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Invasion of *Codium fragile* ssp. *tomentosoides* in northern Chile: A new threat for *Gracilaria* farming

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Abstract

Invasive species are key components of the burgeoning global change in ecological communities. The green alga *Codium fragile* ssp. *tomentosoides* (Chlorophyta) is a recognized invader in marine ecosystems around the world, with described ecological effects ranging from minor changes in native species abundance to major changes in community structure, as well as negative economic effects on aquaculture species. The objective of this work is to provide an assessment of the extension of the *C. fragile* invasion along the coast of Chile, and characterize the pattern of temporal fluctuations in abundance, and potential economic effects of this algal invader in a *Gracilaria chilensis* farm in northern Chile. In 2005 we recorded *C. fragile* at 34 of 123 sites sampled along the Chilean coast, with over half of the invaded sites occurring between 26° and 30°S latitude. At 12 sites *C. fragile* was present only on artificial substrata, suggesting that artificial structures may act as corridors for the dispersal of this alga into subtidal or intertidal habitats where it is otherwise not able to survive. At one site (Calderilla Bay) *C. fragile* has reached high levels of abundance within *G. chilensis* farms. At this site we observed marked seasonality in the monthly *C. fragile* abundance index, with greater *C. fragile* abundances in summer and fall months, associated with higher sea surface temperatures (SST). In addition, we report a significant long-term trend of increasing *C. fragile* abundances over the 5 years of observations in the plantation. If the distribution of *C. fragile* in Chile is largely determined by SST, we expect faster spread of northern populations towards the north. Weedy species had a negative effect on the farmed species, *G. chilensis*. During the 4 months in which algae wet weights were measured, the estimated *C. fragile* biomass averaged 22.9 kg m^{-2}, compared with an estimated average of 18.5 kg m^{-2} of the harvested red alga, *G. chilensis*. In addition, we recorded a negative effect of *C. fragile* abundances on the Catch Per Unit Effort (CPUE) of *G. chilensis* with a significant upper limit to CPUE at the 94th quantile. Since weedy species generate a great loss of time and money in *G. chilensis* farms, it is likely that without intervention, the costs associated with the *C. fragile* invasion threaten the persistence of *G. chilensis* farms in northern Chile. Stakeholders should implement preventative measures to stop *C. fragile* spread from focal points.

Keywords: Algal farming; Invasion ecology; Marine invasion; Non-indigenous species; Seaweed; South America

1. Introduction

Invasive species are key components of the burgeoning global change in the environment (e.g., Vitousek, 1994;

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Simberloff, 2000; D'Antonio et al., 2001; Pimentel et al., 2005), widely recognized for their effects on the biodiversity of native communities (Mack et al., 2000). Much concern has been centered on changes in native species biodiversity when communities receive an aggressive invader (e.g. Elton, 1958; Bertness, 1984; Boudouresque et al., 1995; Kennedy et al., 2002; Sax and Gaines, 2003; Stachowicz and Tilman, 2005) and the changes they cause in the structure and functioning of ecological systems (e.g. *Dreissena polymorpha*, Strayer et al., 1999; *Pyura praeputialis*, Cerda and Castilla, 2001; *Castor canadensis*, Iriarte et al., 2005). These invaders frequently attain vast social importance when they impact economically important species, such as agricultural crops or fisheries (see examples in Naylor, 2000; Mack et al., 2000; Pimentel et al., 2005).

A recognized invasive species in marine ecosystems around the world is the siphonous green alga *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (Van Goor) Silva (Chapman, 1999; Trowbridge, 1998, 1999; Mathieson et al., 2003; Provan et al., 2005). Currently this subspecies has a wide distribution on temperate and tropical coasts, although its invasive capacity (e.g. ability to reach high densities at the invaded site) varies spatially (Chapman, 1999; Trowbridge, 1998, 1999; Mathieson et al., 2003). Originally from Japan, this alga has invaded numerous coastal sites around the world, including the Pacific and Atlantic coasts of North America, the Atlantic coast of Europe, the Mediterranean coast, areas of Australia and New Zealand, as well as the coast of Chile (Provan et al., 2005). Although this alga mainly inhabits protected bays and estuaries, it is also found in semi-exposed coastal areas, where it tends to be smaller, have fewer dichotomies, and occur in lower densities (Chapman, 1999; Harris and Jones, 2005). This alga is found attached to hard substrata in both the intertidal and subtidal zones, down to approximately 15 m depth (Chapman, 1999). On sandy or muddy bottoms *C. fragile* utilizes many types of secondary hard substrata, including mollusk and crustacean shells, rocks, coralline crustose algae, as well as artificial materials such as ropes, plastic structures and stone breakwaters (Carlton and Scanlon, 1985; Trowbridge, 1999; Bulleri and Airoldi, 2005, P.E. Neill, personal observation).

