Modeling the increase and control of *Caulerpa taxifolia*, an invasive marine macroalga

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Abstract

Population modeling based on species' demography makes it possible to predict the pace of an invasion and evaluate the likelihood of success of different control strategies. We modeled the initial (density-independent) rate of increase of *Caulerpa taxifolia* (Vahl) C. Agardh (aquarium strain), a green alga that has markedly altered marine communities where it has invaded in the Mediterranean Sea. Parameter values for patch growth (from stolon extension) and reproduction (by asexual fragmentation and reattachment) were gleaned from published studies. Only the most conservative model, invoking field growth rates and low levels of fragment reattachment (2.5 m^{-2} of existing patch each summer), closely matched observed increases (4–14 × annually). The most effective times for control (greatest reduction in rate of increase) were removal of established patches before summer and removal of fragments after summer. These times correspond to just before maximum growth and just after maximum reproduction, respectively. Only a combined strategy, incorporating 99% removal of all fragments and annual removal of 99% of established patches, was predicted to eliminate *C. taxifolia* entirely ($\lambda < 1$). This level of effort is only likely to be possible during the first few years of an invasion, arguing strongly for careful monitoring and rapid response to potential high-impact invaders.

Introduction

High-impact invasive species are rarely eradicated (Myers et al. 2000) and instead require long-term control to reduce impacts. The costs of control have been minimally estimated at 15% of total costs of non-indigenous species (Pimentel et al. 2000). Better understanding of the ecology and demography of nonindigenous species may be helpful in devising cost-effective methods of control, although the need for research should not be used as an excuse for inaction during the early stages of an invasion (Simberloff 2003). In this paper, we use demographic information about an invasive strain of a marine macroalga, *Caulerpa taxifolia* (Vahl) C. Agardh (Caulerpales, Chlorophyta) in the Mediterranean Sea, to predict its initial rate of increase and evaluate the likely success of different methods of control.

The effectiveness of control is generally judged in terms of reduced population growth of an invasive species. Modeling and empirical studies show that, across large scales, plant invasions are slowed more by the removal of small emerging populations (nascent foci) than by a similar reduction in area of well-established monocultures (Moody and Mack 1988; Cook et al. 1996). This strategy works particularly well when the appearance of small new populations is stochastic, distant, and unrelated to the current size of

the invasion. Simply, new populations grow faster than established ones. In parallel, other studies have addressed the dynamics of invasions within particular locations, focusing on the level of control at different stages of the life cycle necessary to reduce population growth (Shea and Kelly 1998; Parker 2000). Control efforts vary in effectiveness based on the amount of control, the number of times it is carried out, and when – seasonally and during the life cycle – it occurs. Crawley (1986) developed a conceptual model emphasizing multiple factors, including interactions and refuges, leading to increases in invasive plants. However, this degree of ecological understanding is unavailable in many cases, and the model is limited for practical uses (Higgins and Richardson 1996).

Caulerpa taxifolia is a green clonal macroalga that aggressively invades coastal waters (Meinesz and Hesse 1991; Meinesz et al. 2001). Its invasion of the Mediterranean Sea is indicative of its potential rate of spread and impact. It was first reported in 1984 in Monaco covering an area of 1 m^2. The affected area throughout the Mediterranean was 3 ha in 1990, 30 ha in 1991, 427 ha in 1992, and more than 1300 ha in 1993 (Meinesz et al. 1993, 1995). In the spring of 2000, Langar et al. (2000) reported new settlements of *C. taxifolia* on the coast of Tunisia (North-Africa coast). Throughout the Mediterranean Sea, diverse native communities of eelgrass and sessile invertebrates have been replaced by monocultures of *C. taxifolia* (Verlaque and Fritayre 1994; Riggio 1995). Damage in the Mediterranean prompted rapid responses to the alga when it appeared more recently on other continents. *C. taxifolia* was identified in Huntington Harbor near Los Angeles, and Aqua Hedionda near San Diego, California, in 1998 (Jousson et al. 2000), but early detection and lethal removal methods have succeeded in checking these populations (Withgott 2001). Large patches were covered with black plastic over several years and injected with chlorine, with concomitant removal of any newly-established clones produced by asexual fragmentation (Anderson 2002).

Large scale spread of *C. taxifolia* has been successfully modeled using stochastic discrete event simulation with a geographical information system (Hill et al. 1998) and approximated with a neural network trained with simulation data (Aussem and Hill 2000). These models define the depth, substrate and current characteristics where *C. taxifolia* persists and suggest a high risk of invasion in shallow (5–10 m deep) calm waters with sandy bottoms or close to seagrass beds. In contrast to previous models, which emphasize spread over broad geographic areas, we model local dynamics driven by clonal growth and fragmentation. At this scale, management decisions must be made about how often, how much, and which life stage of *C. taxifolia* to remove. Guidelines developed for *C. taxifolia* may apply to other invaders that share similar life history characteristics: clonal growth, associated with high adult survival, and size-specific reproductive rates. In this paper, we parameterize deterministic and stochastic models to examine the initial increase of *C. taxifolia* in a single location. Space is not treated explicitly; we simply use the predicted increase in area of *C. taxifolia* to evaluate different parameterizations and assess the effectiveness of different control strategies. Values for the simulations were based on published studies of stolon growth rates, reproduction by fragmentation, and frond dynamics of the invasive strain of *C. taxifolia* in the Mediterranean Sea. Our goals were to: 1. Explore how uncertainty in parameter values influenced the prediction of local increase in *C. taxifolia*; 2. Use actual observations of local increase to select best demographic parameter values from a suite of conflicting and incomplete published reports; and 3. Compare management strategies, focusing on removal of new recruits vs. existing patches, to determine costs (effort) and effectiveness of control.

Materials and methods

Study species

The invasive strain of *C. taxifolia* tolerates broad temperature ranges (10–30 °C), colonizes a variety of substrates (rocky, sandy, seagrass and algal beds), and grows at broad depth ranges, from 1 to 90 m deep (Belsher and Meinesz 1995). These generalist traits may be partly responsible for its high impacts in the Mediterranean Sea.

C. taxifolia in its native habitat has been described as a non-dominant species living in calm waters, mainly between 10 and 30 m deep intermingled with other algal species (Garrigue 1994).

Where it has invaded, sexual reproduction has not been observed (Zuljevic and Antolic 2000). Instead, new ramets arise through fragmentation of fronds and reattachment. Subsequently, these clones increase in area through the growth of stolons, which grow laterally across the substrate. Although we focus on the growth of stolons, which increases the area covered by *C. taxifolia*, fronds also grow. Fronds are the upright portions of the alga, emerging at intervals from the stolon. Many of the fronds have ramifications (branching points). Frond density, length, and ramifications change seasonally. Frond biomass peaks in mid-summer, primarily through growth in length; in winter and spring fronds ramify and show signs of necrosis, potentially releasing fragments (Meinesz et al. 1995). Meinesz et al. (1995) concluded that *C. taxifolia* has an annual cycle where no single part of the thallus persists for more than a year, but the individual persists by means of indefinite vegetative development. These seasonal patterns of fronds do not affect area covered, but they are expected to influence how many fragments are produced. Once established, clones are believed to have very high survival (Thibaut 2001). The increase in area of *C. taxifolia* is therefore governed by the following rates: fragmentation and reattachment of fronds (reproduction), which is likely to be influenced by frond dynamics, and growth of existing clones.

