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Phytoplankton And The Macondo Oil Spill: A Comparison Of The 2010 Phytoplankton Assemblage To Baseline Conditions On The Louisiana Shelf

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18

19   ABSTRACT

20

21   The Macondo oil spill was likely the largest oil spill to ever occur in United States territorial

22   waters. We report herein our findings comparing the available baseline phytoplankton data from

23   coastal waters west of the Mississippi River, and samples collected monthly from the same

24   sampling stations, during and after the oil spill (May – October, 2010). Our results indicate that

25   overall, the phytoplankton abundance was 85% lower in 2010 versus the baseline, and that the

26   species composition of the phytoplankton community moved towards diatoms and cyanobacteria

27   and away from ciliates and phytoflagellates. The results of this study reaffirm the view that

28   phytoplankton responses will vary by the seasonal timing of the oil spill and the specific

29   composition of the spilled oil. The trophic impacts of the purported lower abundance of

30   phytoplankton in 2010 coupled with the observed assemblage shift remain unknown.

31

32   Keywords: Deepwater Horizon; Gulf of Mexico; phytoplankton; protozoans

33   Capsule: Phytoplankton biomass was 85% lower in 2010 versus baseline. The phytoplankton

34   community moved towards diatoms and cyanobacteria and away from ciliates and

35   phytoflagellates. Trophic impacts remain unknown.

36

1. Introduction

One unfortunate consequence of the extraction, transport, and refining of crude oil is the risk of accidental spillage into the environment and, in particular, into marine environments. Significant oceanic oil spills first began during World War I, with the commencement of transoceanic oil transport and the wartime targeting of commercial shipping (Albers, 1995). A large number of these oil spills adversely affected marine birds (Bourne, 1968). Compared to World War II, however, the spills in World War I pale in comparison. Michel et al. (2005) estimated that more than 75% of the 8569 documented shipwrecks (including 1583 tankers) were the result of World War II hostilities, and that they introduced 567 million to 4.5 billion gallons of oil into the oceanic environment. The environmental impacts of these WWII releases are undocumented.

The *Torrey Canyon* grounded off the coast of England in 1967, releasing 32 million gallons of oil (Smith, 1968). The public concern for such large oil spills grew after this event, leading to a significant increase in research on the fate and impacts of crude oil in the environment in the 1970s (Albers, 1995). As a result, a better understanding of the impacts of crude oil exposure on various marine organisms has been garnered (e.g., Peterson et al., 2003), particularly in cases where the local environment was already under study and baseline data were available before the oil spill (e.g., the *Tsesis*, *Florida*, and *Amoco Cadiz* spills; Teal and Howarth, 1984). Most of the documented impacts, however, were limited to coastal littoral and subtidal regions, with far less information gathered and analyzed on impacts to pelagic and planktonic organisms.

Despite the previous experiences and knowledge gained in earlier oil spills (including the *Exxon Valdez* in Prince William Sound, Alaska; Maki, 1991) and the significant efforts implemented to extract crude oil in the Gulf Mexico (Managi et al., 2005), the petroleum

61   industry, scientific community, and resource managers were under-prepared for the magnitude

62   and complexity of the oil spill that occurred on April 20, 2010 in the northern Gulf of Mexico at

63   the Macondo 252 production site. On this date, the *Deepwater Horizon* drilling rig exploded,

64   resulting in the loss of eleven lives and the release of four million barrels (636 million L) of oil

65   into the northern Gulf of Mexico over the next several months (Camilli et al., 2010). Oil was

66   released at an average of 9.8+ million L of oil per day over an 84 day period (Chen and Denison,

67   2011). A legitimate concern is that the scale of this oil spill (likely the largest ever in U.S.

68   territorial waters) has created a multitude of potentially catastrophic ecological impacts in the

69   northern Gulf of Mexico for years to come.

70   The northern Gulf of Mexico harbors a highly productive coastal ecosystem, including the

71   second largest U.S. fishery by weight (mainly Gulf menhaden, *Brevoortia patronus*), and the

72   fifth largest by value ($300–400 million per year; due primarily to the harvest of penaeid

73   shrimps; de Mutsert et al., 2008). These substantial fishery yields are related (in part) to the large

74   phytoplankton biomass generated by high nutrient loads supplied by the Mississippi River,

75   primarily during the annual spring floods of the river (Lohrenz et al., 1997). The spring blooms

76   are composed primarily of diatoms (Turner et al., 1998; Dortch et al., 2001), and are often

77   dominated by the toxigenic genus, *Pseudo-nitzschia* (Dortch et al., 1997; Parsons et al., 1998;

