Aquatic Invaders THE DIGEST OF
NATIONAL AQUATIC NUISANCE SPECIES CLEARINGHOUSE
Vol.16, No.2, April-June 2005

DISTRIBUTION & DISPERSAL

Reciprocal *Caulerpa* Invasion: Mediterranean native *Caulerpa ollivieri* in the Bahamas supported by human nitrogen enrichment

Brian E. Lapointe[1], Peter J. Barile[1], Michael J. Wynne[2], and Charles S. Yentsch[3]

[1]Division of Marine Science Harbor Branch Oceanographic Institution, Inc. 5600 US 1 North, Ft. Pierce, Florida 34946, lapointe@hboi.edu, pbarile@hboi.edu; [2]Department of Ecology and Evolutionary Biology University of Michigan; Ann Arbor, Michigan 48109, mwynne@umich.edu; [3]Bigelow Laboratory for Ocean Sciences, McKown Point Road, West Boothbay Harbor, Maine 04575, csyentsch@aol.com

Abstract

The genus *Caulerpa* is known for its invasion of tropical, subtropical, and temperate coastal waters. Whereas the role of humans as vectors for the introduction of *Caulerpa* has been well documented, other anthropogenic factors that may mediate the success of an invasion are poorly understood. We provide evidence that a recent invasion of *Caulerpa ollivieri* into shallow Bahamian seagrass meadows is facilitated by anthropogenic nitrogen enrichment from sewage. Considering the accelerating nitrogen enrichment of coastal waters worldwide, our results suggest that reduction of anthropogenic nitrogen inputs must be achieved as a means of controlling similar biotic invasions.

Humans are recognized as the primary vector in the global epidemic of biotic invasions in aquatic ecosystems (Carlton and Geller 1993). Much less is known about how anthropogenic modification of ecosystems facilitate biological invasions. We provide an example of how anthropogenic nitrogen enrichment has supported a successful invasion of the green alga *Caulerpa ollivieri* in coastal waters of Green Turtle Cay, Abacos, Bahamas.

The islands of the Bahamas are surrounded by carbonate-rich subtropical waters that were historically oligotrophic and contained healthy coral reefs and nutrient-limited tropical seagrass ecosystems (Short et al. 1990). The growing resident and tourist populations on Green Turtle Cay, like many small island states globally, are increasing land-based nutrient loads to coastal waters from a variety of sources, especially untreated (raw) and/or partially-treated (septic tanks) domestic sewage. Recent studies have shown that the inshore waters of Green Turtle Cay are experiencing nutrient enrichment[1] and eutrophication primarily as a result of localized sewage pollution (Barile 2001).

Common symptoms of nutrient pollution in shallow, tropical and subtropical seagrass meadows include macroalgal blooms and epiphytization of seagrass blades, which reduce light and cause fragmentation and die-off of seagrasses, especially turtle grass, *Thalassia testudinum* (NRC 2000). Historically, *T. testudinum* meadows surrounding Green

