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Ecological Effects of Brown Seaweed Harvesting

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Intertidal and shallow subtidal rocky substrata of temperate and subpolar areas can be dominated by large brown macroalgae that are harvested for the alginate industry and food. The impact of harvesting on these macroalgal dominated communities is similar to that produced by physical or biological disturbances. Both remove the biomass of the target species and modify the abundance and distribution of associated flora and fauna. In this context, the community stability and/or ecological impact of harvesting are related to the spatial distribution of the harvested population, the seasonality and intensity of harvesting, the relationship between the method of harvesting and location of reproductive structures (sori, sporophylls) and meristematic tissues, the reproductive cycle of the dominant seaweed and its potential competitors, and herbivore abundance. These factors must be considered in management plans for harvesting brown macroalgae.

Introduction

Rocky substrata of temperate and subpolar seas in both hemispheres are usually dominated by Laminariales and Fucales in biomass and cover down to 30 m depth (Dawson *et al.* 1960, Druehl 1970, 1978, North 1971, Barrales and Lobban 1975, Kain 1979, Santelices *et al.* 1980, Choat and Schiel 1982; Dayton *et al.* 1984, Dayton 1985 a, b, Vásquez 1991, 1992 a). These macroalgae are an essential element of these communities (Ghelardi 1971, North 1971, Cancino and Santelices 1981, Ojeda and Santelices 1984, Santelices and Ojeda 1984 a, b, Vásquez *et al.* 1984, Vásquez and Santelices 1984, Vásquez and Castilla 1984, Snider 1985, Vásquez 1993).

Kelp associations have been characterized according to the genus of the dominant seaweed (*e. g.* Mann, 1982 and Table I). Many of these taxa are harvested. In southern California alone 144 000 tons of *Macrocystis pyrifera* (L.) C. Agardh are collected yearly (McPeak and Barilotti 1993). The harvest has a similar effect on a resource to that produced by physical and biological disturbances (*sensu* Sousa 1984, Underwood 1989). Both remove, totally or partially, the dominant population and modify the distribution and the abundance of associated species.

If the disturbance (*e. g.* harvest) is strong enough, changes occur in the abundance of harvested and/or associated species, and in availability of some resources (*e. g.* space and light). It is then expected that community change should follow one of the successional models described by Connell and Slatyer (1977). If, however, the community has high resilience to impact (*sensu* Dayton *et al.* 1984), change in species diversity will be insignificant, and the initial species composition will be restricted to Type III disturbance of Sutherland (1981).

Although the analysis of the consequences of biological disturbance is increasingly used in the study of biological communities, it has rarely been considered with harvested populations (Foster and Barilotti 1990). This approach allows analysis of the many factors that maintain or modify community stability (*sensu* Connell and Sousa 1983) when the dominant organism is intensively removed.

Harvesting and Ecological Impact

The ecological impact of macroalgal harvesting depends on the frequency, intensity and percentage removal of the harvest as well as the characteristics of the life history of the organisms harvested and the phenological attributes of the community. The magnitude of harvesting depends on the harvesting strategies, and should be in accordance with the biological characteristics of the target species to allow a sufficient recovery to maintain a sustainable biomass (Foster and Barilotti 1990). In macroalgae, particularly the Laminariales, *in situ* harvesting includes collection of: (1) vegetative fronds; (2) fronds with vegetative and reproductive structures; and (3) whole plants.

Harvesting of vegetative canopies

The removal of vegetative canopies has no important effect on the target population (Foster and Barilotti 1990). For example, in southern California, harvest of the vegetative canopy only of *Macrocystis pyrifera* has no important ecological effects on the population (Barilotti and Zertuche-González 1990). The features of *M. pyrifera* responsible are: (1) the distribution of the growth meristems; (2) the plant growth rate; (3)

Table I. Kelp-dominated associations at different locations at higher latitudes.