78   Parsons et al., 2013). Much of this phytoplankton biomass is consumed by grazers (Dagg, 1995),

79   but phytoplankton biomass and zooplankton fecal pellets transport significant amounts of

80   organic matter to the benthos (Dortch and Whitledge, 1992; Qureshi, 1995), fueling hypoxia in

81   the calmer, warmer summer months (Rabalais et al., 2002, 2007). Phytoplankton growth rates

82   can be high (up to 3 divisions day^{-1}; Fahnenstiel et al., 1995), but can be limited for diatoms by

83   silica limitation (Dortch et al., 2001). A reduction in diatom biomass as a result of silica

84   limitation can cascade to higher trophic levels, for example causing a reduction in copepod

85   biomass (Turner et al., 1998). In summary, research to date has demonstrated that diatoms

86   dominate the coastal Louisiana phytoplankton assemblage (primarily in the spring months), and

87   support higher trophic levels. When diatom growth is suppressed (e.g., in response to silica

88   limitation), other phytoplankton groups dominate and higher trophic levels may be impacted

89   (Turner et al., 1998). The *Deepwater Horizon* oil spill adds another stressor to the system - the

90   toxic effects of oil on the phytoplankton.

91   Ozhan et al. (2014a) reviewed the studies on the effects of the Macondo oil spill on

92   phytoplankton (i.e., those studies presented or published by spring 2014). Some studies reported

93   evidence of an increase in phytoplankton biomass following the Macondo oil spill, as

94   demonstrated by the higher chlorophyll concentrations in the northeastern Gulf of Mexico soon

95   after the wellhead was capped (e.g., Hu et al., 2011). A relaxation of grazing pressures from

96   micro- and macrozooplankton, however, cannot be discounted as the cause of the increase in

97   phytoplankton biomass. Bacterial activity was also higher during and after the spill in surface

98   and deeper waters (e.g., Hazen et al., 2010; Edwards et al., 2011; Ziervogel et al., 2012).

99   Conversely, there is evidence that the oil spill could have been toxic to (some) phytoplankton

100 (based on the *Pyrocystis lunula*-based QwikLite[®] assay; Paul et al., 2013), although laboratory-

101 and microcosm-based studies indicate that the various phytoplankton species have different

102 tolerance levels to the oil and/or dispersant (e.g., Ozhan and Bargu, 2014a, b). In summary,

103 Ozhan et al. (2014a) concluded that the Macondo oil spill likely stimulated some phytoplankton

104 species, while hindering the growth of others.

105   The Ozhan et al. (2014a) review demonstrated that there are no known published data

106 examining *in situ* phytoplankton community responses to the Macondo oil spill. Phytoplankton

107   populations are notoriously patchy (both temporally and spatially), and so it can be difficult to

108   obtain adequate baseline data to access the impacts of the oil spill on the phytoplankton.

109   Fortunately, the ongoing phytoplankton research described earlier has also produced a database

110   of phytoplankton and associated environmental data for coastal Louisiana, of which 20 years

111   (1990 – 2010) are now formatted for a long-term analysis (Parsons, in prep.). Portions of the

112   database have been used in several publications related to harmful algal blooms and silica

113   limitation (e.g., Dortch et al., 1997; Parsons et al., 1998; Dortch et al., 2001; Brown et al., 2006;

114   Parsons et al., 2013), and several presentations addressing long-term trends have also been given

115   (Maier et al., 2002; Parsons et al., 2007, 2008). Recent efforts have updated and formatted the

116   phytoplankton database to allow for more long-term and baseline studies, including comparisons

117   with the Macondo oil spill. The objective of this study, therefore, was to utilize this long-term

118   dataset to determine if any differences were evident in the 2010 phytoplankton versus previous

119   years, thereby recording possible impacts of the Macondo oil spill on the phytoplankton

120   community.

121

122   **2. Methods**

123

124   2.1 *Sample collection and preparation.*

125   We collected surface (0 to 1 m depth) water samples from 1990 to 2010 at station C6* (C6,

126   C6A, C6B, and C6C) on the Louisiana shelf (Fig. 1). This station was sampled most regularly,

127   generally on a monthly basis, and was therefore the focus of this study. Water samples were

128   prepared for microscopy following the methods of Dortch et al. (1997), in which aliquots were

129   preserved in 0.5% glutaraldehyde, stained with 0.03% proflavine hemisulfate, and size-

130   fractionated through 25 mm diameter polycarbonate 8, 3, and 0.2 μm pore-size filters.