continued on p. 3

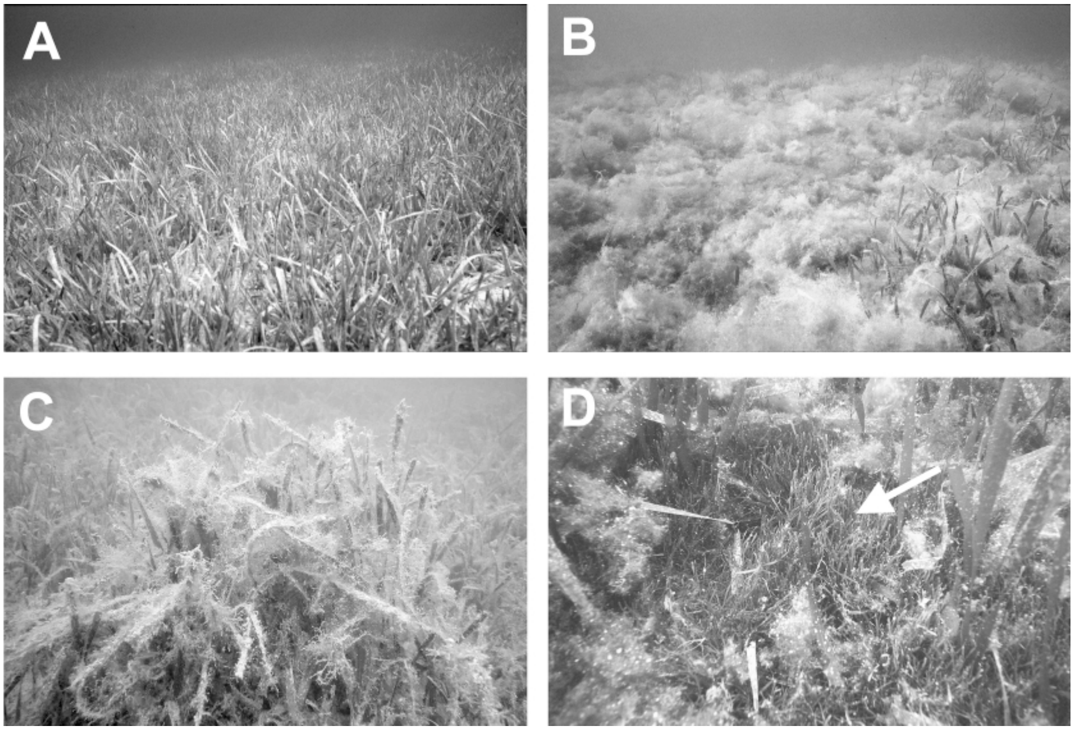

Figure 1. A) A productive turtle grass (*Thalassia testudinum*) meadow in nearshore waters of Green Turtle Cay, Abacos, Bahamas. B) Bloom of a mat-forming filamentous green macroalga (*Cladophora* sp.) causing fragmentation and die-off of *T. testudinum* in the Town Harbor, Green Turtle Cay. C) Micro-filamentous algal epiphytes on blades of *T. testudinum* in Black Sound, Green Turtle Cay. D) Invasive bloom of *Caulerpa ollivieri* (denoted by arrow) causing fragmentation of and die-off of a *T. testudinum* meadow in Black Sound, Green Turtle Cay.

continued from p.1

Turtle Cay were highly productive and had a low biomass of associated macroalgae and few attached epiphytes (Figure 1A). In Black Sound, a confined embayment on Green Turtle Cay, symptoms of nutrient pollution have developed in recent years that include blooms of mat-forming green seaweeds (Figure 1B) and microfilamentous blade epiphytes (Figure 1C), which cause fragmentation and die-off of *T. testudinum*.

During a survey of the degraded seagrass meadows in Black Sound (a popular anchorage for vessels in transit) we discovered extensive areas of organic-rich sediments that supported thick mats of the green rhizomatous macroalga *Caulerpa ollivieri* (Figure 1D). Prior to this discovery, *C. ollivieri* had not been reported for either the Bahamas or Caribbean region (Littler and Littler 2001). This finding suggests that international maritime activities may have been involved with this introduction, as commonly reported for marine bioinvasions (Carlton 2000). *Caulerpa ollivieri* was first recognized in the area of Villefranche-sur-Mer in the Mediterranean by Ollivier (1929), who regarded it as a form of *C. prolifera* and suspected that its proliferation resulted from domestic pollution. Initially, Dostal (1928) published on this plant as *C. prolifera* but in subsequent studies (Dostal 1929) he concluded it was distinct from *C. prolifera* and described it as a new species, *C. ollivieri*. *Caulerpa ollivieri* was recently included in a checklist of seaweeds from the Mediterranean (Gallardo et al. 1993) and it has also been listed as an endangered species in the Mediterranean by the Berne Convention (the European Centre for Nature Conservation, http://www.ecnc.nl). The first report of *C. ollivieri* outside of the Mediterranean was from relatively deep-water collections in the Gulf of Mexico offshore of Tampa Bay (30 m) and Loggerhead Key, Dry Tortugas (60 m, Hine and Humm 1971). Whereas *C. ollivieri* is now rare in the Mediterranean, it is increasingly abundant in the shallow waters (< 5 m) of upper Black Sound where it exhibits invasive attributes. To date, we have not observed *C. ollivieri* growing in other coastal waters around Green Turtle Cay.