Observed population growth

The initial increase in area of *C. taxifolia* has been monitored at a few locations in the Mediterranean Sea. *C. taxifolia* at Cap Martin increased in area from 1 m^2 to 30 ha, (20 ha at Cap Martin and 10 between Rocher de Monaco and Cap d'Ail) between 1984 and 1991, then from 30 to 427 ha one year later (Meinesz et al. 1993). This increase suggests an annual increment of 6.1× in the first 7 years, and 14.2× in 1992. At the Alpes-Maritimes, a 16 m^2 (1992) patch occupied 127 m^2 (1993) after one year (7.9×) and more than 1 ha (1996) after an additional three

growing seasons (4.3×, Thibaut 2001). After this period, the rate of increase is reported to have accelerated, and the biomass and area increased 6-fold during a 7-month period (Thibaut 2001). Over a similar period, *C. taxifolia* in the Strait of Messina increased from 10 m^2 to 480 ha, an annual increase of 6.5× (Meinesz et al. 2001). Altogether, uncontrolled rates of increase have been recorded between 4- and 14-fold annually in terms of area covered by *C. taxifolia* in many places in the Mediterranean Sea. In other parts of the Mediterranean, rate of increase of *C. taxifolia* appears to have been slowed but not stopped by control efforts. Near the island of Elba, *C. taxifolia* increased from 600 m^2 in 1993 to 51 ha in 2000, an annual increase of 2.6×, despite early removal by hand. Peripheral colonies at the Island of Hyar were covered with black plastic, and the area increased from 7 ha in 1995 to 40 ha in 2000, an annual increase of 1.4×. At Mallorca, regular control efforts have also been attempted through both the use of a benthic vacuum and exposure to copper ions, and the invasion, nevertheless, increased from 250 m^2 in 1992 to 65 ha in 2000, an annual increase of 2.7× (Meinesz et al. 2001).

Deterministic population model

We used a non-spatial, discrete, linear model to describe the increase in area covered by patches of *C. taxifolia*. Growth of patches was based on empirical measurements of stolon growth rates derived from literature values (Meinesz et al. 1995; Komatsu et al. 1997; Thibaut 2001). Once established, clones were assumed to be immortal, by the continual renovation of biomass by vegetative growth of the stolon and fronds. Due to the clonal life history of *C. taxifolia*, reproduction was entirely by asexual fragmentation and was assumed to be directly related to the area of existing patches.

The model involved the following governing equations for the production of new patches and growth of existing patches.

$$P_{0,t} = A_{\text{tot},t} f_t r_t, \tag{1}$$

where $P_{0,t}$ is the number of recruits at time t (each time step is one season). $A_{\text{tot,t}}$ is the area

occupied by *C. taxifolia* at time t. f_t is the number of fragments produced per area of *C. taxifolia* in season t and r_t is the probability that a fragment will successfully reattach. The fragmentation parameters take different values depending on whether time step t corresponds to summer, autumn, winter, or spring, but the season-specific values do not change over the course of a simulation.

All patches of age i survive to age $i + 1$ during time step t to $t + 1$:

$$P_{i+1,t+1} = P_{i,t}. \tag{2}$$

Surviving patches also increase in area by radial stolon growth at a season-specific rate g_t. For a circle of radius r extending at its edge, the area (A) at time t for patches of age i is:

$$A_{i,t} = \pi r_{i,t}^2 \tag{3}$$

Similarly, at time $t + 1$,

$$A_{i+1,t+1} = \pi (r_{i,t} + g_t)^2. \tag{4}$$

The total area occupied at time t is then given by

$$A_{\text{tot},t} = \sum_{i=1}^{t} A_{i,t}. \tag{5}$$

This equation adds the area of all patch age-classes, where new patch areas are calculated from the previous area per patch plus the new area added from radial growth of stolons (g_t), which varies seasonally.

Newly recruited patches are approximated as having zero area, and patches are assumed not to overlap or coalesce during the early phase of the invasion. This assumption obviously fails if new patches form close together and rapidly coalesce into meadows. The model is not explicitly spatial, so we cannot at this point incorporate dispersal distance of fragments or patches that abut against each other. Initially, invasions of clonal plants are likely to meet our assumptions. Although the model will tend to overestimate invasion rates as the invasion proceeds, *C. taxifolia* in the Mediterranean Sea appears not to experience self-shading and competition for several years (Thibaut 2001). The model also focuses on demography of a single species, without explicitly incorporating interactions with other species that could impede or foster invasion. Implicitly, however, we include environmental context because field data were available for most parameters in the model.

Growth
Stolon growth measured in the laboratory for the Mediterranean strain of *C. taxifolia* was higher in summer than in winter (Komatsu et al. 1997). These laboratory rates far exceed field observations of 4.6 mm/day in summer (Thibaut 2001). We used both laboratory and field growth rates to parameterize demographic models (Table 1).

Fragmentation
We found four reports in the literature of a reproductive rate for *C. taxifolia* – the number of new clones produced by existing clones. Hill et al. (1998) reported 59 new colonies surrounding

Table 1. Mean (SD) parameter values used to model increase in area of *Caulerpa taxifolia.*

Parameter	Spring	Summer	Autumn	Winter	Reference
Stolon growth (lab, mm/d)	6.17 (1.68)	24 (4.2)	6.17 (1.68)	0 (0)	Komatsu et al. (1997)
Stolon growth (field, mm/d)	2.3 (0.3)	4.6 (0.6)	2.3 (0.3)	0 (0)	Thibaut (2001)
Density of fronds >4 cm per m^2	1554 (172)	4606 (1884)	4378 (1148)	2813 (533)	Meinesz et al. (1995)
Length of fronds (cm/m^2)	24082 (2661)	30844 (12615)	39800 (10433)	58200 (11031)	Meinesz et al. (1995)
Number of ramifications per m^2	16962 (6531)	5913 (8634)	1450 (299)	7693 (3949)	Meinesz et al. (1995)
Loss of fronds >4 cm per m^2	0 (0)	228 (1274)	1565 (730)	1259 (323)	Meinesz et al. (1995)
f_t per m^2 based on frond density	1.98 (0.22)	5.88 (2.41)	5.59 (1.47)	3.59 (0.68)	
f_t per m^2 based on frond length	4.59 (0.51)	5.88 (2.41)	7.59 (1.99)	11.10 (2.10)	
f_t per m^2 based on ramifications	16.87 (6.50)	5.88 (8.59)	1.44 (0.23)	7.65 (3.93)	
f_t per m^2 based on frond loss	0 (0)	5.88 (32.86)	40.38 (18.85)	32.49 (8.34)	
Reattachment probability (r_t)	0.166 (0.046)	0.425 (0.066)	0.09 (0.045)	0.008 (0.002)	Ceccherelli and Cinelli (1999)

f_t values are presented for 2.5 established fragments per m^2 of existing patch in summer.