131   Microorganism counts from the 0.2 μm pore-size filters were not used in the present analysis

132   because of concerns with reduced fluorescence due to a prolonged time between collection and

133   processing of some samples in our target years (we rely heavily on fluorescence to detect the

134   very small organisms usually encountered on the 0.2um filter and thus were concerned some

135   organisms would be artificially under represented). The phytoplankton and heterotrophs on the 8

136   and 3 μm pore-size filters are less dependent on fluorescence for detection (larger cells) and thus

137   were not compromised by delayed counts.

138   All cells were identified to the lowest practical taxonomic unit and enumerated on the filters

139   using an Olympus BH2-RFCA epifluorescence microscope equipped with blue and green

140   excitation light, and transmitted light when necessary. Only seven microscopists identified and

141   enumerated phytoplankton since 1990, with W. Morrison (2000 to present) and M. Parsons

142   (1996 to 1999) conducting the majority of the counts. An extensive identification logbook

143   complete with descriptions and photographs has been maintained since 1990 and departing

144   microscopists would always work with incoming microscopists to ensure that the counts and

145   identifications were consistent. For those taxa where identifications could not be routinely made

146   (e.g., small (< 10 µm diameter) *Cyclotella* species versus other small centric species), a broader

147   classification was adopted (e.g., centric diatom < 10 µm diameter) to ensure consistency.

148   The abundance of phytoplankton and heterotrophic cells (cells L^{-1}) was calculated based on

149   the number of fields counted per filter and volume of water filtered. The taxa were also sorted

150   into higher taxonomic groupings, e.g., diatoms, dinoflagellates, cyanobacteria, etc. The relative

151   abundance of each taxon and group was calculated by dividing the abundance of each

152   taxon/group (cells L^{-1}) by the overall abundance of phytoplankton or heterotrophs (depending on

153   which group the taxa belonged to). The relative abundance values are presented as percentages

154   of the total cell density. Shannon-Wiener diversity indices (Log_e) and species richness were

155   calculated for the overall baseline data (i.e., the average abundance of each phytoplankton taxa

156   across the baseline years for each month) and for the 2010 data to compare the baseline values

157   versus 2010.

158

159   2.2 *Environmental variables.*

160   The environmental variables collected on the most consistent basis between 1990 and 2010

161   were temperature, salinity, and inorganic nutrients (nitrate, nitrite, ammonium, silicate, and

162   phosphate). Temperature and salinity were measured at each site using a Seabird CTD. The

163   concentrations of inorganic nutrients were determined using either a Technicon AutoAnalyzer II

164   or an Alpkem RFA/2 Rapid Flow Analyzer and were reported in μM units.

165

166   2.3 *Data analysis*.

167   Environmental data from C6* (temperature, salinity, and nutrient variables) were arranged by

168   month for each year in preparation for analysis. Sometimes samples were collected more than

169   once per month, in which case the data would be averaged to provide a monthly value. The

170   months between May and October were compared, because this time frame covers the beginning

171   of oil spill (May) and post-oil spill months (September, October) that were sampled in 2010. No

172   samples were collected in November 2010, and April samples were collected before the oil spill

173   occurred and were, therefore, not included in the analysis. The environmental data were square-

174   root transformed and normalized about parameter means. Using PRIMER 7, a resemblance

175   matrix was generated using Euclidean distance calculations, and a group-average cluster analysis

176   (CLUSTER) was conducted with a similarity profile test (SIMPROF) to determine which years

177   had the most similar environmental conditions to 2010 between the months of May and October.

178   The SIMPROF test was conducted at an $\alpha = 0.05$.

179   Based on these results, phytoplankton and protozoan data from the years most similar (and

180   not statistically different) from 2010 were then analyzed by averaging monthly data across the

181   baseline years (e.g., averaging the May data from the baseline years to compare against data

182   from May 2010). Only taxa that were present in at least 25% of these month periods were used in

183   analysis (i.e., 3 out of the 12 month periods), to reduce the influence such infrequent species

184   would have on the subsequent analyses (Clarke and Gorley 2014). The phytoplankton and

185   protozoan data from the averaged baseline months were then compared to the monthly data from

186   2010 by creating a resemblance matrix (Bray-Curtis similarity), followed by the CLUSTER

187   procedure (group-average) with SIMPROF testing to determine if the phytoplankton and

188   protozoans from 2010 differed from the baseline months. Similarity percentages (SIMPER)

189   analyses were then conducted to determine what taxa were most different between the baseline

190   data and 2010. The plankton data were log-transformed ($\ln(\text{cells } L^{-1} +1)$) prior to the PRIMER

191   analysis.