Species	Locations	References
Macrocystis spp	South Africa, New Zealand, Tazmania, Australia and East Pacific Coast.	North 1971, Dayton 1985 a, b, Bold and Wynne 1985.
Ecklonia spp	New Zealand, South Africa.	Novaczek 1981, Bold and Wynne 1985.
Cystoseira spp	Australia, Pacific North America, Asia, Caribbean and Indian Ocean.	Roberts 1967, Bold and Wynne 1985.
Nereocystis spp	Pacific coast of North America.	Druehl 1970, Schiel and Foster 1986.
Alaria spp	North Atlantic and North Pacific coast.	Widdowson 1972.
Pterigophora spp	Pacific coast of North America.	Mann 1982, Bold and Wynne 1985.
Lessonia spp	Perú, Chile and southern Argentina.	Searles 1978, Villouta and Santelices 1986, Vásquez 1992.
Laminaria spp	Cold-temperate coast of Northern Hemisphere	Kain 1967, 1979, Lüning 1970, 1979.

the basal location of the reproductive structures; and (4) the proportion of the harvested surface in relation to the total size of the plant.

Between 30% and 50% of the total standing biomass of *M. pyrifera* available for harvesting is annually extracted (Coon 1981, North 1987). After 25 years of harvesting, recruitment, elongation of haptera, frond production and plant survival have not been affected (Barilotti *et al.* 1985, Barilotti and Zertuche-González 1990). However, the removal of over 75% of the *Macrocystis* fronds may significantly reduce sporophyll production (Reed 1987) and holdfast growth (McCleneghan and Houk 1985).

Post-harvest regeneration of plants depends on the location of growth meristems. Growth in length of Laminariales is based on intercalary meristems and growth in diameter on superficial meristems (Bold and Wynne 1985). If harvesting does not greatly impact intercalary meristems, as is the case for *Macrocystis*, regeneration should occur. Due to the basal location of the sporophylls, harvesting does not adversaly impact them.

In the south-east Pacific, between 18° and 42° S, *Lessonia nigrescens* Bory and *L. trabeculata* Villouta *et* Santelices are the most abundant kelp species in intertidal and subtidal rocky areas, respectively. Experimental pruning of canopies of both species resulted in little regeneration of plant tissue and high mortality rates (Vásquez and Santelices 1990). Experimental cutting of the stipes of *L. trabeculata* and *L. nigrescens* at base level or just over the first dichotomy reduced stipe friction, thus favouring epiphytism (Santelices 1982). Furthermore, whiplash effect of algal fronds on benthic herbivores diminished (Santelices and Ojeda 1984 b, Vásquez 1992 a) and grazing pressure increased (Vásquez and Santelices 1990).

Harvest involving reproductive structures

Ascophyllum nodosum (L.) Le Jolis is the most frequent and abundant macroalgae in mid-littoral zones of the north Atlantic (Bold and Wynne 1985). Harvesting greatly reduces its reproductive output (Sharp and Pringle 1990). Its marked reproductive activity during the winter months (Bold and Wynne 1985) increases the impact of harvesting and restricts recovery of the population based on spore propagation. Furthermore, recovery of the biomass is slow and depends on the volume of the remaining biomass (Sharp 1987, Sharp and Pringle 1990). Removal of plants and the volume of removal permitted depends on the stocks of each locality (Sharp 1987). The time of recovery after harvesting of an *Ascophyllum* bed is directly related to harvest intensity (Sharp 1987, Sharp and Pringle 1990).

Harvesting affects spore production of *Lessonia nigrescens* due to the presence of sori on stipes and fronds (Venegas *et al.* 1992). Thus, extensive harvesting during periods of maximum reproduction (late winter and spring) may be a crucial factor for the recovery of the population by spore propagation (Santelices 1982, Vásquez 1989).

Harvesting of whole plants

Laminaria spp. may be harvested by whole-plant removal (Chapman 1987). Recovery of the biomass depends on spore production and the growth of juveniles and adults remaining after harvest (Chapman 1987, Sharp and Pringle 1990).

The contribution of the residual biomass to the regeneration of the standing stock depends on the selectivity of the harvest method and on the vulnerability of the population harvested. The latter is strongly determined by topography of substrate and frond size. The latter in turn depends on the exposure to the waves, the kind of substrate, the velocity of the bottom currents, and, the depth of the site (Sharp and Carter 1986).