a single patch of~1 m² after 5 months from June to November 1994. We interpret this observation as showing that the product of fragmentation and reattachment is about 35 (59 × 3/5) new patches per m² of existing patch area during the summer. In contrast, Meinesz et al. (1993) give two observations of the number of established fragments around patches of 5 m diameter (20 m²): 50 at Cap d'Ail and 215 at Roquebrune, corresponding to 2.5 and 10 successful fragments per m² of existing clone. Finally, Thibaut (2001) uses a value of 12 successful fragments from each 1 m². We parameterized our model with summer reproductive rates of 2.5, 5, 10, 20, and 40 successful fragments per m² of clone to bracket these reports. Starting with this summer reproductive rate, we calculated reproductive rates in other seasons from empirical data on relative fragmentation and reattachment probabilities.

Native *Caulerpa* species in Hawai'i have been shown to regrow from fragments as small as 1 cm of frond (Smith and Walters 1999). Reattachment probabilities for the aquarium strain of *C. taxifolia* have been documented twice by examining the fate of fragments (15 cm stolon + five fronds) outplanted to field sites over 2–4 weeks. In studies on the coast of Italy, the probability of establishment of fragments was greater during summer than in other seasons (Table 1, Ceccherelli and Cinelli 1999). Following the same procedure, Thibaut (2001) found, on the French coast, that in summer, establishment on sandy bottoms about 10 m deep with low water movement can be as a high as 98%, whereas 50% establishment was found in shallow environments of high water movement. Between 5 and 10 m deep he found 88% probability of establishment. In general, reattachment depends on season, hydrodynamics and water depth. This variability in reattachment may be partly responsible for the varied observations of successful establishment of fragments around existing clones. Therefore, we did not incorporate any additional reported variability, except for seasonal changes (Ceccherelli and Cinelli 1999).

Little information is available on the production of fragments (f_t), but fragment production on a per area basis is likely to depend on how much frond biomass exists that could break into pieces. Data were available on the density of

fronds, length of fronds, frond ramifications and loss of fronds for each season (Meinesz et al. 1995). We used these data to develop four scenarios for fragment production.

First, fragment production might increase with frond density, and large fronds might be more likely to produce fragments than small fronds. For instance, most of the fragments collected after a storm in the Mediterranean Sea were live fragments about 5 cm long, and there were fewer small fragments, almost all of which were necrotic (Thibaut 2001). We assumed that fragment production was related to the density of fronds >4 cm in each season.

Second, fragment production might depend on the total length of fronds if large fronds can break into several pieces. Third, fragments may be produced when fronds ramify, so we assumed that fragment production was related to the number of ramifications. Finally, fragments may be produced when fronds are lost, which we modeled by assuming that fragment production was related to the loss of frond density between each season and the next. We began with the working assumption that a 1 m² patch creates 2.5–40 successful fragments during the summer season (Hill et al. 1998). If fragments have a 42.5% chance of reattaching in summer (Ceccherelli and Cinelli 1999), these came from at most 94 fragments per m².

We calculated the number of fragments produced per area of existing patch in other seasons by adjusting the summer value based on observed ratios of frond properties among seasons. We used ratios of the four frond properties described above. Thus, the mean value of fragment production in each season was

$$f_t = \frac{F_t}{F_{su}} f_{su} \qquad (6)$$

where f_{su} is the number of fragments produced per m² in summer, and F is the frond property in summer (F_{su}) or other season (F_t).

With different combinations of these parameter values (growth rate, fragment production and reattachment probability), we constructed five versions of the *C. taxifolia* deterministic model (Table 2). The basic model used field observations of stolon growth, fragment production based on

Table 2. Alternative parameterizations for modeling increase in area of *Caulerpa taxifolia*.

Model	Parameter value for stolon growth (g_t)	Parameter value for fragment production relative to summer (f_t)
1	Field rates	Frond density
2	Lab rates	Frond density
3	Field rates	Frond length
4	Field rates	Frond ramifications
5	Field rates	Loss of frond density

All models were run assuming a range (2.5–40) of successful reattached fragments from each m^2 of existing clone in summer.

relative frond densities among seasons, and seasonally variable reattachment probabilities. Model 2 substituted laboratory for field stolon growth rates. Models 3–5 incorporated fragment production based on relative frond length, ramifications, and loss of density among seasons. All models were run for a range of observed successful asexual reproduction: 2.5, 5, 10, 20, and 40 reattached fragments per m^2 of existing clone over the summer season. For instance, given observed summer reattachment probabilities (0.425) and the lowest actual reattachment (2.5 per m^2), all models were parameterized with 5.9 fragments produced per m^2 of existing clone over the summer season; however, fragmentation in other seasons varied across models.

These models were compared in terms of the predicted annual increase in area of the invasion. The model was initiated in spring with a single fragment. To assess model performance, we report the area covered by *C. taxifolia* in the 3rd summer relative to the 2nd summer after invasion (5th–9th time step). This proportional increase is robust to choice of seasons and years. This simulation approach allowed us to develop stochastic models that incorporated uncertainty in parameter estimates, but the deterministic version closely approximated a matrix population model (Caswell 1989) and converged on a constant annual increase (commonly denoted λ) within a few years.

Stochastic population model

To establish bounds of uncertainty on model output, we ran the model numerous times (500 simulations) using parameter values drawn at random from distributions around each mean value. Stolon growth, frond length, number of ramifications, and frond number had normal distributions (Table 1). The coefficients of variation of estimates of each frond property (seasonal) were used to generate a standard deviation of f_t calculated from frond density, length, ramifications, or density loss. Reattachment probability was determined without error in the original papers (Ceccherelli and Cinelli 1999; Thibaut 2001), but we selected this parameter from a binomial distribution, given a sample size of 20 fragments in the original study. To assess the match between observation and models, we determined whether the observed increase in *C. taxifolia* fell inside the 95% confidence limits for any model based on the output from 500 simulations with random parameter values. Because we always calculated population growth from the 2nd to 3rd summers, interannual variation in demography was accounted for in different simulation runs.