C. fragile presents a number of traits which seem to favor its ability to invade new habitats, including a high tolerance to fluctuations of abiotic factors such as temperature, salinity, light and nutrients, as well as the possibility of reproducing both sexually via gamete fusion and asexually through parthenogenesis and fragmentation (Chapman, 1999; Trowbridge, 1998, 1999; Mathieson et al., 2003; Harris and Jones, 2005). Within invaded regions, high abundances of *C. fragile* have been reported to be associated with high temperatures, increased illumination, and anthropogenic activities, such as artificial marine structures and aquaculture equipment (Trowbridge, 1998, 1999; Harris and Tyrrell, 2001; Naylor et al., 2001; Mathieson et al., 2003; Bulleri and Airoldi, 2005; Harris and Jones, 2005).

Various studies have reported ecological and economic effects of *C. fragile* ssp. *tomentosoides* within its introduced range (e.g. Trowbridge, 1998; Colautti et al., 2006 and references therein). In a recent study comparing species traits of 113 introduced macroalgal species in Europe, *C. fragile* ssp. *tomentosoides* ranked as the number one most risky macroalgae in terms of dispersal capability, probability of establishment and ecological impact on the receiving community (Nyberg and Wallentinus, 2005). Reported ecological effects of this invasive alga range from minor changes in the abundances of native species (Trowbridge, 1999; Mathieson et al., 2003; Harris and Jones, 2005) to changes in the structure of entire communities (Harris and Tyrrell, 2001). This alga has also been reported to be damaging to the aquaculture industry by fouling nets, as well as by attaching to, uplifting and transporting shellfish (Fralick and Mathieson, 1973; Carlton and Scanlon, 1985; Mathieson et al., 2003). In Canada estimated economic loss to the aquaculture industry as a result of the *C. fragile* invasion was estimated at over \$1.2 million USD per year (Colautti et al., 2006).

In northern Chile, the green alga *C. fragile* ssp. *tomentosoides* was registered for the first time in 1998 (Neill et al., 2003; Castilla et al., 2005; Castilla and Neill, in press), and it soon became a pest affecting the farming operations of the economically important red alga *Gracilaria chilensis* (Neill et al., 2003; González and Santelices, 2004; Provan et al., 2005; Leonardi et al., 2006). This red alga is harvested in both northern and southern Chile as raw material to produce agar, and represents an important economic resource to the country (Buschmann et al., 2001; SERNAPESCA, 2004). Since the introduction of *C. fragile*, red algae farmers must invest additional time and money in removing this pest, which becomes entangled in the thalli of *G. chilensis* and pulls the red alga off the bottom before it can be harvested by divers.

In spite of the known ecological and economic effects of *C. fragile* in other parts of the world, in Chile there is little quantitative information regarding its range of distribution, abundances, and its potential effects on local assemblages of benthic organisms and economic resources (Castilla et al., 2005; Castilla and Neill, in press). The objective of this work is to provide an assessment of the extension of the *C. fragile* invasion along the coast of Chile, and characterize the pattern of temporal fluctuations in abundance, and potential economic effects of this algal invader in a *G. chilensis* farm in northern Chile.