To determine if the invasive growth of *C. ollivieri* is being supported by land-based sewage pollution as suggested by Ollivier (1929), we collected native *Caulerpa* spp. and the invasive *C. ollivieri* from several polluted sites in Black Sound for comparison with native *Caulerpa* species collected at reference locations along an offshore gradient of decreasing nutrient pollution. The

Date	Location	Station	Species	$\delta^{15}N$
Feb-03	sewage polluted harbor	Swanson's	*C. ollivieri*	4.97 ± 0.06
	(Black Sound)	Escape	*C. ollivieri*	2.62 ± 0.19
		Linton's	*C. ollivieri*	3.68 ± 0.64
		Shipyard	*C. ollivieri* (small form)	5.13 ± 0.51
		Shipyard	*C. ollivieri* (large form)	5.19 ± 0.57
		Shipyard	*C. verticillata*	4.34 ± 0.18
			mean (n = 24)	**4.32 ± 1.01**
Jul-03	Sewage polluted harbor	Swanson's	*C. ollivieri*	2.61 ± 0.17
	(Black Sound)	Escape	*C. ollivieri*	2.62 ± 0.19
		Linton's	*C. ollivieri*	3.08 ± 0.60
		Shipyard	*C. ollivieri* (small form)	5.66 ± 1.15
		Shipyard	*C. ollivieri* (large form)	6.07 ± 0.36
		Shipyard	*C. verticillata*	3.07 ± 0.02
			mean (n = 24)	**3.85 ± 1.58**
Jul-03	Seagrass Meadow	Sand Bar	*C. cupressoides*	1.59 ± 0.51
	Coral Reef	Raven's Cliff	*C. verticillata*	1.75 ± 0.06
Feb-04	Coral Reef	Raven's Cliff	*C. racemosa*	0.67 ± 0.43
	Coral Reef	No Name North	*C. racemosa*	0.78 ± 0.37
			mean (n = 16)	**1.20 ± 0.55**

Table 1. Stable nitrogen isotope ($\delta^{15}N$, ‰) values of *Caulerpa ollivieri*, *Caulerpa cupressoides*, *Caulerpa verticillata*, and *Caulerpa racemosa* sampled from several sewage-polluted sites in Black Sound, a nearshore seagrass meadow and offshore coral reefs near Green Turtle Cay, Abacos, Bahamas, in 2003/2004. Values represent means ± SD (n=4).

samples were analyzed for stable nitrogen isotopes ($^{15}N/^{14}N = \delta^{15}N$, see Lajtha and Michener 1994). This biogeochemical technique has been used widely to discriminate between natural and anthropogenic nitrogen sources potentially supporting growth of marine biota, including macroalgae; low $\delta^{15}N$ values close to 0 are indicative of natural N fixation whereas values > + 3.0 ‰ are characteristic of sewage pollution (Costanzo et al. 1999).

Caulerpa ollivieri collected in February (dry season) and July (wet season) of 2003 had mean $\delta^{15}N$ values of + 4.32 ± 1.01 ‰ (n = 20) and + 4.01 ± 1.53 ‰ (n = 20), respectively (Table 1), values characteristic of sewage pollution. Native populations of the sibling species *Caulerpa verticillata* and *Caulerpa cupressoides* were also collected from Black Sound, a nearshore *Thalassia testudinum* meadow (Sand Bar), and two offshore coral reefs (Raven's Cliff, No Name North) and analyzed for $\delta^{15}N$ as reference material. *Caulerpa verticillata* from Black Sound had a mean value of + 4.34 ± 0.18 ‰ in February and + 3.07 ± 0.02 ‰ in July, values within the range of sewage nitrogen and consistent with the results for *C. ollivieri*. In contrast, *C. cupressoides* from the nearshore *T. testudinum* meadow and *Caulerpa verticlllata* from the offshore Raven's Cliff reef in July 2003 had mean values of +1.59 ± 0.51 ‰ and +1.75 ± 0.06 ‰, respectively (Table 1), values significantly below that of sewage. Similarly, *C. racemosa* sampled in February 2004 at Raven's Cliff and No Name North Reef had values of + 0.67 ± 0.43 ‰ and + 0.78 ± 0.37 ‰, well below the sewage signature. This pattern of decreasing $\delta^{15}N$ values with increasing distance from shore reflects the dilution of land-based sewage discharges and possibly an increased importance of natural N-fixation in these more offshore, oligotrophic locations.