Control options

We examined several control options, focusing on removing new patches or reducing the size of existing patches, to determine cost and effectiveness of different strategies. 'Effectiveness' refers to the change in annual increase (λ) achieved with a given control strategy; 'cost' refers to the effort required, for instance, number of fragments removed or area of patch removed. All of these scenarios were modeled with mean (deterministic) parameter values. We considered two general issues reflecting the timing of control: whether control happened each season (four times annually) or once each year, and, if the latter case, what time of year. Clearly, if all new recruits are effectively removed, *C. taxifolia* will increase in area only in the single 'founding' patch. We varied control of recruits from 0 to 99%; in the case of annual control, fragments that established in other seasons were not subject to control. As a proxy for the cost of removing recruits, we also tracked the number of recruits (not simply the proportion) removed between the 2nd and 3rd summers. Control of existing patches was modeled in two ways: by setting a maximum patch size limit beyond which individual patch area

was reduced to this limit, and by removing a proportion of the existing patches in all cohorts. The effect on *C. taxifolia* cover of reducing the size of established patches was explored across a range of maximum patch sizes (0.1–15 m^2) and proportional removal (0–90% seasonally and 0–99% annually). We also tracked the area of *C. taxifolia* that needed to be removed between the 2nd and 3rd summers; this value was expected to scale with costs of control. A final control strategy involved the combination of removal of a proportion of recruits and a proportion of the area of established patches.

Results

Growth of patches

In our model of the initial invasion dynamics of *C. taxifolia*, we focused on patch growth and fragmentation. Based on literature values for stolon growth in the field, patches recruiting in spring and growing radially were expected to increase by a factor of 3.2 (3.4–10.9 m^2) from the 2nd to 3rd summers (Figure 1). Regardless of season of establishment, patches showed rapid growth in summer and no growth in winter,

when stolons did not extend. The area of a single patch increased greater than linearly from year to year, because patches added area more rapidly as they grew. However, on a per area basis, smaller patches grew faster than larger ones (Figure 2). Patches smaller than 1 m^2 increased by a factor of 10 in summer (4× in spring or autumn), whereas patches of more than 1 m^2 did not even double in area over one season. Thus, many small patches cover area more rapidly than an equivalent initial area of large patches.

Growth of the population

Predictions from the deterministic population models varied dramatically with our choice of parameter values. *C. taxifolia* was expected to increase in area by a factor of between 11 and nearly 51,664 annually (Table 3). Major distinctions were visible between models parameterized by lab vs. field stolon growth rates: stolon growth rates in the lab were 3–6 times higher than in the field, but higher linear stolon growth raised the area covered by 1–2 orders of magnitude. In order of lowest to highest population growth, the four methods of parameterizing seasonal differences in fragmentation were arranged: frond density < frond length < frond
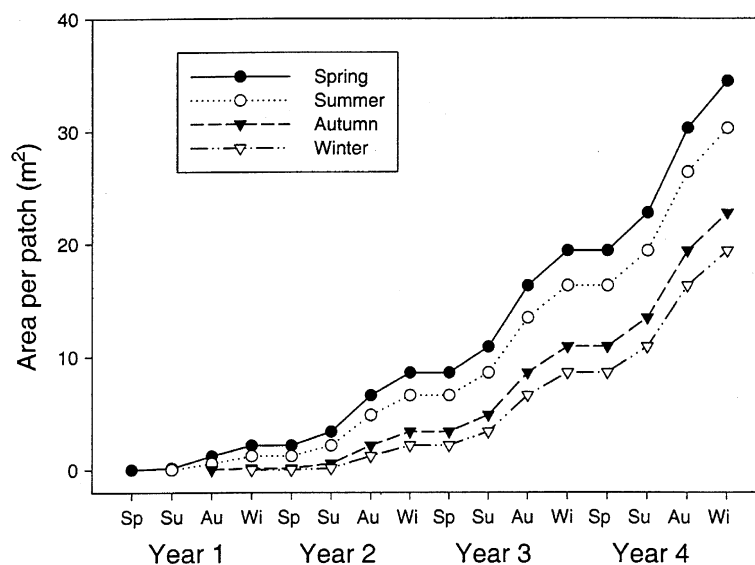

Figure 1. Growth in area of individual patches of *Caulerpa taxifolia* recruited in four seasons. Growth in area is calculated from field measurements of rates of stolon growth.
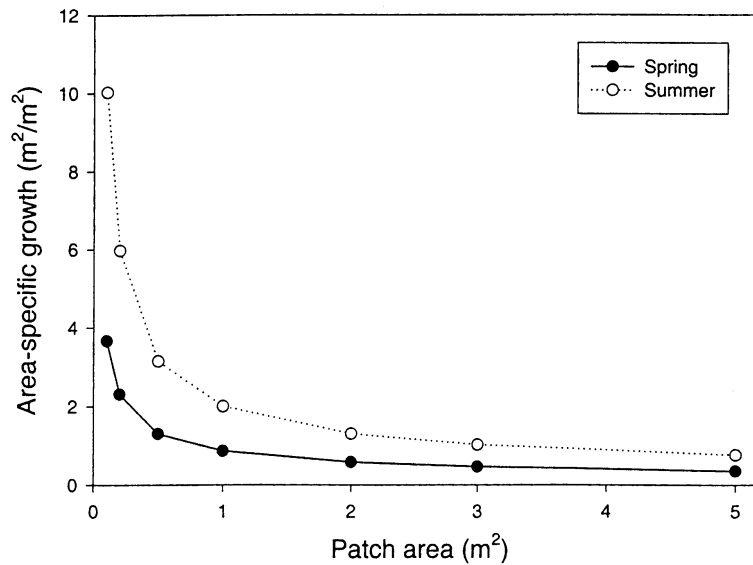
Figure 2. Area-specific growth of *Caulerpa taxifolia* patches ranging in initial size from 0.1 to 5 m^2. Area-specific growth defines proportionally how much new area is added to a patch over one season.

Table 3. Rate of increase as a function of number of successful fragments.

	Established fragments in summer per existing patch area (per m^2)				
	2.5	5	10	20	40
Model 1					
Deterministic	10.9	19.7	40.2	91.0	254.2
Stochastic	11.1	20.1	41.3	98.0	275.1
Model 2					
Deterministic	187.6	591.4	2043.5	8290	37444
Stochastic	217.8	660.7	2380.5	10197	51664
Model 3					
Deterministic	12.7	24.3	50.3	128.8	394.3
Stochastic	13.0	24.7	54.0	140	440
Model 4					
Deterministic	16.0	32.6	64.0	146.6	468.9
Stochastic	16.6	32.5	72.4	186.9	567.6
Model 5					
Deterministic	22.9	41.6	98.2	228.9	918
Stochastic	20.1	42.6	105.9	310	1058

Comparative results between stochastic (median values) and deterministic models. Model numbers are explained in Table 2.

ramifications < loss of fronds. Loss of fronds generated highest population growth rates because very few fronds were lost in summer relative to autumn (Table 1), so high fragmentation coupled with moderate reattachment generated substantial asexual reproduction during autumn.

Successful establishment of fragments, which we varied from 2.5 to 40 reattached fragments per m^2 of existing clone, also resulted in large variation in predicted rate of increase. Population growth scaled approximately linearly with fragment production (Table 3).