2. Materials and methods

2.1. Range of distribution

We evaluated the extension of the invasion by *C. fragile* by conducting visual surveys in the field at 123 sites along the Chilean coast during the austral summers of 2004 and 2005 (Fig. 1A). We selected sites in northern, central and southern Chile, over 26° of latitude. Sites were selected if they fulfilled at least one of the following criteria: (1) a previous record of *C. fragile* in the literature and/or (2) presence of a protected bay, principal port, or aquaculture area (especially aquaculture areas with *Crassostrea gigas*, *Haliotis rufescens*, *Argopecten purpuratus*, or *G. chilensis*). Surveys were made by searching for the presence of *C. fragile* in the intertidal zone (along the drift line, on rocky platforms and in intertidal pools) along 100 m sections of coastline. We also surveyed the subtidal zone, by diving along a 100 m transect parallel to the coastline, examining both natural substrata (e.g. rocks, mollusk shells) and artificial substrata (e.g. scallop farming equipment, tow lines of small boats, plastic "sleeves" used to plant *G. chilensis*) at up to 7 m depth and up to 150 m offshore. In addition, we carried out extensive interviews ($n=103$ sources) with local fishers, divers, algal gatherers, scientists and employees of the Chilean Navy to compile information regarding sites where *C. fragile* is present, how long the alga has been present in the area, and the types of substrata on which it is found. In all cases we confirmed information obtained from interviews regarding the presence of *C. fragile* through field observations, as described above.

2.2. Patterns of abundance of *C. fragile* and effects on *G. chilensis*

A detailed evaluation of the abundance patterns of *C. fragile* was conducted in a farm of *G. chilensis* (Cultivos

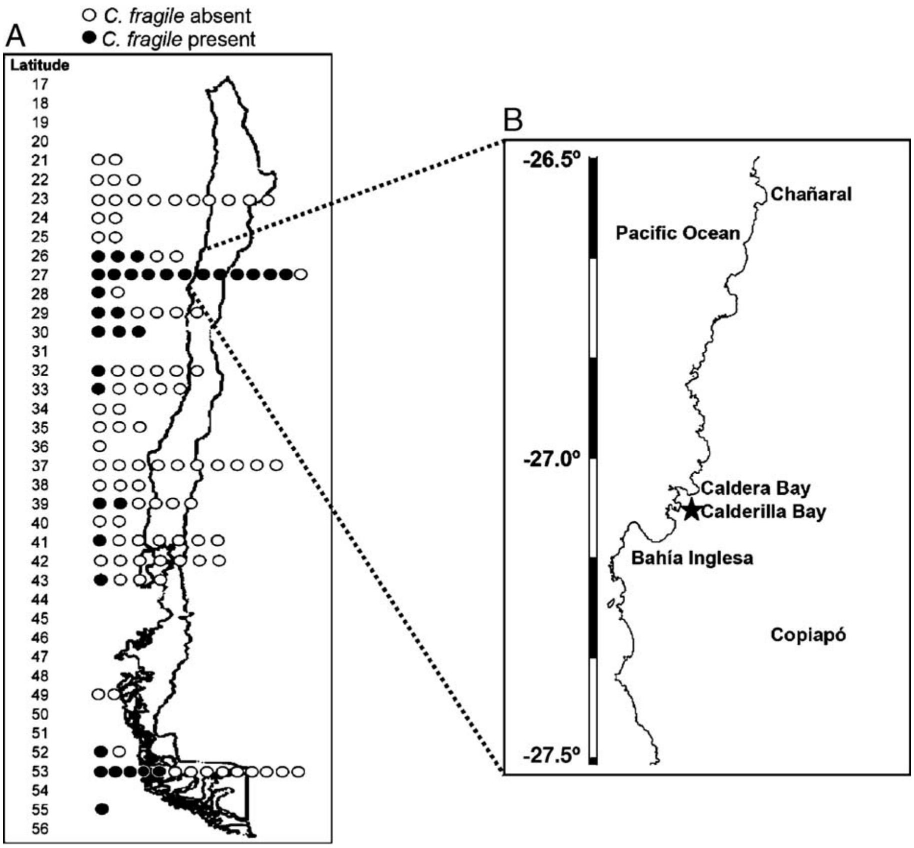

Fig. 1. (A) Range of distribution of *C. fragile* along the Chilean coast. This map is divided into 1° bands of latitude where the number of sites sampled within the band is indicated by the number of circles. Filled circles indicate sites where *C. fragile* is present, unfilled circles indicate sites where the alga was absent. Some latitudinal bands were not sampled. (B) Location of the study site in Calderilla Bay where the effects of *C. fragile* abundances on *G. chilensis* were measured between 1998 and 2003.