192

193   **3. Results**

194

195   The results of the CLUSTER and SIMPROF analyses indicated that the years 1994, 1996,

196   1998, 2001, 2003, and 2008 were not statistically different ($p > 0.05$) from 2010 in terms of the

197   environmental parameters tested (temperature, salinity, inorganic nutrients) between the months

198   of May and October (Fig. 2). Additionally, the CLUSTER and SIMPROF results on the

199   baseline-averaged monthly phytoplankton data versus the 2010 monthly phytoplankton data

200 indicated that the phytoplankton assemblage was different in 2010 compared to the baseline data

201 (Fig. 3; $p < 0.05$).

202 The average dissimilarity between the baseline data and the 2010 phytoplankton assemblages

203 was 38.58, with the taxa for which genus and/or species designations could be attributed are

204 presented in Table 1. All diatom taxa analyzed were less abundant in 2010 versus the baseline,

205 with *Chaetoceros affinis*, *Chaetoceros socialis*, and *Heterocapsa rotunda* responsible for most of

206 the decrease between periods. All of the major taxa (i.e., those with species designations; Table

207 1) were less abundant in 2010 compared to the baseline assemblage, with many of them being

208 absent altogether in 2010 (Table 1).

209 We classified the phytoplankton by higher taxa levels, and found that most groups were less

210 abundant in 2010 compared to the baseline period (Table 2). Cyanobacteria, however, were more

211 abundant in 2010 (39% higher; Table 2). Chlorophytes, ciliates, silicoflagellates, and

212 coccolithophorids were entirely absent in the 2010 samples. Euglenoids and phytoflagellates

213 were dramatically less abundant in 2010 versus the baseline (98% and 95%, respectively),

214 whereas diatoms, cryptomonads, and dinoflagellates were moderately less abundant in 2010

215 (69%, 49%, and 47%, respectively). Overall, phytoplankton abundance was 85% lower in 2010

216 versus the baseline. Diatoms, cryptomonads, dinoflagellates, and cyanobacteria were

217 proportionally higher in 2010 versus the baseline, mainly a result of the decreased representation

218 of phytoflagellates in 2010 (Table 2). Phytoplankton were more diverse in 2010 versus the

219 baseline (H' = 2.135 vs 1.503; 42% higher), although species richness was lower in 2010 versus

220 the baseline (56 vs 67; 16% lower).

221 The SIMPER analysis on the protozoan data demonstrated that the protozoan assemblage

222 from 2010 was not as different from the baseline as the phytoplankton were (protozoans had a

223   dissimilarity value of 24.88 versus the 38.58 for the phytoplankton). Five taxa were less

224   abundant in 2010, whereas eight taxa were more abundant in 2010 versus the baseline (Table 3).

225   Several of these taxa were not identified beyond being armored or naked, and by their size

226   (length), which could be a cause of the ambiguity. Those taxa with higher-resolution

227   identifications show the same result, however; some taxa increased (e.g., *Gyrodinium* spp. > 15

228   µm in length) whereas others decreased (e.g., *Amphidinium* spp.). *Hermesinum* (an Ebridian),

229   heterotrophic ciliates, zooflagellates, and naked dinoflagellates < 15 µm in length were also more

230   abundant in 2010 compared to the baseline period (Table 3). An examination at a higher taxa

231   level reveals that heterotrophic ciliates were 62% more abundant in 2010 versus the baseline,

232   whereas heterotrophic dinoflagellates were 33% less abundant in 2010, and zooflagellate

233   abundance was not different in the two time periods (Table 4). The relative abundances among

234   the groups did not change appreciably, with ciliates becoming more abundant as dinoflagellates

235   were less abundant. Overall, the abundance of protozoans was 1% higher in 2010 compared to

236   the baseline period (Table 4).

237   Our results are consistent with many, but not all, previous studies that we examined (Tables 5

238   and 6). Most studies reported a decrease in diatoms and phytoflagellates, and an increase in

239   cyanobacteria, zooflagellates, and heterotrophic ciliates, all of which corroborate our results

240   (Table 5). On a species level, our results were generally in agreement with previous studies,

241   with some exceptions including the diatom, *Thalassionema nitzschioides*, and the dinoflagellate,

242   *Prorocentrum minimum*, where the majority of studies reported an increase in abundance when

243   exposed to oil versus our reported lower abundance in 2010 (Table 6).