Based on Monte Carlo simulations, stochastic models predicted rates of increase similar to deterministic models (Table 3). Median stochastic predictions rarely varied by more than 10% from deterministic rates of increase (except model 2 [20%]). Because 95% confidence intervals overlapped for models 1 and 3–5, the method of parameterizing fragmentation did not significantly
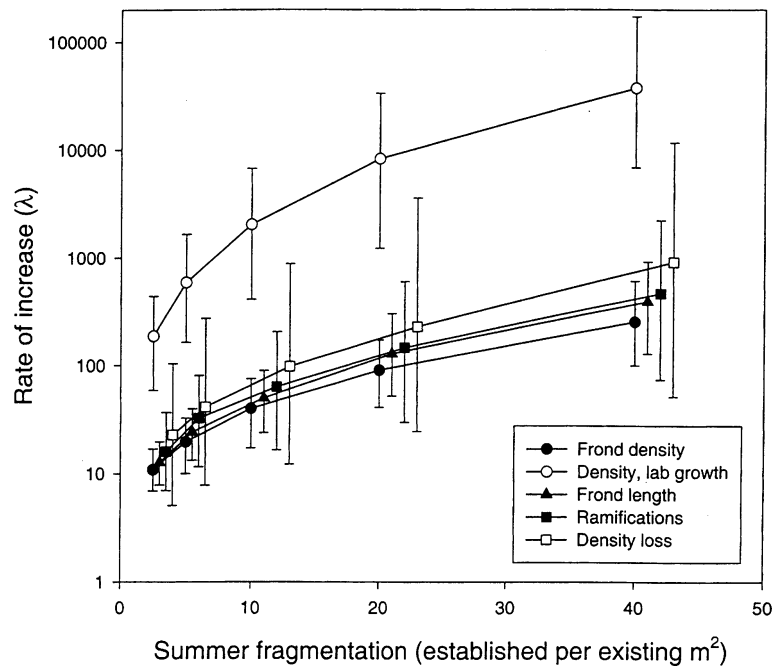
Figure 3. Rate of increase (λ) predicted for *Caulerpa taxifolia* based on literature values for stolon growth and asexual reproduction (fragmentation). The five models differ in stolon growth (lab vs. field rates) and in the method used to calculate fragmentation in seasons other than summer. Results are shown for a range of successful establishment of fragments, from 2.5 to 40 during summer from each m^2 of existing clone. Note that the relationship between successful fragments and population growth is linear and only appears curved because of the log-transformation of the y-axis. Points show median values from 500 simulations incorporating uncertainty in parameter values; error bars are 95% confidence intervals.

affect results (Figure 3). The widest confidence interval was in model 5, with fragmentation parameterized from loss of frond density. This wide variation in stochastic simulations was due to the high coefficient of variation in estimates of frond loss (Table 1). Significantly higher rates of increase were predicted for model 2, which used lab instead of field values for stolon growth.

Throughout Mediterranean locations, *C. taxifolia* has been observed to increase in area by factors of 4–14 annually. These represent extremely rapid rates of increase, but they are below all but the most conservative model predictions. The model that best matched observed increases incorporated low (field) stolon growth and low summer numbers of successfully-attached fragments, which were still lower in other seasons (Model 1, using 2.5 attached fragments per m^2 of existing clone). Most of the observations of increased area of *C. taxifolia* fell within the 95% confidence limit of the stochastic version of model 1.

Control options

Over one year (2nd–3rd summer), *C. taxifolia* was predicted to increase by about 11× in our most conservative scenario. Of this increase, 34% came from the growth of existing patches, whereas 66% came from newly-established patches that subsequently grew. Fragments contributed relatively more when they were assumed to successfully establish at higher numbers (e.g. >2.5 per m^2 of existing clone). These ratios suggest that the removal of fragments is an essential part of an effective control strategy for *C. taxifolia*. However, larger patches are expected to have higher levels of asexual reproduction. Consequently, reducing the area of large patches is also likely to be effective, because asexual reproduction is reduced (unless control actually releases more fragments). Understanding the costs (effort) and benefits (reduced rate of increase) of removing fragments, reducing area or a combination of both

is thus important in defining control strategies. We explored control options using model 1 (field stolon growth, fragmentation based on frond density) and summer fragment reattachment of 2.5 per m^2 of existing patch, because these parameters provided the best overlap with field observations of population growth.

Seasonal control

One control strategy is to prevent patches from growing beyond some maximum size by removing new growth whenever patches exceed this maximum. Beneficial results were only achieved when patches are kept at small sizes throughout the year: rates of increase were similar across all maximum patch sizes >2 m^2 (Figure 4a). The peak in effort (area removed) occurred at an intermediate maximum patch size (1–2 m^2) because few patches reached larger sizes during the simulation, and control at smaller sizes reduced the number of recruits that subsequently grew. This control strategy seemed to us to be a poor choice, because one might try to eliminate patches altogether instead of maintaining them at 1–2 m^2, and we did not explore this strategy further.

A second control strategy is to remove a proportion of newly established fragments. The rate of increase was related negatively and linearly to the proportion of fragments removed (Figure 4b). When nearly all fragments were removed each season, λ approached the rate of growth of the single founding patch (3.2 between the 2nd and 3rd summers). Control costs increased rapidly with the proportion removed, reflecting the fact that, early in an invasion, most fragments are produced by the founding patch. Controlling only fragments allows any established patches to grow, which in turn keep producing new fragments.

A third control strategy involves removing a proportion of all established patches. We only explored in detail the case where entire patches were removed (removal of a proportion of patches rather than a proportion of each patch), and efforts were spread across different cohorts of patches in relation to their abundance. The relationship between rate of increase and proportion of patches removed was negative, with λ dropping most rapidly when small proportions
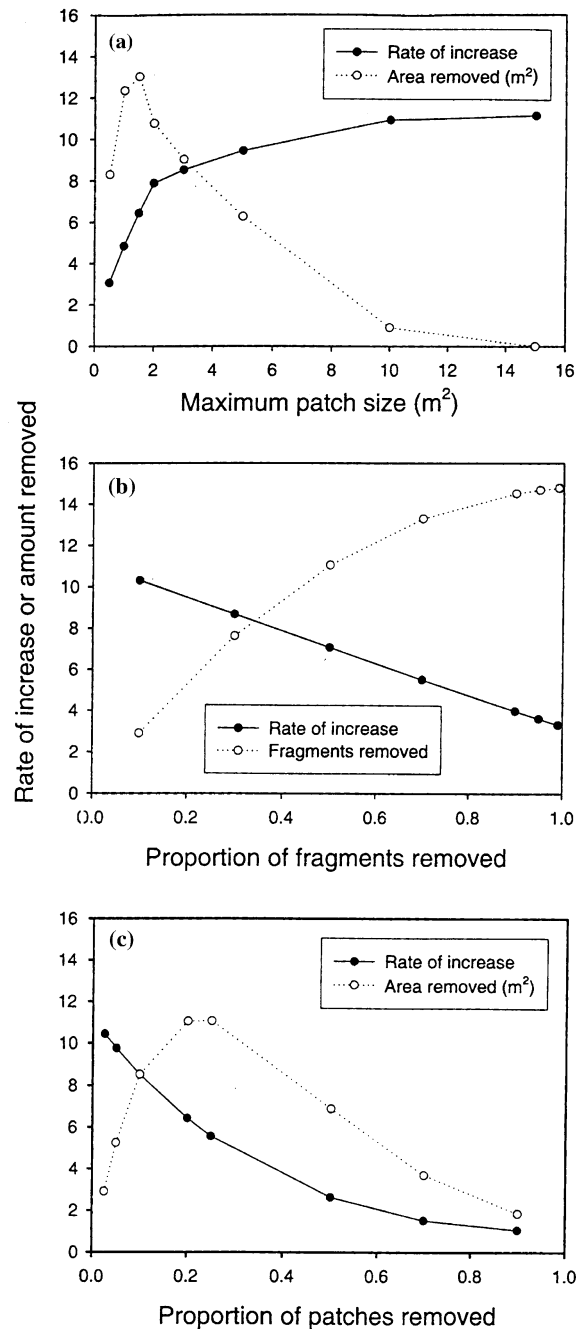