Caldera Ltda.) located in a semi-enclosed bay (Calderilla Bay, 27°04'39"S; 70°50'70"W) in northern Chile (Fig. 1B). Many notable anthropogenic activities occur within the bay, as well as directly southward, in Bahía Inglesa. These activities include cultivation of seaweed (*G. chilensis*), invertebrates (*H. rufescens* and *A. purpuratus*), a fish flour processing plant, and traffic by small to medium sized boats. For the purpose of optimizing the management of the farm, the total planted surface was divided into twenty-two 4900 m^2 quadrats. Between November 1998 and January 2003 the abundance of *C. fragile* was estimated monthly in each of these quadrats. Divers inspected each quadrat and classified *C. fragile* abundance using five qualitative categories: absent, low, medium, medium-high, and high. We assigned numerical values to each qualitative category (absent=0, low=1, medium=2, medium-high=3, high=4). We then calculated the index of abundance for each month as:

$$\text{Monthly abundance index} = \frac{\frac{n_{\text{Codium}}}{n} \times \sum_{i=1}^{n} A}{n \times A_{\max}} \times 100$$

where n is the total number of quadrats (i.e. 22), n_{Codium} is the number of quadrats containing *C. fragile*, A are the abundance values (0 to 4) which are summed over all quadrats, and $A_{\max}$ is the maximum possible abundance value (i.e. 4). This abundance index ranges from 0 to 100.

In order to obtain a coarse estimate of the effect of water temperature on *C. fragile* abundances we made daily measurements of sea surface temperature (SST) at a buoy anchored approximately 50 m offshore. These daily temperature readings were averaged over each month and these values were used in a regression analysis of *C. fragile* abundances vs. average monthly SST.

As a first attempt to obtain a quantitative measurement of *C. fragile* biomass, on four separate occasions in 2003 we measured the wet weight of *C. fragile* plants obtained from one 1 m^2 quadrat containing "high" abundances (i.e. abundance category 4) of *C. fragile*. All of the *C. fragile* plants within the quadrat were removed by hand, placed in a mesh bag, and taken to shore where they were weighed (Precision balance, ±50 g). For comparison with *C. fragile*, on the same dates we also measured the wet weight of *G. chilensis* in 1 m^2 quadrats where the red alga had been planted in high densities.

From September 1996 to July 2003 we recorded the monthly biomass of dry, processed *G. chilensis* obtained from different procedures, each differing in the amount of hand labor required to remove weedy species: (1) "algal masses" refer to tangled masses of different algal species suspended in the water column between 10 and 50 m offshore; these algal masses are collected in nets by divers and brought to shore in small boats. Plants obtained from these masses require the greatest amount of processing to remove weedy species (approximately 3.8 min to obtain 1 kg of clean *G. chilensis*; P.E. Neill and O. Alcalde, unpublished data); (2) "drift algae" refers to plants which have been prematurely pulled out of the plantation by wave action or other causes and end up stranded on the shore. Plants obtained from this source require intermediate amounts of processing (approximately 2.4 min to obtain 1 kg of clean *G. chilensis*; P.E. Neill and O. Alcalde, unpublished data); and (3) "harvested algae" refers