244

245   **4. Discussion**

246

247   The overall results of this study suggest that in 2010, there was a dramatic reduction in

248   phytoplankton concentrations (85%) coupled with a shift in the composition of the

249   phytoplankton community (towards diatoms and cyanobacteria; away from ciliates and

250   autotrophic flagellates). This study does not, however, directly link the Macondo oil spill to these

251   results, although other (but not all) studies have reported a reduction of phytoplankton biomass

252   following exposure to crude oil and/or dispersant (Table 5). A review of these other studies

253   indicates that oil exposure can result in an increase in phytoplankton biomass in some cases

254   (suppression of grazing, direct stimulation, and/or increase in nutrients), but not others (e.g., oil

255   concentrations were too high or toxic compounds were present). González et al. (2013) suggest

256   that the apparent lack of agreement among studies is (partly) due to the initial conditions of the

257   phytoplankton community existing before the oil spill (i.e., if the composition is dominated by

258   species sensitive to oil, one would expect an overall decreased in biomass). Additionally, the

259   differing compositions of the various types of crude oil (and oil concentrations) can cause

260   different phytoplankton responses, as can the presence of dispersants (reviewed in Ozhan et al.,

261   2014a).

262   Although our study indicates that there was an overall decrease in phytoplankton biomass

263   following the 2010 Macondo oil spill, the results were primarily due to phytoflagellates

264   decreasing from 4.75×10^7 cells L^{-1} to 2.60×10^6 cells L^{-1}, which is a decrease of 95% (Table 2).

265   Given that heterotroph biomass was not lower in 2010 versus the baseline (Table 4), grazing

266   likely remained consistent and would not resulted in increased grazing pressure on the

267   phytoflagellates. Additionally, baseline environmental conditions were similar to 2010, which

268   cannot explain the lower phytoflagellate biomass in 2010. Rather, the large decrease in

269   phytoflagellate biomass suggests that the Macondo oil spill may have been detrimental to this

270   group. Many, but not all, studies corroborate this conclusion (Table 5).

271   All of the other phytoplankton groups, with the exception of cyanobacteria, also decreased in

272   abundance in 2010 (Table 2), resulting in a decrease of 65% when compared with the baseline

273   period when phytoflagellates are excluded from the calculation. This result suggests that while

274   the phytoflagellate impact was severe and caused most of the decrease in overall phytoplankton

275   abundance, the decrease was still significant for the other groups. The results of other studies

276   concur with these findings in most cases (Table 5). Interestingly, species diversity was higher in

277   2010 (H' = 2.153) versus the baseline (H' = 1.503), although species richness was lower (56

278   versus 67). These results suggest that there were fewer dominant species present in 2010, as

279   depicted by the lack of *Chaetoceros* species in 2010 (e.g., *C. affinis*, *C. socialis*, and *C. debilis*;

280   Table 1). Vargo et al. (1982) also observed higher phytoplankton diversity in the oil treatments

281   of their experiment, although Nomura et al. (2007) reported higher species richness in control

282   treatments versus oil and/or dispersant treatments in their study.

283   Our protozoan findings are opposite of the phytoplankton results, in that there was an overall

284   increase in these heterotrophs in 2010 versus the baseline period, albeit only a 1% increase

285   (Table 4). As was the case with the phytoplankton results, some previous studies were in

286   agreement with our results whereas others were not (Table 5). For example, Dale (1987)

287   observed a decline in heterotrophic ciliates exposed to oil, whereas we found higher numbers of

288   heterotrophic ciliates in 2010. Gertler et al. (2010), however, observed an increase in

289   heterotrophic ciliates exposed to oil (in line with our results), accompanied by an increase in

290   heterotrophic flagellates (in agreement with our findings). In mesocosm studies, Jung et al.

291   (2012) also documented an increase in heterotrophic flagellates, which they attributed to an

292   increase in bacteria (a food source) that were stimulated by the oil and oil + dispersant

293   treatments. The lower numbers of heterotrophic dinoflagellates observed in our study suggests

294   that these heterotrophs may have been hindered by potential exposure to oil (and possibly

295   dispersant). The fact that heterotrophic ciliates and zooflagellates increased in abundance

296   suggests that bacterial densities may have been higher in 2010, but the lack of bacterial density

297   data (from the baseline years and 2010) prevents further examination of this possibility.

298   An examination of the literature revealed similar results for individual phytoplankton taxa;

299   our results are corroborated by some, but not all, studies (Table 6). For example, only one out of

300   four studies (Nomura et al. 2007) observed a decrease in the diatom *Thalassionema nitzschioides*

301   when exposed to oil (Table 6). Similarly, only one out of three studies (Ozhan and Bargu 2014b)

302   observed a decrease in the dinoflagellate, *Prorocentrum minimum* (Table 6).

