigate the long-term (1997–2000) dynamics of *S. polyceratium* populations at two depths (0 and 18 m) under different disturbance regimes. Specific questions include: (1) does population growth rate differ between shallow- and deep-water populations; (2) which stage class is most important for population growth; (3) what is the relative importance of vegetative growth, reproductive growth and fertility; (4) is recruitment or regeneration of holdfasts more important for population persistence?

Materials and methods

Description of habitats

All data were gathered between January 1997 and January 2000 on the island of Curaçao (Netherlands Antilles), 60 km off the coast of Venezuela. Tidal range is about 0.3 m. General information about the area, intertidal and subtidal vegetation and descriptions of coral-reef bottom components can be found in Engelen et al. (2005) and references therein. Vital rates (i.e., growth, survival and fertility) for *S. polyceratium* were estimated in three bays with different degrees of wave exposure. St. Michiel Bay, on the leeward southwest coast, receives the least wave action with waves of 0–30 cm high during normal conditions. Westpunt Bay, on the northwestern tip of the island, has slightly higher waves (0–50 cm) and is also subjected to oceanic swell, causing occasional wave heights of approximately 1 m or more. Boca Canoa, on the windward northeast coast, is the most wave-exposed bay with waves of 2–3.5 m high (Van Duyl 1985). The bays will hereafter be referred to as Michiel, Westpunt and Canoa. More detailed descriptions of the three bays are given in Engelen (2004).

During the study period, populations experienced several major disturbance events. Each year during the rainy season (roughly between October and March) the easterly trade wind can change for a number of days to westerly directions, causing very rough seas on the normally sheltered leeward coast. In January 1998, the western leeward coast was hit by a particularly severe winter storm. The following year, Hurricane Lenny had an impact on the study sites. Hurricanes rarely hit the Lesser Antilles, and Lenny (category IV) was the first hurricane in the 113-year Atlantic tropical cyclone record to have an extended west-to-east track across the central and eastern Caribbean Sea (Guiney 2000). Lenny generated large waves and swell that propagated across much of the southern and eastern Caribbean, affecting the Guajira Peninsula, Aruba, Bonaire, Curaçao, and much of the rest of the Leeward and Windward Islands. Lenny's unusual approach from the west produced unprecedented wave and surge impact on the usually sheltered coasts of Aruba, Bonaire and Curaçao on 16 November 1999 (Bries et al. 2004). Both disturbance events were used to investigate differences in life history strategies between shallow- and deep-water populations of S. polyceratium.

Demographic model

Data for model parameterisation

In algae, it is often difficult to distinguish genets (e.g. Åberg 1989). Genetic characterization based on RAPD markers for *S. polyceratium* has confirmed that branches of a common holdfast are genetically identical, whereas those on different holdfasts are genetically distinct (Engelen unpublished). Thus, individual plants were distinguished by their holdfast. Between 1997 and 2000 the fate of marked individuals in five populations was followed. At Michiel and Westpunt a shallow, intertidal population (0 m) and a deep, subtidal population (18 m) were selected. But, due to the exposed conditions at Canoa, only a deep subtidal population could be censused in this bay. Plants were marked by nailing numbered tags in the substratum close to their holdfast and

by a numbered tag around their main axis. The stage of every individual was identified and its fate (transition to another stage class, stasis or death) was recorded at the next census. In total about 2,500 plants were marked in the study. Each census was carried out in January or February of each year. During this time of year populations reached the maximum density of receptacle bearing plants, both in shallow- and deep-water populations (Engelen et al. 2005).

Matrix models

Projection matrices were constructed based on the lifecycle graph shown in Fig. 1. Within the monophasicdiplontic life history, four different and biologically relevant stages were distinguished: juveniles (J; small rosettes of leaf-like fronds without a detectable holdfast and without upright main axes), non-fertile adults (A), fertile adults (F) and plants consisting only of a basal holdfast (H). These stages were chosen so that the relative importance of sexual reproduction and vegetative regeneration from holdfasts could be studied. Juveniles arise from zygotes as a result of sexual reproduction; asexual reproduction by means of spores does not occur in Sargassum. Stage-specific mortality was estimated based on the number of marked plants of each stage class that disappeared between censuses. Transition probabilities among stage classes were estimated by calculating the relative frequencies of each transition from one year to the next. Only those plants on which the labels remained intact were considered. After the hurricane, all labels were lost in the shallow-water populations of the two leeward bays. However, no older adult plants with large holdfasts remained in the study area, and therefore it was assumed that all labelled plants had died.

Fertility was calculated by dividing the number of juveniles present in year t+1 by the number of fertile adults in year t (from quadrat data). This estimate is



subject to error since non-fertile adults at time t may contribute to recruitment later in the year, and juveniles formed right after a census may have developed into fertile plants before the next census. However, it is believed that relating the recruitment to the maximum number of fertile plants is the best fertility estimate that can be got from the data. This fertility estimate also led to an implicit model assumption that it is a closed population where all recruits are locally produced (99% of recruits settle within 1 m; Kendrick and Walker 1991; Stiger and Payri 1999, and populations separated by 150 m are genetically differentiated; Engelen et al. 2001), or that an input of recruits from other populations is balanced with an output from the local population.

Analyses of models

Basic analyses of deterministic models (e.g. population growth rate) for one matrix per population and year were all performed using standard methods as described by Caswell (2001).

Trade-offs among matrix elements (fitness components) were studied by analysing the correlations among matrix elements, using Spearman's rank correlation. When matrix elements comprise life cycle components involved in a trade-off relation due to limited resources, a change in one matrix element will lead to a change in the opposite direction of another element. This trade-off relationship can be detected as a significant negative correlation among the variables involved.

The stochastic models consisted of a set of three matrices per population (3 years). In model simulations the sequence of matrices was generated by a stochastic process, i.e., a first-order finite-state ergodic Markov chain. It was assumed that the hurricane year was a rare event and because it had been 125 years since a disturbance of similar magnitude had occurred on Curaçao, the current year was given a probability of 1/125 in the model simulations. The other 2 years were assumed to be equally common so each year was assigned a probability of occurrence of 0.496 in the model simulations. The mean matrices were calculated as the weighted mean using the probabilities mentioned herewith (Åberg 1992a; Caswell 2001).