Figure 4. Rate increase of Caulerpa taxifolia (λ) when control efforts occur seasonally. In the panels, (a) patches are reduced in area whenever they exceed the maximum size, (b) a proportion of newly established fragments is removed, and (c) a proportion of established patches is removed across all cohorts. In all cases, control is assumed to occur four times a year, once in each season. Area and fragments removed are also shown, as these indicate the magnitude of the task of different levels of control between the 2nd and 3rd summers.

were removed (Figure 4c). Intermediate levels of control actually required the most effort from the 2nd to 3rd summer: the relationship between area removed and proportion removed is concave down because low removal proportions require small change in a large area, whereas high removal proportions require large change in an area that has been kept small through prior control efforts.

Annual control

We explored how removal of fragments and removal of area affected rate of increase when control occurred annually instead of seasonally as detailed above. In Figures 5a–f, the timing of control differs (after summer, after winter, after spring). The most effective time to control fragments was after summer, because λ dropped most steeply with proportion of fragments removed
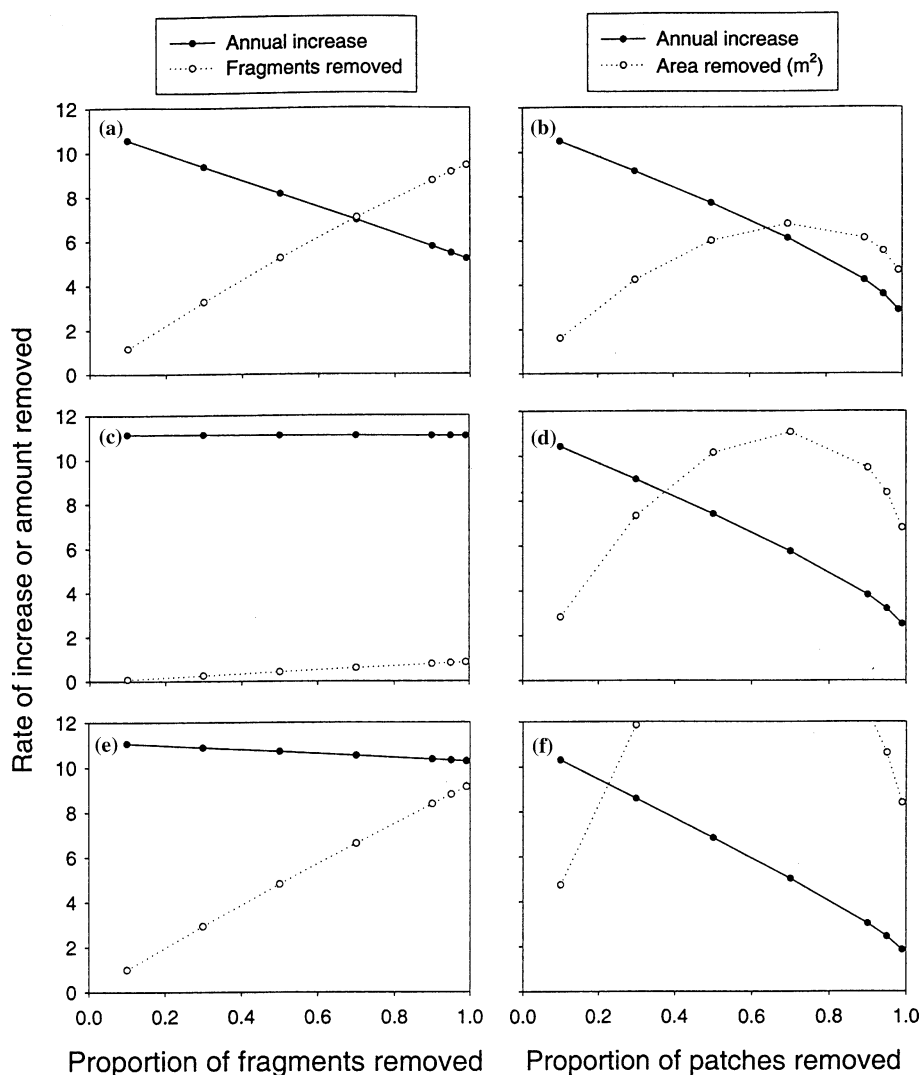

Figure 5. Rate of increase of *Caulerpa taxifolia* (λ) when control efforts occur one time per year. (a, b) Control occurs after summer. (c, d) Control occurs after winter. (e, f) Control occurs after spring. Two strategies for control are pictured: removal of a proportion of fragments that have recruited in the past season, or removal of a proportion of the established patches across all cohorts. Fragments removed and area removed between the 2nd and 3rd summers are presented as an indication of the effort required to achieve each proportional control. However, area removed cannot be compared well among graphs as the invasion progresses from the 2nd to 3rd summer.

(compare Figures 5a–c and e). The worst time to control fragments was after spring, which had little effect on λ but a relatively high cost in terms of number of fragments removed. As in seasonal control, the cost of controlling fragments, in terms of the number removed, increased steadily with proportion removed.

The most effective time to control established patches was after spring (compare Figure 5f to 5b and d). High proportions of patches removed (99%) after spring reduced λ to 1.8, relative to $2.5 < \lambda < 2.9$ if 99% of area was removed in other seasons. Compared to seasonal control, the costs of annual control peaked at higher proportions of patches removed ($\sim$70% removed vs. 30% removed). Rate of increase declined steadily with the proportion of patches removed, whereas with seasonal control, λ was most sensitive to small proportions removed.