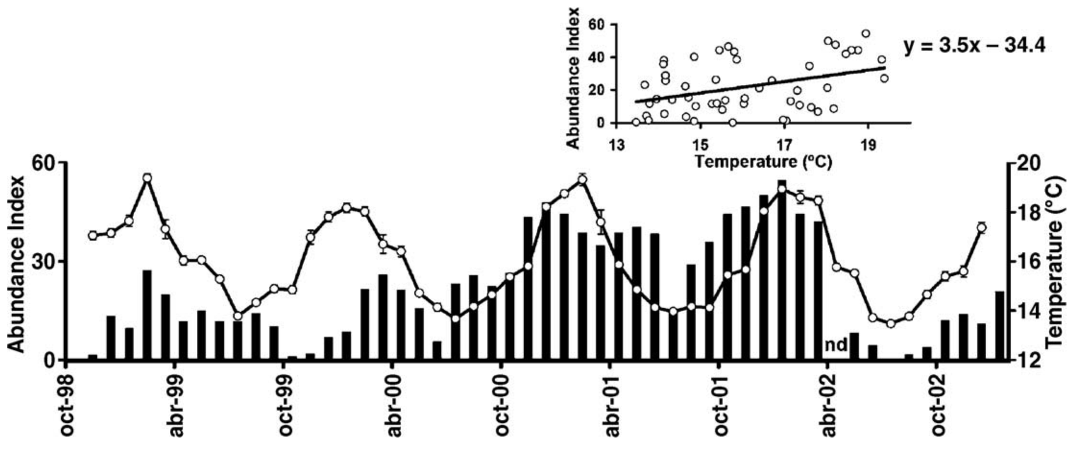

Fig. 2. Time series depicting the annual cycles of *C. fragile* abundance and temperature in the Caldera *Gracilaria* farm from October 1998 to January 2003. Bars represent the monthly *C. fragile* abundance index based on the number of quadrats in which *C. fragile* was present, weighted by a 5 category measure of algal abundance (see Materials and methods for details). Circles indicate average monthly sea surface temperature within the algae farm in Caldera Bay. Error bars are included for temperature data, but not for the *C. fragile* abundance index since the latter data are based on single monthly evaluations. The inset graph shows a regression of monthly *C. fragile* abundances on average monthly sea surface.

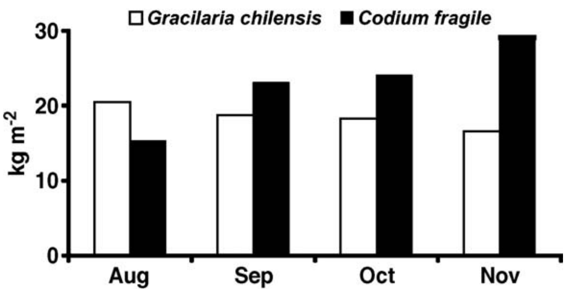

Fig. 3. Wet biomass of *Gracilaria chilensis* (white bars) and *Codium fragile* (black bars) based on four monthly evaluations made in 2003.

to *G. chilensis* obtained from direct harvesting by divers (approximately 0.03 min to obtain 1 kg of clean *G. chilensis*; P.E. Neill and O. Alcalde, unpublished data). Plants obtained in this way are hand selected by divers and do not require additional processing for weedy species removal. These plants are immediately set out to be dried and then compacted into cubes and packaged for shipping. The principal weedy species requiring removal are *Ulva* spp. (a native species) and *C. fragile*, however we were not able to separate the time required for weed removal between these two species. Finally, we estimated capture per unit effort (CPUE) as the total dry biomass of *G. chilensis* (in tons) obtained from direct harvest by divers ("harvested algae"), divided by the total number of divers harvesting per month. Since divers are only allowed to dive for 6 h per day, the total number of divers varied monthly according to the amount of work needed to collect the planted *G. chilensis*. To test for the presence of a declining upper limit on the extraction of *G. chilensis* (CPUE) given by the abundance of *C. fragile*, we searched for an upper limit in the relationship CPUE–*C. fragile* abundance, determining the linear regression of significant quantiles for the greatest quantile. This analysis was conducted using the program BLOSSOM developed by the Fort Collins Science Center (FORT, U.S. Geological Survey, http://www.fort.usgs.gov/products/software/blossom/blossom.asp), which establishes the significance of the slope (with the null hypothesis of a slope equal to 0) using the rank score test for quantile regression (Koenker, 1994; Koenker and Machado, 1999). This test evaluates the probability (p) of a Chi-square distribution, using a randomization approach (for this analysis we used 50,000 randomizations).