The population growth rate from the mean matrices (μ) was calculated. The average stochastic population growth rate (ln λ_s) was estimated by averaging a number of one-step (from time *i* to *i*+1) estimates of ln λ_s over *T* time units (Heyde and Cohen 1985).

$$\ln \lambda_{\rm s}(i) = \ln N(i+1) - \ln N(i), \tag{1}$$

$$\ln \lambda_{\rm s} = 1/(T-1) \sum_{i} \ln \lambda_{\rm s}(i). \tag{2}$$

In the model simulations *T* was set to 10,000 but to avoid transients, only the last 9,000 steps were used in the calculation of $\ln \lambda_s$. Intra-population variances in λ were decomposed into contributions from the variances



in (and covariances among) the matrix entries as described by Caswell (2001). The mean stochastic stage structure (w) was calculated as the mean population structure from time 1,000 to 10,000.

Generation time was estimated using stochastic model simulations so that a cohort of individuals was followed for 30 time-steps and at each time-step the number of recruits was recorded. The fertility elements in the first row of each matrix **A** were set to zero and placed into a separate vector **b**. For each time-step, two calculations were performed: $\mathbf{n}(i+1) = \mathbf{A} \mathbf{n}(i)$ to calculate cohort survival and $D(i) = \mathbf{b} \mathbf{n}(i)$ to calculate the number of recruits per time step (D). Generation time (G) was calculated as

$$G = \sum t(i) D(i) / \sum D(i),$$

where t is a vector with cohort age (in this case 1, 2, 3, ..., 30). In other words, G is the sum of the yearly recruits scaled by the cohort age divided by the total sum of recruits produced by the cohort. The mean stochastic generation time was calculated as the average of G from 300 replicate model simulations. The mean cohort survival curve was calculated by averaging the vector n at each time-step.

Reproductive values were calculated from the mean population matrices as described in Caswell (2001).

Elasticity analysis

Elasticities (e_{ii}) of the stochastic population growth rate λ_s were calculated using a numerical method described by Åberg (1992a). A 5,000-year long stochastic sample path was simulated and the last 2,000 years were used to estimate λ_s . Elasticities (e_{ij}) were calculated by measuring the proportional change in the estimated λ_s caused by: (1) a proportional change in one of the matrix elements a_{ii} in all matrices in the set; (2) a proportional change in one of the matrix elements a_{ii} in one matrix in the set at a time. The first calculation is analogous to a deterministic elasticity analysis of the population growth rate of the mean matrix and provides information on disturbances that will take place in all years. In the second calculation the disturbance affects only one matrix at a time. This can be used to study the variation between years and to determine which life-cycle components are most important for the overall stochastic growth.

Since elasticities sum to one, each elasticity value may also be interpreted as the contribution of each matrix element to the population growth rate (De Kroon et al. 1986; Caswell 2001). Thus, elasticities allow identification of the most vulnerable/important phases of a species' life history (De Kroon et al. 1986; Caswell 2001). In addition, elasticities may be summed across selected regions of a matrix, corresponding to different demographic processes, for instance, to compare the relative importance of growth, stasis or retrogression, and fertility. Elasticity elements in each row of the elasticity matrices were summed, to give the relative contribution of each stage to the stochastic growth rate (since a row represents the stasis and all transitions to that stage). The rows of the A and H stages were summed up in order to compare the relative contribution of vegetative growth (A+H), with sexual reproduction (the row of the J stage) and survival as reproductive individuals (the row of the F stage). Elasticity values of sexual reproduction were compared with the summed elements of regeneration from holdfasts.

All model simulations and analyses were performed in MATLAB (The Math Works).

Model validation

Validation of models is usually performed by either dividing the data-sets into two parts, or using a bootstrapping procedure to estimate the reliability of model outputs. In the first case the first half of the data-set is used to parameterise the model and after simulations, predicted estimates of the viability of the species are compared to the second half of the data-set (Brook et al. 2000; Kindvall 2000). Although one would have preferred to validate the models using bootstrapping procedures, or by reserving half the data to test model predictions, the data were too variable and too limited to permit this. However, the model outputs conformed in general to the data on population stage structure obtained from a study, using random quadrats at all studied sites (Engelen 2004). In addition, transition probabilities that were relatively poorly estimated from labelled individuals in general did not make a large contribution to λ and so estimation errors in these cases are unlikely to affect the model significantly.

Results

Population projections

Population projection matrices differed between years in all populations. In the hurricane year (1999), there was a marked increase in mortality and a low number of stage transitions in all leeward populations. Only in the deepwater population of the windward bay (Canoa) did total mortality remain relatively constant over the years.

Adult, non-fertile plants generally dominated the stage structure (A stage; Table 1). Only populations at Westpunt showed an increased proportion of fertile plants (F stage) in years without and with a moderate disturbance event (1997, 1998). After the hurricane, the stage structure was altered dramatically mainly because of the absence of fertile plants.

The mean stochastic stage distribution was very similar to the *mean* observed stage distribution in all populations, except the shallow-water population at Michiel (Table 1). The mean stochastic stage distribution differed among populations, although non-reproductive adults were generally the dominant stage class. Shallow-water populations had a higher proportion of juveniles and fewer non-reproductive adults than those in deep-water. The holdfast stage contributed noticeably to the overall population composition in the deep-water population at Canoa.

Correlations among stage transitions were strongly significant in two out of 60 cases (P < 0.01). The probability to grow from the A stage into the F stage was positively correlated with the probability to grow from the J stage into the F stage, and with the probability to grow from the H stage into the F stage. Thus, conditions that promote non-fertile adults to become fertile also promote growth of juveniles and holdfasts into fertile adults. No strongly significant negative correlations were found, indicating that there are no major trade-offs between matrix elements.

Reproductive values

Reproductive values increased with plant development $(H \le J \le A \le F)$ in all leeward populations (Table 1). However, in the deep-water population of Canoa, reproductive values of the A and F stages were about equal, and lower than for the J and H stages. In general, reproductive value's were higher at Westpunt than at Michiel. The Canoa population showed the lowest values.

Stochastic population growth rate and generation time

Population growth rates based on the mean matrices (μ) showed variation between populations: strong positive

growth in both populations at Michiel and in the shallow-water population at Westpunt, whereas growth rates at Canoa were very low (Table 2). The stochastic population growth rate (λ_s) varied strongly among populations (Table 2), and differences were not related to depth. Only the deep-water population at Michiel showed positive population growth, whereas all other populations showed values (well) below 1. For all populations μ was larger than λ_s . The large difference between μ and λ_s at the shallow-water population at Michiel indicates high variance in growth rate $(V(\lambda))$ over the years. Decomposition of the intrapopulation variances of this population showed that variances and covariances involving the transition from the F to the J stage were responsible for $V(\lambda)$.