Control of fragments and established patches
It is clear that removing only fragments or only area will lead to new area addition by either patch growth or fragment reattachment. Figure 6
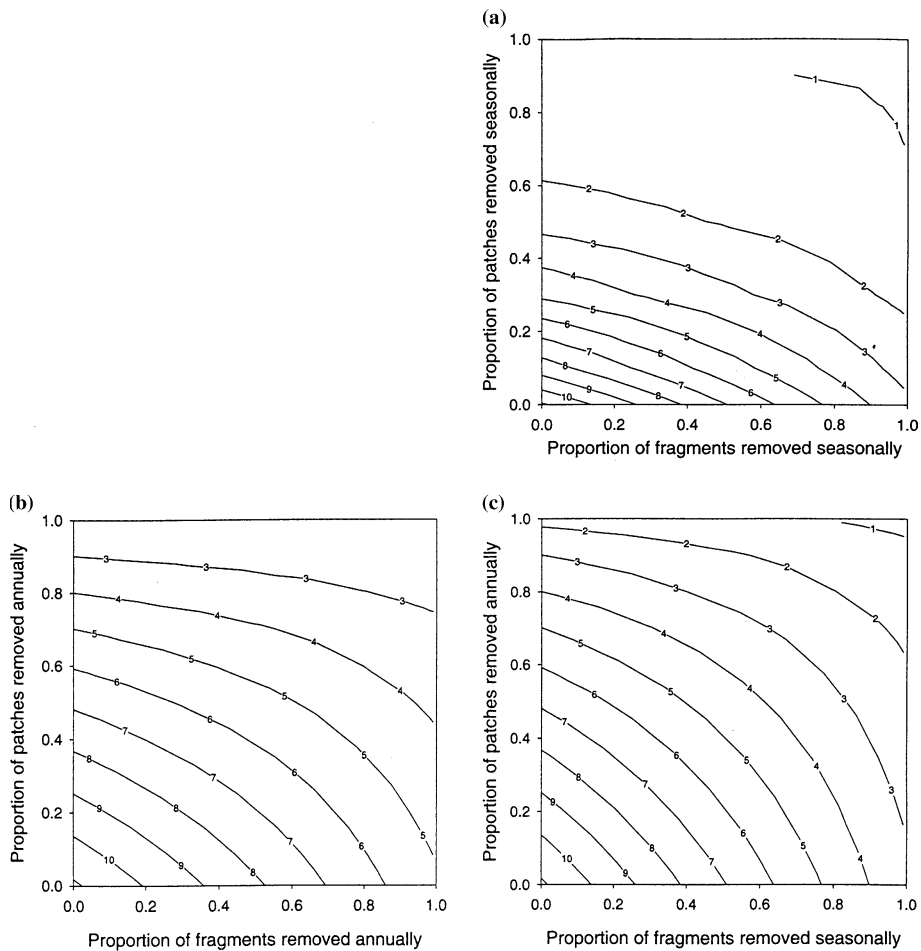

Figure 6. Rate of increase of *Caulerpa taxifolia* when control efforts include a combination of removal of fragments and removal of established patches. Contours show values of the change in area from the 2nd to 3rd summer (λ). (a) Seasonal control efforts in which fragments and patches are reduced four times annually. (b) Annual control efforts in which fragments are reduced just after the summer season of peak recruitment and established patches are removed just prior to the summer season of peak growth. This scenario represents the best possible case for effective annual control. (c) Seasonal control of fragments and annual control of established patches. This scenario explores the strategy of diligent efforts to remove new recruits all year, coupled with intense annual efforts to reduce area just before summer. The lower left hand corner of all contour plots shows the case of no control, where $\lambda = 11.2$.

compares the effect on *C. taxifolia* population growth of proportional removal of both fragments and established patches. We interpret these results to favor a strategy of removing established patches, rather than fragment control, if control efforts can be implemented seasonally. Removal of 50% of established patches each season reduced population growth below 3, whereas removal of 50% of fragments each season only reduced population growth to 7 (Figure 6a). However, if control efforts only occur once annually, then removal of fragments becomes a more important component of effective control. We focused on the best-case scenario of annual control, in which patches were removed before summer growth, and fragments were removed after summer reattachment (reattached fragments in other seasons were not removed). Removal of half of the patches or fragments reduced the rate of increase to $\lambda \sim 7$–8, whereas the combined strategy reduced λ well below 6 (Figure 6b). Only at very high levels of patch removal did control of fragments become relatively unimportant. Finally, we explored a control strategy in which fragments were removed year-round but established patches were only controlled annually just before summer. This strategy seemed more realistic than seasonal control of patches: large-scale removal efforts are unlikely to be applied to an area more than once a year, but smaller efforts could be directed at removal of fragments whenever they appear. Relative to annual control, this mixed strategy markedly reduced the rate of increase (e.g. $\lambda = 5$ at 50% removal of patches and fragments). Relative to seasonal control, the mixed strategy showed a much more consistent reduction in rate of increase across all levels of control. Importantly, controlling an area once a year always was more effective than removing one-fourth the proportion, four times a year. Although a reduction in rate of increase of *C. taxifolia* occurred over a wide range of control efforts, few of these efforts were actually predicted to cause *C. taxifolia* to decline. This occurred because stolon growth was fast enough to recover from almost any proportional removal short of 100%. Using the mixed strategy, almost 99% removal of fragments and 99% removal of area were required to reduce λ below 1. If all control occurred seasonally, then less effort was required in any given season: controlling 90% of patches and 80% of fragments reduced λ to 1, but only if carried out four times a year.

Discussion

In keeping with its reputation as an invader that rapidly transforms benthic marine communities, *C. taxifolia* has consistently increased by a factor of 4–14× annually during the initial stage of invasion in areas throughout the Mediterranean Sea (Meinesz et al. 1993, 2001; Thibaut 2001). Our population models, parameterized from entirely independent demographic studies, generally predicted even higher rates of increase than were actually observed (Figure 3). The most conservative model invoked relatively slow stolon growth (field rates), fragmentation based on frond density (highest in summer), and summer establishment of only 2.5 new patches per m^2 of existing patch. Nevertheless, the deterministic population model predicted rates of increase of 11.2. Five of six observations of uncontrolled invasions fell within the 95% confidence interval of the stochastic version of this model; the other observation was lower. Three additional observations of controlled invasions fell below the 95% confidence interval, although in all cases *C. taxifolia* did continue to increase ($\lambda = 1.4$, 2.6, and 2.7).

We are hampered, in trying to assess the fit between models and data, by uncertainty in how to model asexual reproduction. *C. taxifolia* in the Mediterranean Sea reproduces entirely by fragmentation, yet rates of fragmentation are essentially unknown. We had to back-calculate, based on a few observations of established fragments, the number of fragments produced by existing patches. We also explored several options for how fragmentation might vary through the year (related to frond density, length, ramifications [branches], or loss of density). The models were relatively insensitive to the method of defining seasonal differences in fragmentation (95% confidence intervals of models 1 and 3–5 overlapped), but quite sensitive to the number of established fragments. We varied the number of established fragments from 2.5 to 40 per m^2 of existing patch, and λ responded linearly across this range (Figure 3).