The harvesting methods used for *Durvillaea antarctica* (Chamisso) Hariot, one of the most dense and abundant seaweed population on the coasts of New Zealand and southern Chile (Hay and South 1979, Hay 1988, Santelices *et al.* 1980), removes the entire plant.

The stipes and fronds of *Durvillaea* pruned experimentally above the holdfast showed a regenerative rate of only 32% of the initial biomass after 15 months in New Zealand. If the plant is totally removed, the regeneration of new germlings over the same period was 1.5 times the initial biomass (Hay and South 1981). As this regeneration is conditional on the winter/spring reproductive peak, harvesting of whole plants should be carried out between April and June (Hay and South 1979).

Occasionally, the collection of *Lessonia nigrescens* in Chile is by the removal of whole plants from intertidal populations. The effect of these harvests on the population (recruitment, growth of remaining juveniles and adults) and on the community depends mostly on the size of the denuded area (Santelices 1982). If the area does not exceed 2 m^2, the removal of adult plants minimizes intra-specific competition, favouring spore recruitment and the growth of pre-existing juveniles. If denudation exceeds 2 m^2 the whiplash effect of the fronds over the substrate decreases, allowing access of benthic grazers to the remaining population, and thereby reducing or slowing juvenile recruitment. Similar effects occur in subtidal populations of *L. trabeculata* in northern Chile (Vásquez and Santelices 1990).

In terrestial communities, individual plants within a dense population have lower reproduction, growth and survival rates compared to plants from less dense populations (Harper 1977). Experimental field kelp studies have shown that inter- and intra-specific interactions generate both negative and positive combined effects on the process of recruitment and survival of adult plants. Choat and Schiel (1982) indicated that in exposed environments, individuals of *Ecklonia radiata* (C. Ag.) J. Ag. and *Sargassum sinclairii* Hook. *et* Harv. are larger when in high densities. These authors suggested that dense aggregations of the plants reduce mortality and selective pruning by water movement. Black (1977) showed that mortality and growth rate of juvenile *Egregia* are dependent on high density, at least over the three first months of life. Santelices and Ojeda (1984 b) found similar results in intertidal habitats of central Chile, where the interference of conspecific adults were crucial for juvenile settlement. For seaweeds living in highly disturbed areas and subjected to frequent local extinctions, such as Laminariales, the competition among early microscopic stages modifies the ways in which spore settlement influenced sporophyte recruitment (Reed 1990). The effects are interactive, and their relative importance vary with species, location, and time (Reed 1990). Other factors like overgrowth, crowding, shading, sweeping effect, allelopathic effect, and positive effects such as facilitation for recruitment have been discussed by Santelices (1990).

Effects of Harvesting on the Community

The harvesting tools, the harvest frequency, magnitude and seasonality can strongly influence the ecological effects of commercial harvesting, with an ensuing low survival of the affected population and/or a high instability of the community (Foster and Barilotti 1990). In Canada, for instance, biannual commercial harvesting and the consequent substrate displacement significantly decrease the abundance and diversity of flora (Pringle and Mathieson 1987) and fauna (Pringle and Sharp 1980, Michaud 1986) associated with *Laminaria longicruris* de la Pyl.

Holdfasts of *Macrocystis* spp, *Lessonia* spp and *Laminaria* spp, support an extremely diverse macroinvertebrate community (Ghelardi 1971, Vásquez and Santelices 1984, Ojeda and Santelices 1984, Michaud 1986, Vásquez 1993). Harvesting causes great disturbance to these populations (Vásquez and Santelices 1984).

In New Zealand, *Durvillaea antarctica* fronds produce a whiplash effect on the substrate, keeping it free from organisms (Schiel and Nelson 1990). Thus the removal of adult plants allows other species to settle and growth on the free substrata. If harvesting is carried out in the warmer months, when *Durvillaea* is not reproductive, the recruitment of other species precludes the settlement of *Durvillaea* (Hay 1988).