303   The results of our analysis suggest that the Macondo oil spill may have had an impact on the

304   phytoplankton community in Louisiana coastal waters west of the Mississippi River. The overall

305   phytoplankton abundance was almost an order of magnitude lower (a decrease of 85%)

306   compared to the baseline years, primarily due to lower numbers of phytoflagellates, although all

307   phytoplankton groups decreased in abundance with the exception of cyanobacteria (Table 2).

308   The trophic impacts of this decrease in phytoplankton biomass remain unknown, although such a

309   large loss of trophic level one biomass would hypothetically cascade to higher trophic levels.

310   Our results are in agreement with other studies in some cases, but are conflicting in others.

311   Interestingly, our results are in almost complete disagreement with Nomura et al. (2007), which

312   could be due to different oil sources (purported Macondo oil versus Bunker A), or experimental

313   methods employed (*in situ* versus mesocosm). Such variability in methods and source oils

314 demonstrate the need to examine phytoplankton responses to oil (and dispersant) exposures on a

315 case-by-case basis (Ozhan et al. 2014a).

316   Admittedly, this study is indirect, relying on an analysis of baseline data versus

317 phytoplankton data collected during and immediately following the Macondo oil spill. There are

318 means, however, to further examine the direct impacts of Macondo oil exposure to Louisiana

319 phytoplankton, either through additional lab-based exposure experiments (e.g., Ozhan and

320 Bargu, 2014a), or through the examination of additional field samples from 2010 (Parsons et al.

321 in prep.). This study, however, represents the best opportunity to date of utilizing available

322 baseline data to examine the impacts of the Macondo oil spill on local phytoplankton

323 communities, and the results suggest that the impacts were plausible.

324

325 **Acknowledgments**

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336 **References**

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Table 1. The results of a SIMPER (similarity percentage) analysis displaying the phytoplankton taxa for which genus and/or species designations could be attributed, and were moderately abundant in the samples ($>10^3$ cells L^{-1} total abundance in baseline or 2010). The class of each phytoplankton taxon is given. The abundance values for the baseline and 2010 are displayed as cells L^{-1}, and were computed as total abundance across all months for the baseline and 2010. The average dissimilarity is based on Bray-Curtis similarity, and is computed by calculating the dissimilarity between the overall baseline average (i.e., species abundance averaged May – October across baseline years) versus the dissimilarity in 2010 for each species. The % contribution values indicate how much each taxon contributes to the overall dissimilarities between the two time frames.

taxon	class	baseline abundance	2010 abundance	average dissimilarity	% contribution
Chaetoceros affinis	diatom	5.94×10^7	0.00	1.14	2.95
Chaetoceros socialis	diatom	1.44×10^7	0.00	1.04	2.7
Heterocapsa rotundata	dinoflagellate	7.98×10^5	0.00	0.85	2.2
Chaetoceros debilis	diatom	6.60×10^5	0.00	0.83	2.16
Chaetoceros diadema	diatom	3.85×10^5	0.00	0.8	2.07
Asterionellopsis glacialis	diatom	2.68×10^5	0.00	0.77	2.01
Dinophysis caudata	dinoflagellate	2.45×10^5	0.00	0.77	1.99

Chaetoceros laciniosus	diatom	2.33×10^5	0.00	0.76	1.98
Mesodinium rubrum	ciliate	2.18×10^5	0.00	0.76	1.97
Chaetoceros didymus	diatom	1.75×10^5	0.00	0.75	1.93
Asterionellopsis kariana	diatom	1.61×10^5	0.00	0.74	1.92
Chaetoceros lorenzianus	diatom	1.40×10^5	0.00	0.73	1.89
Hemiaulus sinensis	diatom	1.05×10^5	0.00	0.71	1.84
Chaetoceros constrictus	diatom	9.20×10^4	0.00	0.7	1.82
Eucampia cornuta	diatom	2.43×10^4	0.00	0.61	1.59
Ceratium fusus	dinoflagellate	1.84×10^4	0.00	0.59	1.54
Stauropsis membranacae	diatom	1.90×10^4	0.00	0.6	1.54
Ditylum brightwellii	diatom	1.55×10^4	0.00	0.58	1.51
Ceratium tripos	dinoflagellate	1.16×10^4	0.00	0.56	1.46
Prorocentrum micans	dinoflagellate	1.21×10^6	3.65×10^2	0.55	1.42
Cylindrotheca closterium	diatom	4.74×10^5	3.65×10^2	0.48	1.25
Rhizosolenia setigera	diatom	4.17×10^5	7.28×10^2	0.43	1.11
Skeletonema costatum	diatom	5.84×10^6	2.20×10^4	0.38	0.97