Why do observed rates of increase fall at the low end of predictions from even our most conservative model? The model does not appear to overestimate clonal growth. The growth of patches in the model was consistent with observations reported in the literature, for instance patches growing 2 m (3 m^2 in area) in a summer or 5 m (20 m^2) in two years (Meinesz et al. 1993; compare to Figure 1). In contrast, poor field data were available for asexual reproduction, so we had no way of assessing the likelihood of low fragmentation rates that generate our best model. Alternatively, we may have overestimated the survival of small clones, which we assumed immortal. Furthermore, if density dependence sets in much earlier than we believe, then either patch growth or reattachment of fragments could be reduced through intraspecific competition. Finally, it is well known that demographic parameters vary dramatically across habitat types, for instance, reattachment rarely occurs on shifting sand (Thibaut 2001). Our models did not account for this variation, which could cause some observed increases to fall below model predictions. Clearly, there is a real need for additional empirical field data on appearance and survival of newly reattached fragments. In addition, better data on how far fragments travel from their patch of origin would help determine when patches begin growing into each other, which affects density dependence. The founding patch, for instance, reaches an area of almost 20 m^2 (2.5 m radius) after the third summer (Figure 1), which means that fragments must travel beyond this distance to grow unimpeded.

Although vegetative growth certainly increases colony size, colonization of new areas by fragments is the major way that *C. taxifolia* has spread through the Mediterranean Sea (Belsher and Meinesz 1995; Meinesz et al. 1995; Sant et al. 1996; Ceccherelli and Cinelli 1999). In our models we did not examine increases due to new colonization events, but only the early post-invasion dynamics in a particular place. These dynamics are most relevant to the management decision of how to respond to new incursions, focusing attention on the restoration of local ecosystems.

We found that, when control efforts were mounted just once per year, the most effective strategy was to control existing patches after spring (Figure 5f) or remove newly established fragments after summer (Figure 5a). These periods coincided with reducing area just before the season of highest growth and fragment reattachment, and then removing any fragments that nevertheless appeared. Other parameterizations (models 3–5) also involved highest appearance of reattached fragments in summer, which means that the best time to control fragments was robust to model choice. In general, a strategy of removing patches or fragments four times annually was more effective at reducing rates of increase for a given proportional removal (compare Figures 4 and 5). However, it is important to keep in mind that mounting control efforts seasonally will require more resources than annual control, at least in terms of organization.

We explored the costs of control using, as a proxy, the number of fragments or area of established patch that had to be removed between the 2nd and 3rd summers. The number of fragments removed scaled approximately linearly with proportion removed (Figures 4 and 5), but the areal removal of established patches peaked at intermediate proportions. High proportions of patches removed early in an invasion actually kept *C. taxifolia* in check such that control subsequently required removal of a high proportion of only a small area.

Overall, a focus on removing a proportion of established patches was generally more effective at reducing rates of increase than removing the same proportion of newly attached fragments, whether control occurred seasonally or annually (Figures 4 and 5). This result matches rules of thumb about intervening in different phases of the life cycle to reduce the rate of increase of an invader (Buhle et al. 2004): species with high adult survival, such as the essentially immortal patches of *C. taxifolia*, can be controlled effectively by reducing adult survival. Two caveats must be added, however. First, the relative costs of intervening at different points in the life cycle can actually switch best management practices (Buhle et al. 2004), and eliminating a large area of *C. taxifolia* is likely to take more time and effort than removing fragments. For instance, reducing rates of increase by about half (to $\lambda = 5.5$) using seasonal control required the

removal of about 11 m^2 of established patch or just 14 fragments between the 2nd and 3rd summers (Figure 4). In addition, for control of established patches to be effective, it cannot result in the production of additional fragments, which would raise asexual reproduction. Instead, all of the material must be removed during control. Second, we assumed that the proportion controlled was spread across all cohorts and resulted in the elimination of patches, rather than a reduction in their size. On a per-area basis, small patches grow faster than large patches (Figure 2). Thus, if the removed area consisted disproportionately of large patches, rates of increase would be higher than predicted, and if it consisted disproportionately of small patches, rates of increase would be lower than predicted. The worst-case scenario is a reduction in the size (rather than number) of large patches, which would raise their per-area growth, causing the invasion to proceed faster than expected despite control.

The combination of different models presented here is a simple approach to evaluate invasion risk under different control options for clonal plants without sexual reproduction. The information needed is not difficult to obtain from field observations. It is also a guide for better measurements of useful parameters to build population models and explore different alternatives for management. Macroalgae are underrepresented in studies of biological invasions, although 18 macroalgae are likely non-indigenous in the Strait of Georgia (US/Canada western border; Lindstrom 1999), 34 in the USA (Ruiz et al. 2000), 24 in Hawai'i (Eldredge and Carlton 2002), and 200 in the Mediterranean Sea (Verlaque 1994; Ribera and Boudouresque 1995; Muller 2000). Several of these species, in addition to *C. taxifolia*, have had demonstrable negative impacts on local ecological communities (Curiel et al. 1998; Walker and Kendrick 1998; Garbary et al. 2000; Muller 2000; Schaffelke et al. 2000). Many invasive algae are able to reproduce asexually, for instance, several of the most conspicuous algal invaders in Hawai'i readily regrow from fragments (Rodgers and Cox 1999; Smith et al. 2002). We suspect that clonal growth may be one trait that contributes to high-impact invasions of some macroalgae, as well as making control difficult through asexual growth and reproduction.

In sum, three lessons emerge relevant to the control of invasive species with clonal growth. First, it is not surprising that seasonal control efforts occurring four times per year more effectively reduced λ than annual control. However, removing a large proportion of the invasion once per year was often more effective than removing smaller proportions several times per year (Figures 4 and 5). This result emerged for control of both fragments and established patches. Second, the most effective seasons for annual control were just before peak growth for established patches and just after peak reproduction for fragments (Figure 5). Third, the removal of a proportion of established patches generally reduced λ more than the same proportional removal of fragments. However, because the effort required to remove established patches undoubtedly exceeds fragment removal, a more feasible control strategy might emphasize removing newly established clones.

The applied message from modeling early invasion dynamics of *C. taxifolia* is that it will increase rapidly in the absence of immediate and rather draconian control measures. This conclusion should come as no surprise to those who have witnessed its arrival and spread. Based on our most conservative model (which also best matched observed population growth), *C. taxifolia* can only be reduced in area ($\lambda < 1$) by seasonal removal of about 90% of both established patches and fragments (Figure 6a) or by annual removal of 99% of area, combined with year-round control of fragments (Figure 6c). A strictly annual program of control is expected to be ineffective (Figure 6b). Such high levels of proportional removal are only likely to be possible during the first few years of an invasion, arguing strongly for careful monitoring and rapid response to potential high-impact invaders. Risk assessment has received high priority for evaluating new introductions (Ruesink et al. 1995; Kolar and Lodge 2002), but could be much more fully developed to evaluate costs and benefits of different methods of controlling established invasions.

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