3. Results

3.1. Distribution of C. fragile in Chile

C. fragile was present at 34 of the 123 sites evaluated in northern, central and southern regions of the country (Fig. 1). *C. fragile* populations were observed in both subtidal and intertidal zones, with plants attached to a variety of substrata. At 16 sites *C. fragile* was present only on natural substrata (e.g. rocks), at 12 sites the alga was present only on artificial substrata (e.g. aquaculture equipment, ropes, buoys, etc.), and at 6 sites plants were present on both natural and artificial substrata. This alga presented a discontinuous, patchy distribution at the regional scale (thousands of km; Fig. 1), with high plant

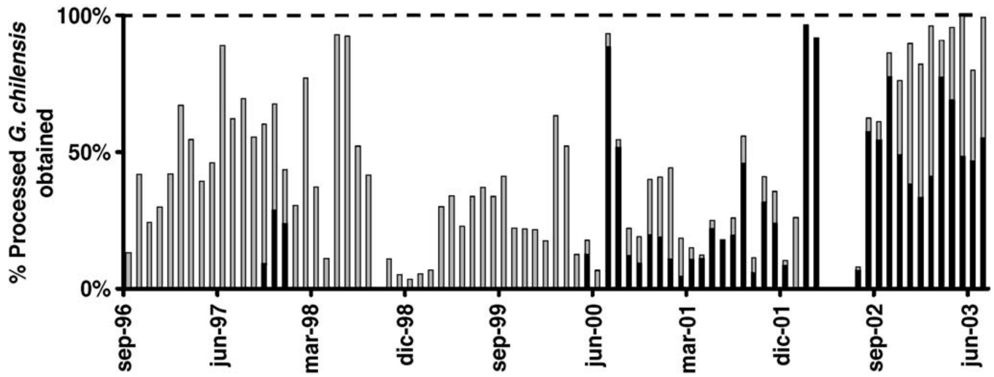

Fig. 4. Time series depicting the influence of weedy species (*Ulva* sp. and *C. fragile*) on total monthly dry biomass of *G. chilensis*. Bars indicate the relative contribution of different collecting methods to total *G. chilensis* obtained each month. The area between the top of the bar and the dashed line at 100% is made up of *G. chilensis* obtained from "direct harvesting" by divers, which does not require additional processing for weedy species removal. The gray shaded portion of the bar represents the percentage of *G. chilensis* obtained from the shore as "drift algae"; *G. chilensis* obtained from this source requires intermediate amounts of processing for weedy species removal. The black portion of the bar represents *G. chilensis* obtained from "algae masses" floating offshore; *G. chilensis* obtained from these masses requires the greatest amount of processing to remove weedy species. We observed an increase in the amount of processing required to clean *G. chilensis*, beginning around the winter of 2000. Throughout 2003 until the end of the data series more than 80% of all *G. chilensis* production was comprised of algae requiring intermediate to high amounts of processing to remove weedy species.

densities occurring only over short distances at the local scale (ones to tens of meters; P. Neill, personal observation). Over half of the invaded sites (61.8%) occurred between 26° and 30°S latitude, suggesting a focal point of the *C. fragile* invasion along the Chilean coast.

3.2. Patterns of abundance and effects on *G. chilensis*

A significant long-term linear trend of increasing *C. fragile* abundances was observed over the 5 years of observations in the plantation (Abundance Index $=-334.146+0.010$[Date], $p=0.046$, $R^2=0.078$). Strong seasonal variation in biomass was apparent all years with higher values in summer–fall months and lower values in winter–spring months. The minimum abundance value was 0.21, occurring in spring of 1998 when *C. fragile* was only present in 2 quadrats at low levels, and the maximum abundance value was 54.55, occurring in summer of 2002 when *C. fragile* was present in all 22 quadrats at intermediate to high levels (Fig. 2). The seasonal trend explained 49.4% of the total variance in *C. fragile* abundance after removing the long-term trend. In addition, abundances of *C. fragile* were significantly and positively correlated with average monthly SST inside the bay (Fig. 2, inset; $F_{[1,47]}=8.17$, $p<0.01$).

During the 4 months in which algae wet weights were measured, the estimated *C. fragile* biomass averaged 22.9 kg m^{-2}, compared with an estimated average of 18.5 kg m^{-2} of the farmed species, *G. chilensis* (Fig. 3). With the exception of the winter month of August, *C. fragile* wet weight per 1 m^2 was greater than *G. chilensis* wet weight, reaching 1.8 times greater mass per area during the summer month of November.