The ability of *Caulerpa ollivieri* to replace *Thalassia testudinum* in eutrophic Bahamian coastal waters may be related to several physiological factors. Under natural conditions, *T. testudinum* relies largely on N-fixation for its nitrogen supply (Patriquin and Knowles 1972) and may not be competitive with faster growing macroalgae like *C. ollivieri* when anthropogenic nitrogen sources, such as sewage, become available. Additionally, coastal waters impacted by anthropogenic nutrient pollution, including sewage, typically have increased light attenuation (Yentsch et al. 2002). Because the minimal light requirement of seagrasses is > 10 % of incident surface irradiance (Duarte 1991) compared to < 1 % for *Caulerpa* spp. (Gacia et al. 1996), increased light limitation[2], coupled with nitrogen enrichment, could favor expansion of invasive *C. ollivieri* at the expense of native *T. testudinum*.

Ironically, these recent findings from the Bahamas support Ollivier's (1929) hypothesis that domestic pollution may be supporting proliferation of *Caulerpa* in the Mediterranean Sea. Since the accidental introduction of *C. taxifolia* at Monaco in the early 1980s (Jousson et al. 1998), this alga has spread towards both Italy and Spain and was recently estimated to cover up to 30,000 ha. of the Mediterranean sea bottom (Withgott 2002), although this estimate has been challenged by Jaubert et al. (2003). The invasion has resulted in extensive, monospecific stands of *C. taxifolia* and controversy continues as to the potential for deleterious alterations of the native *Posidonia oceanica* communities (Meinesz and Hesse 1991, Jaubert et al. 1999). Bioassays of *C. taxifolia* in the Mediterranean suggest nutrient-replete growth year-around (Delgado et al. 1996) and areas of explosive growth of *C. taxifolia* are consistently centered adjacent to land-based stormwater and sewage discharges (Chisholm et al. 1997). *Caulerpa taxifolia* has also invaded coastal waters of California (Jousson et al. 2000), and a sibling species from southwestern Australia, *C. racemosa* var. *cylindracea*, has recently formed a second *Caulerpa* invasion in the Mediterranean (Verlaque et al. 2003).

Considering that human activities are rapidly increasing nitrogen inputs to nitrogen-limited coastal waters from domestic and industrial wastewaters, fertilizers, top soil loss, and fossil fuel combustion (Ryther and Dustan 1971, NRC 2000, Vitousek et al. 1997), invasive blooms of *Caulerpa* may become even more commonplace in the future. In Hillsborough Bay, Tampa, Florida, for example, increasing sewage pollution in the 1960's and 1970's led to fragmentation and die-off of seagrasses with parallel increases in macroalgae, including *C. prolifera* (Avery 1997). In the Indian River Lagoon on the east coast of Florida, *C. prolifera* also expanded in areas receiving sewage pollution and experiencing loss of seagrasses (White and Snodgrass 1990). To moderate the conditions supporting invasive *Caulerpa* blooms, planners and resource managers must consider methods to reduce nitrogen loads from sewage and other sources. For example, *C. prolifera* decreased from 280 ha in 1988 to less than 0.2 ha in 1995 as seagrasses expanded following reductions in wastewater nitrogen loading into Hillsborough Bay that began in 1979 (Avery 1997). More broadly, it is likely that nitrogen enrichment has already facilitated successful invasions of other macroalgal taxa in tropical coastal waters, such as Hawaii (Rodgers and Cox 1999).

Acknowledgements

We thank MM Littler, DS Littler, and D Tomasko for helpful comments on the preparation of this manuscript. Linton's Beach and Harbour Cottages and *Reef Relief* provided logistical support for the work and Michael Braynen (Bahamas Department of Fisheries) assisted with the research permitting. This work was supported by the US Environmental Protection Agency's Science to Achieve Results (STAR - R-83041401-0) Program and the Harbor Branch Oceanographic Institution, Inc. Although the research in this article has been funded in part by the US Environmental Protection Agency's STAR program, it has not been subjected to any EPA review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred. This is contribution # 1590 from the Harbor Branch Oceanographic Institution, Inc.