Mean generation times (G), i.e. the average time needed for completion of the monophasic life history, varied between about 3 and 8 years (Table 2). No consistent differences between shallow- and deep-water populations were found. G was highest in the shallowwater population at Westpunt and lowest in the shallowwater population at Michiel.

Elasticities

The elasticity matrices with the proportional change in one of the matrix elements a_{ii} in all matrices in the set (Table 3: 1997–2000) showed that in the shallow-water populations fertility (Michiel) or persistence of the F stage (Westpunt) were most important for λ_s . In all deep-water populations, however, the highest elasticity values were associated with persistence/stasis of the A

Table 1 Observed and projected stochastic population stage structure and reproductive values of shallow- (0 m) and deep-water (18 m) populations of S. polyceratium in two leeward bays (Michiel and Westpunt) and a windward bay (Canoa)

Bay	Depth	Stage	Observ	ed stage st	ructure		Mean observed	Mean stochastic	Reproductive
			1997	1998	1999	2000	stage structure 1997–2000	stage structure	values"
Michiel	0 m	J	0.06	0.08	0.11	1.00	0.31	0.39	1.00
		А	0.68	0.67	0.71	0.00	0.52	0.08	1.33
		F	0.25	0.15	0.13	0.00	0.13	0.49	2.01
		Н	0.01	0.10	0.04	0.00	0.04	0.04	0.47
	18 m	J	0.29	0.12	0.19	0.22	0.21	0.18	1.00
		А	0.64	0.54	0.69	0.73	0.65	0.61	1.36
		F	0.07	0.34	0.11	0.00	0.13	0.17	2.98
		Н	0.00	0.00	0.01	0.05	0.01	0.04	0.53
Westpunt	0 m	J	0.19	0.01	0.22	0.40	0.20	0.27	1.00
1		А	0.32	0.44	0.43	0.58	0.44	0.41	2.30
		F	0.47	0.49	0.30	0.00	0.32	0.28	4.52
		Н	0.02	0.06	0.05	0.02	0.04	0.04	1.15
	18 m	J	0.07	0.19	0.22	0.50	0.24	0.06	1.00
		Α	0.23	0.41	0.46	0.50	0.40	0.48	2.09
		F	0.70	0.41	0.32	0.00	0.35	0.31	2.65
		Н	0.00	0.00	0.00	0.00	0.00	0.15	0.70
Canoa	18 m	J	0.38	0.14	0.15	0.07	0.19	0.02	1.00
		А	0.48	0.70	0.78	0.93	0.72	0.69	0.65
		F	0.10	0.15	0.06	0.00	0.08	0.09	0.63
		Н	0.03	0.00	0.01	0.00	0.01	0.20	1.02

Stage classes: J juveniles; A adults; F fertile adults; H holdfasts. Dominant stage in bold print

^aCalculated from mean matrices

polyceratium population	ons at three bays (in order of inc	creasing chronic wave disturbance	ce) and at two depths (0 and 18 i	m)
Bay	Depth	μ	$\lambda_{ m s}$	G
Michiel	0 m	1.0455	0.7528	2.8
	18 m	1.0722	1.0316	7.1
Westpunt	0 m	1.0155	0.9919	8.4
•	18 m	0.7814	0.7649	5.9
Canoa	18 m	0.5498	0.5438	4.9

Table 2 Population growth rates for the mean matrices (μ), stochastic population growth rate (λ_s) and mean generation time (*G*) of five *S*. *polyceratium* populations at three bays (in order of increasing chronic wave disturbance) and at two depths (0 and 18 m)

stage (Table 3). In years without disturbance events, fertility and persistence of the F stage were generally the most important for overall stochastic growth (Table 3). In the winter storm year, the same life cycle components were important for the shallow-water populations but in the deep-water populations persistence of the A stage was most important. The deep-water population at Canoa was the only one showing retrogression to the H stage in that year. In the hurricane year, population growth was totally dependent on fertility in the shallowwater populations, whereas in the deep-water population persistence of the A stage (Michiel and Canoa) or vegetative growth from the H stage (Westpunt) contributed primarily to population growth (Table 3). Thus, shallow- and deep-water populations have different survival strategies when exposed to episodic strong disturbance events.

Vegetative growth, sexual reproduction and survival of reproductive individuals

Ordination of the populations by the relative contribution of vegetative growth (stage A+H), sexual reproduction and survival as reproductive individuals showed large differences between shallow- and deep-water populations (Fig. 2). Shallow-water populations have a higher contribution of fertility and survival of reproductive individuals than deep-water populations (Fig. 2). Plotting of values for years with increasing disturbance (no disturbance versus winter storm versus hurricane) clearly showed the strong shift in shallowwater populations from survival of reproductive individuals to fertility. In the deep-water populations, however, there was a strong increase in the contribution of vegetative growth to overall population growth (Fig. 2).

Sexual reproduction versus regeneration from holdfasts

In both the shallow-water populations sexual reproduction was of greater importance to population growth than regeneration from holdfasts. This contribution increased strongly with increasing disturbance (Fig. 3). In leeward deep-water populations sexual reproduction was more important than regeneration from holdfasts during the year without a disturbance event, and much less important in the hurricane year. In the windward deep-water population, regeneration from holdfasts was more important during all years (Fig. 3).

Model simulations

The effect of a change in hurricane frequency was simulated in all populations. The sensitivity of λ_s to small changes in hurricane frequency was small. A doubling of the current hurricane frequency (e.g. proportion of hurricane years increasing from 0.008 to 0.016) caused a maximum decrease of only 2.34% and a maximum increase of 2.55% in the stochastic population growth rate. The deep-water population of Michiel and both populations at Westpunt behaved similarly to changes in hurricane frequency showing a decrease of λ_s with increasing hurricane frequency. The shallow-water population at Michiel, however, showed an increase of λ_s with increase of requency of hurricanes. Hurricane frequencies did not affect λ_s at Canoa.

Cohort survival differed strongly among populations but no relationship existed with depth or level of wave disturbance. During their first year, plants at the deepwater populations of Michiel and Canoa had the highest survival probability, while deep-water plants at Westpunt had the lowest ones. After 1 year, cohort survival became constant. Cohort survival was the smallest in the shallow-water population at Michiel (cohort size reduced to 1% in ca. 6 years), and the largest in the shallow water population at Westpunt (cohort size reduced to 1% in ca. 22 years).