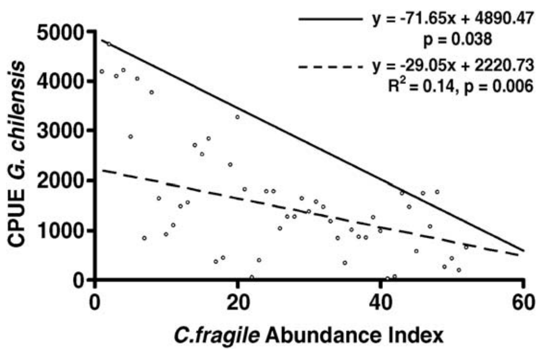

Fig. 5. We observed a significant negative effect of *C. fragile* presence on the Catch Per Unit Effort (CPUE) of *G. chilensis*. CPUE was measured as the total dry biomass of *G. chilensis* (in tons) obtained from direct harvest by divers, divided by the total number of divers extracting, per month. A significant upper limit to CPUE was observed at the 94th quantile.

The increasingly negative influence of weedy species (principally *Ulva* spp. and *C. fragile*) on the monthly production of *G. chilensis* is apparent in the data presented in Fig. 4. We observed an increase in the amount of processing required to clean *G. chilensis* beginning around the winter of 2000. Throughout 2003 and until the end of the data series more than 80% of all *G. chilensis* production was comprised of thalli requiring intensive manual labor to remove weedy species. Regression analysis revealed that the CPUE of *G. chilensis* was significantly, negatively correlated with the *C. fragile* abundance index ($F_{1,49}=8.17$, $p=0.006$, Fig. 5), with a significant upper limit to CPUE at the 94th quantile (Fig. 5). The x-intercept of the upper limit corresponded to a *C. fragile* abundance index of 68.3, indicating that CPUE values of *G. chilensis* fall to zero at intermediate to high values of *C. fragile* abundance.

4. Discussion

Despite its effects as an invasive species in many parts of the world, and its relatively easy identification in the field, especially in the absence of congeners, the distribution of *C. fragile* in Chile has received little attention. Earlier reports indicated that *C. fragile* was present in only a few sites at the southern extreme of Chile (Ramírez and Santelices, 1991). Recently, however, *C. fragile* ssp. *tomentosoides* has been observed and reported in the northern part of the country (Neill et al., 2003; Castilla et al., 2005; González and Santelices, 2004; Provan et al., 2005; Castilla and Neill, in press), however it remains to be elucidated whether the stands in the south belong to the same subspecies (*tomentosoides*). Here we provide records of the presence of *C. fragile* populations at 34 sites along the Chilean coast, expanding the northern limit to Obispito (26°45’19”S; 70°44’09”W). Now that *C. fragile* has been documented at a variety of sites in Chile, future observations will allow researchers to characterize the direction and rate of range expansion. Studies in other parts of the world indicate that expansion rates of *C. fragile* are variable. Some authors report that *C. fragile* populations required at least a decade prior to any significant expansion (e.g. 250 km) while others have reported a much more rapid spread (1200 km in 10 years) (Carlton and Scanlon, 1985, and references in Mathieson et al., 2003).