The lower vegetational strata associated with *Macrocystis pyrifera* respond differentially to canopy harvest between southern Chile and southern California populations. In Chile, canopy cutting triggers an increase in cover and density of conspecific plants (Santelices and Ojeda 1984 a). In contrast, canopy removal of *Macrocystis* in California favours the growth of other understory kelp species (Dayton 1985 a, Vásquez 1992 a). These changes in diversity and relative abundance of species in *Macrocystis* communities depend on the expression of different competitive hierarchies of the coexistent macroalgae, and of the timing of the disturbance (Dayton *et al.* 1984, Dayton 1985 a, Schiel and Foster 1986, Santelices and Ojeda 1984 b).

In the absence of grazers, the effect of the commercial harvesting on the community depends on the seasonality of the removal and on reproductive phenology. In central Chile, experimental removal of *Lessonia nigrescens* generated different communities, depending on seasonality of disturbance (Santelices 1982). Since *L. nigrescens* is fertile during winter–spring, summer removal generated communities dominated by opportunistic algae like *Ulva* and *Enteromorpha*. They were replaced after 3 to 4 months by *Gelidium chilensis* (Montagne) Santelices *et* Montalva, inhibiting the settlement of *Lessonia* (Santelices and Ojeda 1984 b). The substrate was settled by opportunistic algae and *Lessonia* following winter harvest. Eventually *Lessonia* holdfast overgrew other species, recovering the original density. Unlike *Lessonia nigrescens*, *L. trabeculata* does not have a defined reproductive seasonality. Experimental removal of *L. trabeculata* in the absence of herbivores significantly increased juvenile settlement, independent of perturbation time (Vásquez 1989).

Harvesting in the presence of benthic grazers can, in extreme cases, produce barren areas (*sensu* Mann and Breen 1972), even when a sufficient algal biomass exist in adjacent localities for natural repopulation (Vásquez and Santelices 1990). This will depend on the sociability (distance between plants) of the population and on the density of benthic herbivores (Vásquez 1989, 1992 a). It has been suggested that reduced spacing among plants in intertidal communities would hamper grazers (Dayton *et al.* 1984; Santelices and Ojeda 1984 b). This spatial arrangement, when interrupted by harvesting, can be a highly destabilizing agent, switching communities dominated by macroalgae to crustose algae and grazers dominated areas (Mann 1982, Vásqzez 1992 b).

Experimental removals that increased the distance among plants in intertidal populations of *Lessonia nigrescens* in northern Chile favoured herbivores, causing a significant decrease in juvenile recruitment (Santelices and Ojeda 1984 b). Experimental reduction of subtidal plant density (from 3 to 0.5 plants m^2) of *L. trabeculata* significantly increased the herbivory by sea urchins and gastropod snails thus reducing the number of stipes per plant by 50%. The stipes not cut by the grazers increased in length and width, and became more rigid. The resultant decrease in stipe flexibility and the grazing of the holdfast surface weakened its resistance to currents and significantly augmented mortality rates (Vásquez 1989, 1992 a, Vásquez and Santelices 1990).

Harvesting *L. trabeculata* modifies the morphology of plants similarly to that induced by grazing by sea urchins. The stipes of these plants have little flexibility and are cast ashore by winter storms. The selective mortality that would result from harvesting might interrupt the sociability of kelp populations and affect community structure.

Biological Management

The ecological effects of harvesting can be of both negative and positive value, both on the target species and its community. Thus the ecological effects of harvesting must be analyzed in biological management. If maintaining sustainable standing stock through time depends on the biological knowledge of the target species and its community, a management plan should maximize the profitability of harvesting and minimize the deleterious effects produced by this disturbance.

Evaluation of the available biomass

The evaluation of the resource availability is essential when planning commercial exploitation. In the frame of an adequate temporal and spatial scale, it should determine the optimal conditions for a rational extraction plan.

The use of macroalgae for the alginate industry demanded early extensive samplings in order to evaluate the standing stock and standing crop. The methodology for determing algal biomass varies from simple methods of coastal qualitative evaluation (Chapman 1948, Parke 1948), to complex methods of submarine and aerial assessment methods (McPeak and Barlotti 1993). One should consider the following when estimating standing stocks: (1) the distribution (local and geographical) of the resource; (2) the pattern of spatial and temporal changes in standing crop; (3) the ecological conditions related to temporal phycocolloid variation; and (4) the relative age of the population. These parameters permit one to concentrate the extraction in the most productive areas (as to biomass and gel content). Furthermore, it is possible to determine the minimum standing stock regenered to allow harvest sustainability.