Discussion

Population growth rate and the importance of life history components

No consistent differences in population growth rates (λ) of shallow- and deep-water populations of *S. polycera-tium* were found. However, λ depended on different components of the life history at different depth. Such habitat-specific differences have also been reported among species/populations of terrestrial plants (Valver-de and Silvertown 1998). In longer-lived algal species elasticity values for survival are, generally, an order of magnitude higher than those for fertility [e.g. *Asco-phyllum nodosum* (Åberg 1992a, b), *S. siliquosum*

$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\mathbf{B}\mathbf{a}\mathbf{y}$	Depth	Stage	1997–2	000^{a}			Stage	1997–1	998 no d	listurban	ice ^b	Stage	1998–1	999 wint	er storm	P.	Stage	1999–2	000 hurr	icane ^b	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$				- -	A	ц	Н		ſ	A	ц	Н		ſ	A	Ц	Н		5	A	ц	Н
A 0.079 0.000 0.0	Σ	0 m	J	0.000	0.000	0.330	0.000	J	0.000	0.000	0.061	0.000	J	0.000	0.000	0.595	0.000	J	0.000	0.000	1.000	0.000
F 0.251 0.079 0.238 0.010 0.000 0.000 0.015 0.000 <th0.000< th=""> 0.000 0.00</th0.000<>			A	0.079	0.000	0.000	0.000	A	0.153	0.000	0.000	0.000	A	0.000	0.000	0.000	0.000	A	0.000	0.000	0.000	0.000
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			Ц	0.251	0.079	0.238	0.010	Ц	0.170	0.096	0.472	0.021	Ц	0.346	0.059	0.000	0.000	Ц	0.000	0.000	0.000	0.000
			Η	0.000	0.000	0.010	0.003	Н	0.000	0.000	0.021	0.007	Η	0.000	0.000	0.000	0.000	Η	0.000	0.000	0.000	0.000
A 0.149 0.310 0.075 0.008 A 0.138 0.255 0.001 E 0.000 0.363 0.104 0.011 A 0.000 0.371 0.000 0.731 W U J 0.000 0.230 0.067 0.000 0.161 0.005 0.000 0.341 0.017 A 0.104 0.011 A 0.000 0.000 1.47 W U J 0.000 0.115 0.000 0.161 0.000 1.000 0.000 1.47 0.000 0.001 1.47 0.000 0.001 1.47 0.000 0.001 1.47 0.000 0.001 1.47 0.000		18 m	ſ	0.000	0.000	0.152	0.000	ſ	0.000	0.000	0.287	0.000	J	0.000	0.000	0.015	0.000	ſ	0.000	0.000	0.000	0.000
F 0.000 0.230 0.067 0.000 F 0.000 0.304 0.037 0.007 F 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.147 0.000 0.000 0.147 0.000			A	0.149	0.310	0.075	0.008	A	0.138	0.255	0.051	0.004	A	0.160	0.363	0.104	0.011	A	0.000	0.73I	0.000	0.123
W 0 m J 0.003 0.002 0.003 0.000 H 0.000 0.002 0.007 0.000 H 0.006 0.000 0.000 H 0.000 J 0.000 0.000 0.000 0.000 A 0.116 0.152 0.039 0.005 A 0.145 0.150 0.003 0.002 A 0.092 0.158 0.042 0.071 A 0.000 0.000 0.000 F 0.000 0.151 0.400 0.005 F 0.000 0.139 0.452 0.003 F 0.000 0.147 0.350 0.000 F 0.000 0.000 0.000 H 0.000 0.000 0.000 7 0.000 0.013 0.000 1.007 H 0.000 0.0147 0.350 0.000 7.000 0.000 0.000 F 0.000 0.000 0.000 0.007 H 0.000 0.013 0.000 J 0.007 H 0.000 0.0147 0.350 0.000 7.000 0.000 H 0.000 0.000 0.003 0.000 F 0.000 0.013 0.000 J 0.000 0.0147 0.350 0.000 J 0.000 0.000 F 0.000 0.000 0.000 0.000 J 0.000 0.010 0.000 J 0.000 0.013 0.236 0.000 0.000 0.000 0.000 0.000 F 0.000 0.000 0.000 0.000 J 0.000 0.011 0.002 H 0.000 0.013 0.236 0.000 J 0.000 0.000 0.000 0.000 H 0.000 0.000 0.000 0.000 J 0.000 0.011 0.002 H 0.000 0.000 0.000 J 0.000 J 0.000 0.000 J 0.000 0.000 H 0.000 0.000 0.000 0.000 0.016 0.000 0.011 0.002 0.134 0.013 0.236 0.000 J 0.000 0.000 H 0.000 0.000 0.000 0.000 0.016 0.000 0.011 0.002 0.134 0.013 0.000 H 0.000 0.000 H 0.000 0.000 H 0.0000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.00			Ц	0.000	0.230	0.067	0.000	Ц	0.000	0.161	0.096	0.000	Ц	0.000	0.304	0.037	0.000	Ĺ	0.000	0.000	0.000	0.000
W 0 m J 0.000 0.016 0.000 0.116 0.000 J 0.000 0.029 0.000 J 0.000 0.0191 0.000 J 0.000 0.000 F 0.000 0.151 0.400 0.005 F 0.000 0.159 0.452 0.009 F 0.000 0.147 0.350 0.000 F 0.000 0.000 H 0.000 0.0151 0.400 0.005 F 0.000 0.139 0.452 0.009 F 0.000 0.147 0.350 0.000 7.000 0.000 I8 m J 0.000 0.003 0.000 J 0.001 J 0.000 0.013 0.000 J 0.000 0.013 0.236 0.000 J 0.000 0.000 F 0.000 0.000 0.000 J 0.000 0.000 J 0.000 0.013 0.000 J 0.000 0.013 0.236 0.000 0.000 0.000 F 0.000 0.000 0.000 J 0.000 0.000 J 0.000 0.013 0.000 J 0.000 0.013 0.236 0.000 J 0.000 0.000 F 0.000 0.000 0.000 J 0.000 J 0.000 0.011 0.002 H 0.000 0.013 0.236 0.000 J 0.000 0.000 F 0.000 0.000 0.000 J 0.000 0.000 0.011 0.002 H 0.000 0.013 0.236 0.000 J 0.000 0.000 F 0.000 0.000 J 0.000 J 0.000 0.011 0.002 J 0.000 J 0.000 0.013 0.236 0.000 J 0.000 0.000 H 0.000 0.004 0.011 0.002 P 0.000 0.011 0.002 J 0.000 0.004 0.013 0.200 0.000 0.000 F 0.000 0.000 0.024 0.010 0.000 F 0.000 0.0146 0.020 0.000 F 0.000 0.000 0.000 0.000 0.000 0.000 H 0.000 0.000 0.000 P 0.000 0.0146 0.020 0.000 F 0.000 0.000 0.000 F 0.000 0.000 H 0.000 0.000 0.000 P.000 P 0.000 0.0146 0.020 0.000 0.000 0.000 0.000 0.000 F 0.000 0.000 0.000 H 0.000 0.000 0.000 P.000 P.000 0.0146 0.020 0.000 0			Η	0.003	0.002	0.003	0.000	Η	0.000	0.002	0.007	0.000	Η	0.006	0.000	0.000	0.000	Η	0.000	0.147	0.000	0.000
A 0.116 0.152 0.039 0.0145 0.150 0.036 0.002 A 0.092 0.158 0.042 0.071 A 0.000	M	0 m	J	0.000	0.000	0.116	0.000	J	0.000	0.000	0.029	0.000	J	0.000	0.000	0.191	0.000	J	0.000	0.000	1.000	0.000