It is interesting to note the patchiness of *C. fragile* populations at regional and local scales on the Chilean coast, as has been observed in other introduced areas (e.g. Atlantic coast of North America, Carlton and Scanlon, 1985). Such patchiness could indicate multiple introductions of the invader to different locations at different times or via different vectors (e.g. the alga may have been introduced to a site along with a specific mariculture, or may have arrived as a drift alga), and/or that the species requires specific environmental conditions for successful colonization (e.g. warm water temperatures or high nutrients). Several authors have pointed to warm water affinities of *C. fragile*, which is able to survive over a wide range of temperatures, however 10 °C or higher is required for normal growth and 21–24 °C for optimal growth (Fralick and Mathieson, 1972; Mathieson et al., 2003). Temperatures above 13 °C are present year-round in Calderilla Bay. Affinity of this alga for warm water is supported by the observed seasonality of *C. fragile* abundances within the *G. chilensis* farm, and the positive correlation of *C. fragile* abundance with monthly SST in the bay. Our observations are consistent with studies conducted in the Gulf of Maine, where *C. fragile* growth was greatest during peak summer temperatures, with growth and reproduction being restricted by cold water temperatures during winter months (Mathieson et al., 2003), however it should be noted that average winter water temperatures in Calderilla Bay never fell below 13.5 °C, while in the Gulf of Maine average winter temperatures can reach below 4 °C. In the northern hemisphere, some studies have reported that *C. fragile* populations expand more rapidly towards the south than the north likely due to warm-water affinities (Fralick and Mathieson, 1972; Mathieson et al., 2003, but see references in Trowbridge, 1998 for rapid northward spread on Scottish shores). If the distribution of *C. fragile* in Chile is largely determined by SST, we expect faster spread of northern populations towards the north. In addition, conditions imposed by the El Niño Southern Oscillation (ENSO), characterized by warmer northern waters moving into the south, may provide an important opportunity for further invasion by *C. fragile* to the south. Nutrient enrichment due to aquaculture and fishery activities may further promote the growth and establishment of *C. fragile* (as well as other weedy species, such as *Ulva* spp.) in source populations, such as Calderilla Bay. Climate change, especially increased environmental temperatures may then provide further opportunities for range expansion from established source populations. Observations of *C. fragile* abundances within northern Chile suggest that artificial substrata may act as corridors for the dispersal of *C. fragile* into subtidal or intertidal habitats where it is otherwise not able to survive (P.E. Neill, unpublished data). This phenomenon has been documented for non-indigenous species (including *C. fragile*) in the north Adriatic Sea, where artificial marine structures such as jetties and breakwaters provide habitat in otherwise unsuitable areas (Bulleri and Airoldi, 2005). As noted by Trowbridge (1998) for Mediterranean and Scottish shores, in Chile the spread of this species is likely due to a combination of natural, local dispersal and human-assisted spread.

The negative effect of *C. fragile* on the *G. chilensis* plantation is of concern to algal farmers in Chile. The average biomass of *C. fragile* per m^2 at the study site was more than double the greatest biomass reported in the Gulf of Maine (i.e. a maximum of 10.2 kg m^{-2} in the Gulf of Maine vs. an average of 22.9 kg m^{-2} in Calderilla Bay, Mathieson et al., 2003). Furthermore, the negative relationship between monthly *C. fragile* abundance and CPUE of *G. chilensis* indicates that farmers must hire more divers to extract the planted *G. chilensis*. In addition to this cost, farmers must also employ more workers to manually remove the weedy species and pay for trucks to dispose of tons of rotting, unprofitable biomass. This is both time consuming and costly. While we are not yet able to predict the dynamics of *C. fragile* populations at the farm, it is apparent that this species has increased as a pest in mariculture facilities since 1998. The spread of *C. fragile* is also worrisome for other people working in mariculture, given the costs associated with increased fouling of equipment, direct damage to the farmed species, as well as the costs associated with its removal and disposal. During the course of this study the *Gracilaria* plantation where we worked became insolvent as a result of the increased costs associated with weedy species removal, and the farm closed in 2005.

Options for dealing with *C. fragile* in northern Chile could include direct attempts to eradicate the invasive alga via chemical treatment or manual removal in winter time, when abundance is low and growth and reproduction limited. However, such attempts for eradication will be futile if investigators and policy makers are not able to identify and control the sources of the *C. fragile* introduction(s). Furthermore, it is important to identify which kinds of propagules are most important for colonization of new sites in Chile (e.g. drifting plants vs. algal spores), given that different types of propagules likely present different dispersal capacities. If artificial structures, such as equipment used in the aquaculture industry, allow dispersing propagules to persist at otherwise unsuitable sites, it is in the interest of managers and owners to implement measures to prevent further introductions. Such measures should include removing or increasing the distance between artificial structures so that it is greater than the maximum distance over which propagules can disperse (Bulleri and Airoldi, 2005) as well as renewing or treating equipment (e.g. lantern nets, ropes), which are often shared between aquaculture facilities.

It is difficult to anticipate whether *C. fragile* can be completely eradicated from northern Chile and, therefore, management plans should focus on preventing its spread from focal points. This could be accomplished by implementing a comprehensive plan to control local transport vectors, such as small fishing boats and nets or untreated aquaculture equipment, direct removal during months of low abundance so as to reduce the population size, and increasing spacing among aquaculture operations. Beyond the economic effects reported in this study, more detailed research should be conducted to characterize and quantify the effects of *C. fragile* on native algae and invertebrate species in the subtidal and intertidal communities of northern Chile.

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