Footnotes

[1] Mean concentrations of dissolved inorganic nitrogen (DIN = ammonium + nitrate + nitrite) we measured around Green Turtle Cay in 1998/1999 were over ten-fold higher in nearshore waters directly impacted by sewage discharges (Town Harbor, White Sound, and Black Sound, 14.0 ± 6.60 μM, n = 12) compared to seven offshore coral reef sites (0.87 ± 0.47 μM, n = 28).

[2] Laboratory measurements of photosynthesis (oxygen evolution) vs. irradiance curves with *Caulerpa verticillata*, *Caulerpa brachypus*, and *Caulerpa racemosa* collected from reefs off Palm Beach County, Florida, during 2003 indicated that the compensation irradiance for these species was consistently < 20 μmol photons $\cdot$ $m^{-2} \cdot s^{-1}$, a value ~ 1% of full natural surface irradiance.

About the Author

Brian E Lapointe is an Associate Research Scientist in the Division of Maine Science at Harbor Branch Oceanographic Institution, Inc., in Ft. Pierce, FL. For over thirty years he has focused his studies on the physiological ecology and environmental biology of marine macroalgae in South Florida, the Bahamas, and Caribbean region.

References

Avery W. 1997. Distribution and abundance of macroalgae and seagrass in Hillsborough Bay, FL from 1986 to 1995. *Proceedings of Tampa Bay Area Scientific Information Symposium 3*, Tampa Bay National Estuary Program, p151-165.

Barile PJ. 2001. Local, regional, and global biogeochemical linkages to the physiological ecology of macroalgae on coral reef communities near Green Turtle Cay, Abacos Cays, Bahamas. [dissertation]. Melbourne (FL): Florida Tech, 231 p.

Carlton JT. 2000. Quo vadimus exotica oceanica? Marine bioinvasion ecology in the twenty-first century. In: Pederson J, (ed) Marine Bioinvasions, Cambridge, MA, Proceedings 1st National Conference, Jan 24-27 1999. Massachusetts Institute of Technology, p6-23.

Carlton JT, Geller JB. 1993. Ecological roulette: the global transport of non-indigenous marine organisms. *Science* 261:78-82.

Chisholm JRM, Fernex FE, Mathieu D, Jaubert JM. 1997. Wastewater discharge, seagrass decline and algal proliferation on the Cote d' Azur. *Marine Pollution Bulletin* 34:78-84.

Costanzo SD, O'Donohue MJ, Dennison WC, Loneragan NR, Thomas M. 1999. A new approach for detecting and mapping sewage impacts. *Marine Pollution Bulletin* 42:149-156.

Delgado O, Rodriguez-Prieto C, Gacia E, Ballesteros E. 1996. Lack of severe nutrient limitation in *Caulerpa taxifolia* (Vahl) *C. agardh*, an introduced seaweed spreading over the oligotrophic northwestern Mediterranean. *Botanica Marina* 39:61-67.

Dostál R. 1928. Observations morphogénetiques sur le *Caulerpa prolifera* de la baie de Villefranche-sur-Mer. *CR hebd Séanc Acad Sci*, Paris 185:1298-1299.

Dostál R. 1929. *Caulerpa ollivieri* n. sp., la seconde espece européenne des Caulerpacées, *Bull Inst Océanogr*, Monaco No. 531. 12 pp.

Duarte CM. 1991. Seagrass depth limits. *Aquatic Botany* 40(4):363-377.

Gacia E, Rodriguez-Prieto C, Delgado O, Ballesteros E. 1996. Seasonal light and temperature responses of *Caulerpa taxifolia* from the northwestern Mediterranean. *Aquatic Botany* 53(3):215-222.

Gallardo TA, Gomez-Garreta A, Ribera MA, Cormaci M, Furnari G, Giaccone G, Boudouresque CF. 1993. Check-list of Mediterranean seaweeds. 2. Chlorophyceae Wille s. l. *Botanica Marina* 36(5):399-421.

Hine AE, Humm HJ. 1971. *Caulerpa ollivieri* in the Gulf of Mexico. *Bulletin of Marine Science* 21:552-555.