Management plan

Although harvesting may be planned for a group of similar resource species, every species harvested will need a particular management plant to suit its characteristics. It has been suggested (Santelices and Doty 1989, Santelices 1989) that a good management plan for economically important algal species should consider: (1) intensity and frequency of the harvestings, (2) temporal variability of the biomass in representative localities, (3) seasonality of the reproductive phenomena, (4) temporal variability in polysaccharides content and, (5) harvesting methodologies.

This management program, originally proposed for *Gracilaria*, and later suggested as a general methodology for other commercial seaweed species, does not consider the harvesting effects on the community. However, it should be stressed that there are marked differences between the diversity of species associated

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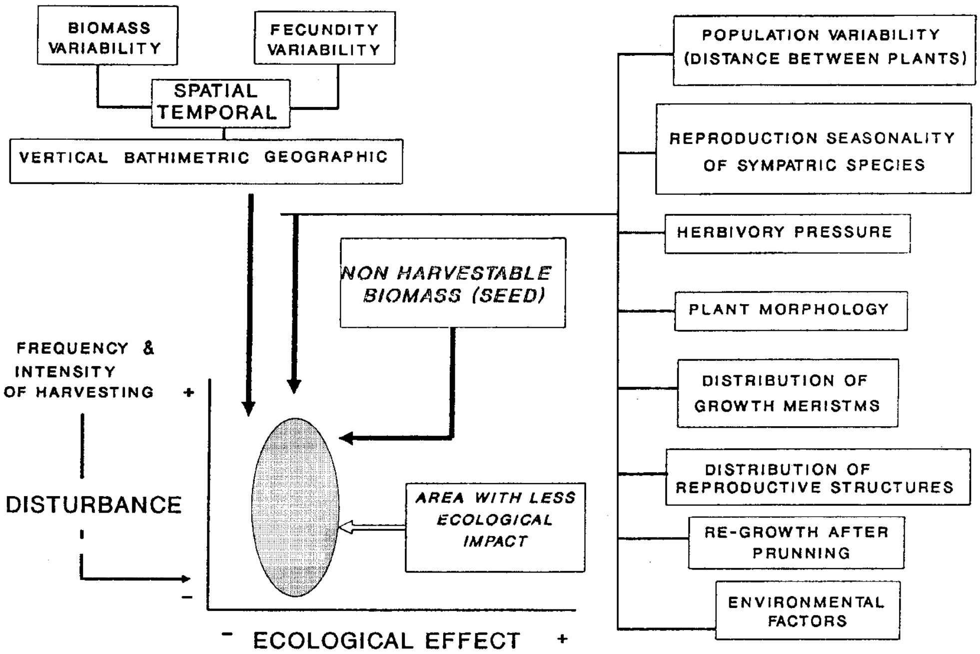

Fig. 1. Population and community factors envolved in a management plan for brown macroalgae.

with *Gracilaria* (in practice a monoculture) and the species richness associated with communities dominated by brown macroalgae (*e. g. Macrocystis*). Hence, a management plan for this group of macroalgae, where the interspecific interactions are strong (Dayton and Tegner 1984, Dayton 1985 a, Dayton *et al.* 1992) should consider additional factors such as: (1) sociability (distance between plants) of the population, (2) plant morphology, (3) competitive hierarchies that may have a bearing on the post-harvest successional processes, (4) abundance of benthic grazers associated with the community and, (5) exposure and vulnerability to natural physical disturbance, such as the pattern and intensity of water movement (Fig. 1).

The interaction of these factors must be considered in a management plan in order to minimize impacts on target species and its community (Fig. 1). The level of importance of each of these factors to the persistence and stability of a community exposed to intensive harvesting will depend on the resilience of the dominant species and its structuring effect on the associated community. Consequently, management models for economically important kelp species must incorporate elements that allow for prediction of community responses to intense, widespread and frequent disturbance.

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