F 0.000 0.151 0.400 0.005 F 0.000 0.147 0.350 0.000 F 0.000			A	0.116	0.152	0.039	0.005	A	0.145	0.150	0.036	0.002	A	0.092	0.158	0.042	0.071	A	0.000	0.000	0.000	0.000
H 0.000 0.009 0.000 0.007 H 0.000 0.013 0.000 0.007 H 0.000 0.005 0.000 0.081 H 0.000 0.000 18 m J 0.000 0.003 0.000 J 0.000 J 0.000 0.060 0.000 J 0.000 0.005 0.000 J 0.000 0.000 A 0.025 0.349 0.120 0.008 A 0.023 0.287 0.083 0.007 A 0.025 0.426 0.159 0.000 A 0.000 0.000 F 0.008 0.149 0.285 0.006 F 0.016 0.167 0.331 0.013 F 0.000 0.133 0.236 0.000 F 0.000 0.000 H 0.000 0.004 0.011 0.002 H 0.000 0.011 0.002 H 0.000 0.004 0.13 0.026 H 0.000 0.000 C 18 m J 0.000 0.020 0.317 0.025 A 0.015 0.485 0.054 0.211 A 0.000 0.001 0.024 0.000 J 0.000 0.000 A 0.020 0.317 0.022 0.257 A 0.015 0.248 0.001 J 0.000 0.000 0.000 0.001 0.000 0.000 0.000 0.000 J 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.014 0.000 0.014 0.020 0.000 0.000 0.000 0.000 0.000 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.014 0.000 0.014 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000			ĹĻ	0.000	0.151	0.400	0.005	ĹĿ	0.000	0.159	0.452	0.009	ц	0.000	0.147	0.350	0.000	ĹĹ	0.000	0.000	0.000	0.000
18 m J 0.000 0.003 0.003 0.003 J 0.000 J 0.000 0.060 0.000 J 0.000 0.000 0.000 J 0.000 J 0.000 0.000 0.000 F 0.000 0.000 0.000 F 0.000 0.000 F 0.000 0.000 0.000 F 0.000 0.000 0.000 F 0.000 0.000 0.000 F 0.000 0			Н	0.000	0.009	0.000	0.007	Н	0.000	0.013	0.000	0.007	Н	0.000	0.005	0.000	0.08I	Н	0.000	0.000	0.000	0.000
A 0.025 0.349 0.120 0.008 A 0.023 0.287 0.083 0.007 A 0.025 0.426 0.159 0.000 A 0.000 0.000 F 0.008 0.149 0.285 0.006 F 0.016 0.167 0.331 0.013 F 0.000 0.133 0.236 0.000 F 0.000 0.000 H 0.000 0.004 0.011 0.002 H 0.000 0.001 0.002 H 0.000 0.044 0.013 0.024 10.000 0.000 C 18 m J 0.000 0.002 0.000 J 0.000 0.016 0.016 0.000 J 0.000 0.024 0.013 0.000 H 0.000 0.000 F 0.000 0.024 0.017 0.045 0.257 A 0.015 0.485 0.054 0.211 A 0.025 0.134 0.034 0.300 J 0.000 0.000 F 0.000 0.074 0.010 0.000 F 0.000 0.146 0.020 0.000 F 0.000 0.000 0.000 F 0.000 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.035 0.018 0.000 H 0.000 0.000 P.000 0.000 F 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.035 0.018 0.000 H 0.000 0.000 0.000 F 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000		18 m	J	0.000	0.000	0.033	0.000	ſ	0.000	0.000	0.060	0.000	J	0.000	0.000	0.005	0.000	ſ	0.000	0.000	0.000	0.000
F 0.008 0.149 0.285 0.006 F 0.016 0.167 0.331 0.013 F 0.000 0.236 0.000 F 0.000 0.000 0.000 F 0.000 0.000 0.000 F 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.269 C 1 0.000 0.002 0.000 1 0.000 0.011 0.000 0.0124 0.000 1 0.000 0.269 A 0.020 0.017 0.016 0.016 0.016 0.000 1 0.000 1 0.000 0.000 F 0.000 0.014 0.020 0.0146 0.025 0.134 0.339 A 0.000 F 0.000 0.000 H 0.000 0.248 0.000 0.0146 0.025 0.134 0.399 A 0.000 0.000 H 0.000			A	0.025	0.349	0.120	0.008	A	0.023	0.287	0.083	0.007	A	0.025	0.426	0.159	0.000	A	0.000	0.000	0.000	0.644
H 0.000 0.004 0.011 0.002 H 0.000 0.000 0.000 0.011 0.002 H 0.000 0.004 0.013 0.000 H 0.000 0.269 C 18 m J 0.000 0.020 0.020 0.000 J 0.000 0.016 0.000 J 0.000 0.024 0.000 J 0.000 0.000 F 0.000 0.074 0.010 0.000 F 0.015 0.485 0.054 0.211 A 0.025 0.134 0.034 0.309 A 0.018 0.756 H 0.000 0.248 0.009 0.000 H 0.000 0.146 0.020 0.000 F 0.000 0.000 0.000 F 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.035 0.018 0.000 H 0.000 0.474 0.000 0.000 H 0.000 0.000			ĹĻ	0.008	0.149	0.285	0.006	Ц	0.016	0.167	0.331	0.013	ĹĻ	0.000	0.133	0.236	0.000	ĹĿ	0.000	0.000	0.000	0.000
C 18 m J 0.000 0.000 0.020 0.000 J 0.000 0.016 0.000 J 0.000 0.015 0.000 J 0.000 0.024 0.000 J 0.000 0.000 F 0.020 0.317 0.045 0.257 A 0.015 0.485 0.054 0.211 A 0.025 0.134 0.034 0.309 A 0.018 0.756 F 0.000 0.074 0.010 0.000 F 0.000 0.146 0.020 0.000 F 0.000 0.000 0.000 F 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.035 0.018 0.000 H 0.000 0.474 0.000 0.000 H 0.000 0.000			Η	0.000	0.004	0.011	0.002	Η	0.000	0.000	0.011	0.002	Η	0.000	0.004	0.013	0.000	Η	0.000	0.269	0.000	0.087
A 0.020 0.317 0.045 0.257 A 0.015 0.485 0.054 0.211 A 0.025 0.134 0.034 0.309 A 0.018 0.756 F 0.000 0.074 0.010 0.000 F 0.000 0.146 0.020 0.000 F 0.000 0.000 0.000 F 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.035 0.018 0.000 H 0.000 0.474 0.000 0.000 H 0.000 0.000	U	18 m	ſ	0.000	0.000	0.020	0.000	ſ	0.000	0.000	0.016	0.000	J	0.000	0.000	0.024	0.000	ſ	0.000	0.000	0.030	0.000
F 0.000 0.074 0.010 0.000 F 0.000 0.146 0.020 0.000 F 0.000 0.000 0.000 0.000 0.000 F 0.000 0.000 H 0.000 0.248 0.009 0.000 H 0.000 0.035 0.018 0.000 H 0.000 0.474 0.000 0.000 H 0.000 0.000			A	0.020	0.317	0.045	0.257	A	0.015	0.485	0.054	0.211	A	0.025	0.134	0.034	0.309	A	0.018	0.756	0.000	0.169
H 0.000 0.248 0.009 0.000 H 0.000 0.035 0.018 0.000 H 0.000 0.474 0.000 0.000 H 0.000 0.000			ĹĹ	0.000	0.074	0.010	0.000	ĹĹ	0.000	0.146	0.020	0.000	Ц	0.000	0.000	0.000	0.000	ĹŢ	0.000	0.000	0.000	0.028
			Η	0.000	0.248	0.009	0.000	Η	0.000	0.035	0.018	0.000	Η	0.000	0.474	0.000	0.000	Η	0.000	0.000	0.000	0.000