Jaubert JM, Chisholm JRM, Ducrot D, Ripley HT, Roy L, Passeron-Seitre G. 1999. No deleterious alterations in *Posidonia oceanica* beds in the Bay of Menton 8 years after *Caulerpa taxifolia* colonization. *Journal of Phycology* 35:1113-1119.

Jaubert JM, Chisholm JRM, Minghelli-Roman A, Marchioretti M, Morrow JH, Ripley HT. 2003. Re-evaluation of the extent of *Caulerpa taxifolia* development in the northern Mediterranean using airborne spectrographic sensing. *Marine Ecology Progress Series* 263:75-82.

Jousson O, Pawlowski J, Zaninetti L, Meinesz A, Boudouresque CF. 1998. Molecular evidence for the aquarium origin of the green alga *Caulerpa taxifolia* introduced to the Mediterranean Sea. *Marine Ecology Progress Series* 172:275-280.

Jousson O, Pawlowski J, Zaninetti L, Zechman FW, and Others. 2000. Invasive alga reaches California. *Nature* 408:157-158.

Lajtha K, Michener HH. 1994. Methods in ecology: Stable isotopes in ecology and environmental science. In: Lawton JH, Likens GE (eds) Oxford, England. Blackwell Scientific Publications. 301 p.

Littler DS, Littler MM. 2001. Caribbean Reef Plants. Washington, DC. Offshore Graphics, 542 pp.

Meinesz A, Hesse B. 1991. Introduction et invasion de l'algue tropicale *Caulerpa taxifolia* en Mediterranee nord-occidentale. *Oceanol Acta* 14:415-426.

National Research Council. 2000. Clean coastal waters: understanding and reducing the effects of nutrient pollution. Washington, DC. National Academy Press.

Ollivier G. 1929. Etude de la flore marine de la Cote d'Azur. *Ann Inst Océanogr*, Monaco, Tome VII, fasc III, p 1-173.

Patriquin DG, Knowles R. 1972. Nitrogen fixation in the rhizosphere of marine angiosperms. *Marine Biology* 16:49-58.

Rodgers SK, Cox EF. 1999. Rate of spread of introduced rhodophytes *Kappaphycus alvarezii*, *Kappaphycus striatum*, and *Gracilaria salicornia* and their current distributions in Kaneohe bay, Oahu, HI. *Pacific Science* 53(3):232-241.

Ryther JH, Dustan WM. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* 171:1008-1013.

Short FT, Dennison WC, Capone DG. 1990. Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Marine Ecology Progress Series* 62(1):169-174.

Verlaque M, Durand C, Huisman JM, Boudouresque CF, La Parco Y. 2003. On the identity and origin of the Mediterranean invasive *Caulerpa racemosa* (Caulerpales, Chlorophyta). *European Journal of Phycology* 38(4):325-339.

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman D. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737-750.

White C, Snodgrass JW. 1990. Recent changes in the distribution of *Caulerpa prolifera* in the Indian River Lagoon. *Florida Scientist* 53(2):85-88.

Withgott J. 2002. California tries to rub out the monster of the lagoon. *Science* 295:2201-2202.

Yentsch CS, Yentsch CM, Cullen JJ, Lapointe BE, Phinney DA, Woodman SF. 2002. Sunlight and water transparency: cornerstones in coral research. *Journal of Experimental Marine Biology and Ecology* 268:171-183.

FISH BASE

Invasive Species in FishBase[1]

Christine Marie V. Casal, Research Associate

FishBase Project, WorldFish Center Philippine Office, Khush Hall, IRRI Campus, Los Baños, Laguna, Philippines. Email: c.casal@cgiar.org

Background

The impact of species movement beyond their natural boundaries has been regarded as a major problem in the conservation of aquatic resources. Introduced species have been implicated in bringing some native species to the brink of extinction through competition for food and niche space, predation, genetic deterioration, introduction of parasites, pathogens and diseases, spatial, habitat and trophic modifications (Lever 1996).

However, the introduction of species is also instrumental in the production of aquatic protein through aquaculture, complementing fish catch. Fish catch worldwide has been slowly declining since the late 1980s, aquaculture production on the other hand, has been steadily increasing through the years (FAO 2004). It is not surprising therefore that over 36%