Chaetoceros decipiens	diatom	9.65×10^5	4.11×10^3	0.37	0.95
Torodinium spp.	dinoflagellate	6.17×10^4	7.28×10^2	0.3	0.78
Lioloma pacificum	diatom	2.68×10^5	3.64×10^3	0.29	0.75
Leptocylindrus danicus	diatom	1.23×10^6	2.10×10^4	0.27	0.71
Cerataulina pelagica	diatom	3.58×10^6	7.92×10^4	0.26	0.67
Karenia brevis	dinoflagellate	4.39×10^4	1.09×10^3	0.25	0.65
Prorocentrum gracile	dinoflagellate	9.20×10^4	2.19×10^3	0.25	0.65
Chaetoceros compressus	diatom	1.56×10^6	4.09×10^4	0.25	0.64
Dactyliosolen fragilissimus	diatom	1.31×10^7	7.67×10^5	0.19	0.5
Guinardia striata	diatom	6.67×10^5	4.22×10^4	0.19	0.48
Guinardia delicatula	diatom	2.79×10^6	2.03×10^5	0.18	0.46
Leptocylindrus minimus	diatom	1.18×10^6	8.84×10^4	0.17	0.45
Odontella sinensis	diatom	1.05×10^5	9.41×10^3	0.16	0.42
Gymnodinium cf. *pulchellum*	dinoflagellate	2.58×10^5	2.56×10^4	0.16	0.4
Ceratium hircus	dinoflagellate	2.09×10^5	2.27×10^4	0.15	0.39
Pseudo-nitzschia spp.	diatom	2.21×10^7	2.42×10^6	0.15	0.38

Proboscia alata	diatom	1.34×10^6	2.22×10^5	0.12	0.32
Prorocentrum minimum	dinoflagellate	9.27×10^5	1.66×10^5	0.12	0.3
Guinardia flaccida	diatom	1.68×10^5	3.19×10^4	0.11	0.29
Pseudosolenia calcar-avis	diatom	2.36×10^5	5.42×10^4	0.1	0.26
Trichodesmium spp.	cyanobacteria	1.36×10^5	3.93×10^4	0.08	0.22
Thalassionema nitzschioides	diatom	1.30×10^6	3.62×10^5	0.09	0.22
Akashiwo sanguinea	dinoflagellate	3.45×10^4	1.05×10^4	0.08	0.21
Heterocapsa niei	dinoflagellate	3.70×10^5	1.23×10^5	0.07	0.19
Chaetoceros curvisetus	diatom	5.24×10^5	2.01×10^5	0.06	0.17
Hemiaulus hauckii	diatom	4.53×10^4	2.10×10^4	0.05	0.13
Scrippsiella spp.	dinoflagellate	1.68×10^5	1.11×10^5	0.03	0.07

Table 2. Summary of abundance changes of the phytoplankton classes differentiating the baseline assemblage versus 2010. The class abundance values are given as cells L^{-1} and are summed across all six months analyzed in the study for the baseline and 2010. The % change was calculated by dividing the difference of the 2010 and baseline abundance by the baseline abundance for each class. Relative abundance values are the proportion of total phytoplankton represented by each class.

class	baseline abundance	2010 abundance	% change	baseline relative abundance	2010 relative abundance
autotroph – other	1.68×10^5	0	- 100%	0.2%	0.0%
chlorophytes	1.08×10^6	0	- 100%	1.5%	0.0%
ciliates	2.12×10^4	0	- 100%	0.05%	0.0%
coccolithophorids	7.79×10^2	0	- 100%	0.01%	0.0%
cryptomonads	3.35×10^6	1.72×10^6	- 49%	4.8%	16.2%
cyanobacteria	5.15×10^5	7.18×10^5	+ 39%	0.7%	6.8%
diatoms	1.71×10^7	5.22×10^6	- 69%	24.3%	49.3%
dinoflagellates	6.27×10^5	3.34×10^5	- 47%	0.9%	3.2%
euglenoids	7.23×10^3	1.33×10^2	- 98%	0.02%	0.0%
phytoflagellates	4.75×10^7	2.60×10^6	- 95%	67.5%	24.5%

silicoflagellates	1.89×10^3	0	- 100%	0.02%	0.0%
Total	7.04×10^7	1.06×10^7	- 85%	100%	100%