^aThe proportional change in one of the matrix elements a_{ij} in all matrices in the set ^bThe proportional change in one of the matrix elements a_{ij} in one matrix at a time

676

Fig. 2 Triangular ordination of the relative contribution of vegetative growth, survival of reproductive individuals, and fertility to population growth for five populations of S. polyceratium located in two leeward bays: Michiel (circles) and Westpunt (squares) and one windward bay: Canoa (triangles) and at two depths (0 m: *closed symbols*; 18 m: open symbols) in 3 years (small symbols; n no disturbance event, w winter storm and h hurricane year) and in the stochastic simulation (large symbols)



(Ang and De Wreede 1990) and Gelidium sesquipedale (Santos and Nyman 1998)]. In shorter-lived algae elasticity values for fertility are generally higher, although still lower than those for survival [e.g. Laminaria longicruris (Ang and De Wreede 1990), Fucus distichus (Ang and De Wreede 1993)]. In this ordination (Fig. 2), S. polyceratium generally took a position similar to that of longer-lived algae/plants. However, with the occurrence of disastrous disturbance events, shallow-water plants have the possibility to switch to characteristics, typical for shorter-lived plants and algae that depend on their recruitment capabilities. S. polyceratium shows large changes in life history to survive a variety of environmental conditions. Recruitment is important for the long-term stability of populations regardless of the contribution of fertility to population growth (Reed et al. 1988; Ang and De Wreede 1993). In this case it can be shown that the importance of fertility may only become apparent during exceptional circumstances such as after extreme disturbance events. Other longer-lived macroalgae [e.g. Macrocystis pyrifera and other kelps (Dayton et al. 1992; Ladah et al. 1999)] also show limited recruitment in established populations but massive recruitment events occur after storm disturbance/ENSO event create empty space.

Recruitment versus regeneration

The relative importance of recruitment versus vegetative regeneration has been a matter of some debate in *Sargassum* (e.g. Ang 2000; Paula and Eston 1987; Kendrick

and Walker 1991). The opposite opinions found in the literature, can probably be attributed to differences in the temporal scales and environmental conditions at which populations were studied. The results in this study clearly demonstrate that the importance of recruitment versus regeneration from holdfasts varies strongly from year to year, both within and among populations. Although recruitment often makes a considerable contribution to population growth, populations have the possible alternative of holdfast persistence and vegetative regeneration when strong disturbance events eliminate all mature plants that would have contributed to the annual reproductive output.

Hurricane Lenny caused mass mortality of *S. poly-ceratium* plants. In the leeward bays, the destruction was nearly 100% in shallow-water populations and only holdfasts and non-fertile adults survived in the deepwater populations. A similarly strong impact of stochastic disturbance was found by Åberg (1992a) for *A. nodosum* along the Swedish west coast, where an unusually strong ice-scouring year effectively wiped out local populations.

The effect of Hurricane Lenny was simulated over longer time periods with a hurricane frequency based on the last documented disturbance event of similar severity, 125 years ago. Hurricane frequencies over a longer time scale are unknown. However, simulations showed that λ_s was not particularly sensitive to small changes in the frequency of such destructive events. This implies that the projected doubling of hurricane frequencies in the Caribbean due to global warming (O'Brien et al. 1992) would have no large impact on population growth Fig. 3 Relative contribution of sexual reproduction and regeneration from holdfasts to population growth rate for five populations of *S. polyceratium* at two depths (0 and 18 m) in 3 years (no disturbance event, winter storm and hurricane year). Populations were located in two leeward bays (Michiel and Westpunt) and one windward bay (Canoa)



in *S. polyceratium.* However, with increasing hurricane frequencies, large changes in life history can be expected with higher dependence on sexual reproduction (in shallow-water) and on survival of non-reproductive adults and regeneration from holdfasts (in deep-water populations) (Fig. 3).

Position of *S. polyceratium* populations in triangular ordination plots

The distribution of the data in the triangular plot (Fig. 2) is comparable to the hypothetical successional sequence, described by a parabolic trajectory from the lower left hand corner (early successional states) to the lower right hand corner (late successional states), as described by Silvertown and Franco (1993). In the case of S. poly*ceratium*, a single species covers the entire trajectory, normally covered by several species with different life histories (e.g. herbs, shrubs and trees). Shallow-water populations covered the early to mid-successional part (herb-like), whereas deep-water populations occupied the mid to late successional part of the plot (tree-like). Disturbances tend to push populations towards earlier successional states (Silvertown and Franco 1993). In this study, this state is clearly shown by the shallow-water populations with the occurrence of both the winter storm and the hurricane. Disturbance events and high chronic disturbance (windward Canoa population) unexpectedly pushed deep-water populations in the corner normally occupied by late successional states.

Evolutionary context

Demographic models provide an insight into the evolutionary processes related to adaptation. The population growth rate λ_s is analytically equivalent to the

relative fitness of the mean phenotype of the population and sensitivities measure the relative strength of selection on life history parameters (Van Groenendael et al. 1988; Caswell 2001). This means that high elasticities indicate fitness advantages for associated life history components.

In S. polyceratium, the high elasticity values for fertility and/or persisting in the reproductive state found for the shallow-water populations indicate that there is a strong advantage for individual plants to be able to reproduce throughout the year and have a high reproductive output. In contrast, deep-water populations depend on persistence and low-turnover, with fitness advantages for individuals with well-attached holdfasts and sturdy main axes. These differences are reflected in differences in morphology and reproductive periodicity at the two depths. Shallow-water plants show yearround instead of seasonal reproduction. They have a higher number of main axes and lateral and, consequently, a much higher reproductive output as compared to deep-water plants (De Ruyter van Steveninck and Breeman 1987; Engelen et al. 2005). Elasticity values varied strongly among years. On an evolutionary time scale, the elasticity values of the matrices for the three different years would have to be weighted according to the frequency of each type of year in order to become equivalent to the overall selection pressure on life history components. However, hurricane frequencies would have to increase strongly before sexual reproduction (in shallow water) or regeneration from holdfasts (in deep water) would carry the main fitness advantages (Fig. 3). Therefore, persistence of fertile adults in shallow-water and of non-fertile adults in deep-water populations suggests that these are probably the life history components with the strongest overall fitness advantages. The different selective regimes encountered by shallowand deep-water individuals suggest possible ecotypic differentiation within this species, as is reflected in the life history strategies (this study), the morphology (De Ruyter van Steveninck and Breeman 1987; Engelen 2004) and in genetic differentiation between these habitats (Engelen et al. 2001).

Coral-reef ecology

Populations of S. polyceratium dominate the shallow reef platform and reef slope on the windward shore of the island of Curaçao. The flexible life history strategy towards both chronic and episodic wave disturbance probably contributes strongly to this dominance. Only lower substrate availability [bare artificial substrates incubated in leeward populations for 6 months bore up to 400 plants m⁻² (Engelen 2004)], less water motion [correlating with smaller plants, fewer reproductive organs and a shorter reproductive season (Engelen 2004)] and probably more herbivore pressure on the calm 'healthy' leeward reefs might inhibit this alga from dominating the reefs all around the island. S. polyceratium also recovers fast from catastrophic disturbance events. Only 2 months after the hurricane, young plants were growing at both depths, and 1-year later visual inspection showed complete recovery of shallow-water populations (AHE, personal observation). In contrast, recovery of coral communities may take several decades (e.g. Connell et al. 1997). This difference in recovery time between fleshy algae and corals has attributed to many phase-shifts on coral reefs in the Caribbean (e.g. Hughes 1994).

Little is known about the life history strategies in benthic coral reef populations (e.g. of any algal species, or of coral species for that matter), let alone "shifts in strategies". However, shifts in resources from vegetative (re)growth to sexual recruitment are a relative common survival strategy for sessile benthic organisms.

Model limitations

Parameter estimates for the model were based on stage transitions for single years. The robustness of the simulations would have been improved if three "consistent" years had been recorded at each bay and depth. However, the unforeseen storms provided the opportunity to observe how strong disturbance events (hurricane) cause different shifts in reproductive strategies in shallow- and deep-water populations.

The robustness of the parameter estimates depends on retrieval of labelled plants. Because of the loss of plant labels, transition probabilities are less reliable for some projection matrices than for others. Loss of labels was a problem in the shallow-water population of Michiel during all years, and after the hurricane in all other populations. However, the high mortality estimates for both leeward shallow-water populations during the hurricane year are well supported. At the census after the hurricane only juveniles and very young adults with tiny holdfasts were found, and these plants had evidently developed after the hurricane. Fertility was measured indirectly, based on the number of fertile plants in year 1 and the number of juveniles in year 2. Higher fertility values do not necessarily imply that the reproductive output of fertile plants has increased. In this case it is more likely that development of juveniles is facilitated by the absence of the adult population.

Population growth rates of some of the populations of S. polyceratium estimated in this case appear to be lower than those reported for other perennial seaweeds, which have λ_s around one (brown seaweeds, Ang and De Wreede 1990; Åberg 1992a, b; red seaweeds; Ang et al. 1990; Engel et al. 2001). Given the long-term persistence of S. polyceratium, this discrepancy is probably caused by the fact that the data were gathered under some of the most extreme disturbances these populations can experience. Discrepancies can also be caused by artefacts associated with data sets covering a short time span, which miss rare recruitment events that provide population persistence over long time spans. Comparison of λ_s with μ showed that there is considerable variation in growth rate between years and that the majority of the populations has µ values close to unity. This indicates that S. polyceratium populations are resistant to disturbance events and can persist over long time periods.

In conclusion, S. polyceratium has a flexible life history that allows it to persist in different habitats and survive strong stochastic disturbance events. In the year without abnormal wave disturbance, plants generally persisted in the stages with the higher reproductive values (F stage in the shallow-water and A stage in most deep-water populations). With the occurrence of catastrophic disturbance events, like the surge storm of a hurricane, vegetative growth (mainly in deep-water populations) and fertility (mainly in shallow-water populations) ensure population persistence. Over a long time frame shallow-water populations persist by survival of reproductive individuals and fertility, whereas deepwater populations do so by survival of non-reproductive individuals and vegetative growth. Over a short time frame of years plants change their life history strategy in order to cope with strong stochastic disturbance events.

Acknowledgements We would like to thank Prof. P. Sale for helpful comments on the manuscript. We thank Prof. Wim J. Wolff for enabling the study on the impact of Hurricane Lenny. We also thank Ria Siertsema, Deniz Haydar and Dr. Mark J.A. Vermeij for their assistance with fieldwork and comments, and the director and staff of the Ecological Institute CARMABI (Curaçao) for working facilities and assistance. This study was supported by a grant from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), project W85-287.

References

Åberg P (1989) Distinguishing between genetic individuals in Ascophyllum nodosum populations on the Swedish west coast. Brit Phycol J 24:183–190

- Åberg P (1992a) Size-based demography of the seaweed Ascophyllum nodosum in stochastic environments. Ecology 73(4):1488–1501
- Åberg P (1992b) A demographic study of two populations of the seaweed Ascophyllum nodosum. Ecology 73(4):1473–1487
- Ang PO (2000) Relative importance of recruitment versus regeneration in maintaining the populations of *Sargassum henslowianum* in Ping Chau, Hong Kong. J Phycol 36(3):2–3
- Ang P, De Wreede RE, Shaughnessy F, Dyck L (1990) A simulation model for an *Iridaea splendens* (Gigartinales, Rhodophyta) population in Vancouver, Canada. Hydrobiologia 204/205:191– 196
- Ang PO Jr, De Wreede RE (1990) Matrix models for algal life history stages. Mar Ecol Prog Ser 59:171–181
- Ang PO Jr, De Wreede RE (1993) Simulation and analysis of the dynamics of a *Fucus distichus* (Phaeophyceae, Fucales) population. Mar Ecol Prog Ser 93:253–265
- Bries JM, Debrot AO, Meyer DL (2004) Damage to the leeward reefs of Curaçao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. Coral Reefs 23:297–307
- Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akçakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387
- Caswell H (2001) Matrix population models, 2nd edn. Sinauer, Sunderland, MA, USA
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67(4):461–488
- Coston-Clements L, Settle LR, Hoss DE, Cross FA (1991) Utilization of the *Sargassum* habitat by marine invertebrates and vertebrates, a review. NOAA Technical Memorandum NMFS-SEFSC-296, 32pp
- Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62:421–445
- De Kroon H, Plaisier A, van Groenendael J, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431
- De Ruyter van Steveninck ED, Breeman AM (1987) Population dynamics of a tropical intertidal and deep water population of *Sargassum polyceratium* (Phaeophyta). Aquat Bot 29:139–156
- Diaz-Piferrer (1969) Distribution of the marine benthic flora of the Caribbean Sea. Caribb J Sci 9:151–178
- Engel C, Aberg P, Gaggiotti OE, Destombe C, Valero M (2001) Population dynamics and stage structure in a haploid-diploid red seaweed, *Gracilaria gracilis*. J Ecol 89:436–450
- Engelen AH (2004) Flexibility without compromise. The population biology of the brown seaweed *Sargassum polyceratium* around Curaçao. PhD Thesis, University of Groningen, The Netherlands, p 180; ISBN 90-9017581-4
- Engelen AH, åberg P, Olsen JL, Stam WT, Breeman AM (2005) Effects of wave exposure and depth on biomass, density and fertility of the fucoid seaweed *Sargassum polyceratium* (Phaeophyta, Sargassaceae). Eur J Phycol 40:149–158
- Engelen AH, Olsen JL, Breeman AM, Stam WT (2001) Genetic differentiation in *Sargassum polyceratium* (Fucales, Phaeophyceae) around the island of Curaçao (Netherlands Antilles). Mar Biol 139:267–277
- Guiney JL (2000) TPC Preliminary report Hurricane Lenny 13–23 November 1999. National Hurricane Center, USA
- Heyde CC, Cohen JE (1985) Confidence intervals for demographic projections based on products of random matrices. Theor Popul Biol 27:120–153
- Hilderbrand RH (2002) Simulating supplementation strategies for restoring and maintaining stream resident cutthroat trout populations. N Am J Fish Man 22(3):879–887

- Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. Science 265:1547–1551
- Inchausti P, Weimerskirch H (2001) Risks of decline and extinction of the endangered Amsterdam albatross and the projected impact of long-line fisheries. Biol Conserv 100(3):377–386
- Kendrick GA, Walker DI (1991) Dispersal distances for propagules of Sargassum spinuligerum (Sargassaceae, Phaeophyta) measured directly by vital staining and venturi suction sampling. Mar Ecol Prog Ser 79:133–138
- Kindvall O (2000) Comparative precision of three spatially realistic simulation models of metapopulation dynamics. Ecol Bull 48:101–110
- Ladah LB, Zertuche-González JA, Hernández-Carmona G (1999) Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. J Phycol 35:1106–1112
- May RM (1975) Stability and complexity in model ecosystems, 2nd edn. Princeton University Press, Princeton, NJ
- McCook LJ, Price IR (1997) Macroalgal distributions on the Great Barrier Reef: a review of patterns and causes. In: Proceedings of the Great Barrier Reef: science, use and management, a national conference, vol 2, GBRMPA, Townsville, pp 37–46
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367
- O'Brien ST, Hayden BP, Shugart HH (1992) Global climatic change, hurricanes, and a tropical forest. Clim Change 22(3):175–190
- Paula EJ, Eston VR (1987) Are there other Sargassum species as invasive as S. muticum. Bot Mar 30:405–410
- Reed DC, Lewis RJ, Anghera M (1988) Variation in algal dispersal and recruitment: the importance of episodic events. Ecol Monogr 58:321–335
- Roughgarden J (1975) A simple model for population dynamics in stochastic environments. Am Nat 109:713–736
- Santos R, Nyman M (1998) Population modelling of *Gelidium* sesquipedale (Rhodophyta, Gelidiales). J Appl Phycol 10:261– 272
- Silvertown J, Franco M (1993) Plant demography and habitat: a comparative approach. Plant Species Biol 8:67–73
- Stiger V, Payri CE (1999) Spatial and temporal patterns of settlement of the brown macroalgae *Turbinaria ornata* and *Sargassum mangarevense* in a coral reef on Tahiti. Mar Ecol Prog Ser 191:91–100
- Tsukidate J (1992) Ecology of *Sargassum* spp. and *Sargassum* forest formation. NOAA Tech Rep NMES 106:63–72
- Tuljapurkar SD (1990a) Delayed reproduction and fitness in variable environments. Proc Nat Acad Sci USA 87:1139–1143
- Tuljapurkar SD (1990b) Population dynamics in variable environments. Springer-Verlag, New York
- Valverde T, Silvertown J (1998) Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. J Ecol 86:545– 562
- Van Duyl FC (1985) Atlas of the living reefs of Curaçao and Bonaire (Netherlands Antilles). Foundation for Scientific Research in Surinam and The Netherlands Antilles, vol 117. Utrecht, The Netherlands, p 37
- Van Groenendael J, De Kroon H, Caswell H (1988) Projection matrices in population biology. Trends Ecol Evol 3:264–269
- Wanders JBW (1976) The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles)II: Primary productivity of the Sargassum beds on the North-East coast submarine plateau. Aquat Bot 2:327–335
- Yoshimura J, Clark CW (1991) Individual adaptations in stochastic environments. Evol Ecol 5:173–192