Table 3. The results of a SIMPER (similarity percentage) analysis displaying the total overall abundance of the heterotrophic taxa differentiating the baseline assemblage versus 2010. The class of each taxon is given. The abundance values are given as cells L^{-1}. The average dissimilarity is based on Bray-Curtis similarity, and is computed by calculating the dissimilarity between months (May – October) of the baseline versus 2010. The % contribution values indicate how much each taxon contributes to the overall dissimilarities between the two time frames.

taxon	class	baseline abundance	2010 abundance	average dissimilarity	% contribution
dinoflagellate – naked, > 15 µm in length	dinoflagellate	1.59×10^5	0	5.68	23.19
dinoflagellate – other, > 15 µm in length	dinoflagellate	3.01×10^4	0	4.89	19.97
Protoperidinium spp.	dinoflagellate	7.54×10^2	0	3.14	12.83
Amphidinium spp.	dinoflagellate	7.41×10^2	0	3.13	12.80
Gyrodinium spp. other	dinoflagellate	6.00×10^2	0	3.03	12.39
Hermesinum spp.	Ebridian	1.80×10^1	2.00×10^3	2.21	9.02
Gyrodinium spp. > 15 µm in length	dinoflagellate	5.79×10^3	2.86×10^4	0.76	3.09

Gyrodinium spp. < 15 µm in length	dinoflagellate	2.68×10^3	8.53×10^3	0.55	2.25
dinoflagellate – armored, < 15 µm in length	dinoflagellate	3.82×10^4	9.02×10^4	0.41	1.67
dinoflagellate – armored, > 15 µm in length	dinoflagellate	7.70×10^3	1.50×10^4	0.31	1.28
ciliate	ciliate	7.21×10^4	1.17×10^5	0.23	0.93
dinoflagellate – naked, < 15 µm in length	dinoflagellate	7.83×10^4	1.04×10^5	0.14	0.55
zooflagellate , < 10 µm in length	composite	7.87×10^7	7.97×10^7	0.01	0.02

Table 4. Summary of abundance changes of the heterotroph classes differentiating the baseline

assemblage versus 2010. The abundance values are given as cells L^{-1} and are summed across all

six months analyzed in the study for the baseline and 2010. The % change was calculated by

dividing the difference of the 2010 and baseline abundance by the baseline abundance for each

taxon.

class	baseline abundance	2010 abundance	% change	baseline relative abundance	2010 relative abundance
ciliates	7.21×10^4	1.17×10^5	+ 62%	0.1%	0.2%
dinoflagellates	3.65×10^5	2.46×10^5	- 33%	0.5%	0.3%
zooflagellates	7.87×10^7	7.97×10^7	+ 1%	99.4%	99.5%
Total	7.92×10^7	8.01×10^7	+ 1%	100%	100%

Table 5. A comparison of the results of this study versus other studies conducted on phytoplankton and protozoan (higher taxa) exposures to crude oil and/or dispersant. For this study, a decrease refers to lower abundance in 2010 versus the baseline data (and vice versa for increase). For the other studies, a decrease indicates a lower abundance when exposed to oil (and/or dispersant) during a spill or in a mesocosm experiment. "Resistant" means the taxon was not affected by the oil. WAF = Water Accommodated Fraction; WSF = Water Soluble Fraction.

Taxa	This study	Other studies	Their results	Petroleum type	Comments
phytoplankton	decrease	Taş et al. (2011)	decrease	*Volgoneft-248* (heavy fuel oil)	
		Cabioch et al. (1981)	mixed	*Amoco Cadiz* (light crude oil)	Reduced biomass near spill; increase farther away
		Johansson et al. (1980)	increase	*Tsesis* (no. 5 fuel oil)	Increase could have been due to reduced grazing
		Hu et al. (2011)	increase	Macondo (MC) 252	River discharge could have played a role
diatoms	decrease	Taş et al. (2011)	decrease	*Volgoneft-248*	

			(heavy fuel oil)	
		Harrison et al. (1986)	decrease	Prudhoe Bay crude oil and Corexit® 9527	Mesocosm experiments; shift from diatoms to microflagellates
		Pérez et al. (2010)	decrease	naphthalene, phenanthrene, pyrene, fluoranthene	
		Gilde and Pickney (2012)	resistant	South Louisiana crude	
		Nomura et al. (2007)	decrease	Bunker A oil (and Corexit®)	
		González et al. (2009)	resistant	*Prestige* - WAF	
		Ozhan and Bargu (2014a)	resistant	South Louisiana crude	
dinoflagellates	decrease	Taş et al. (2011)	increase	*Volgoneft-248* (heavy fuel oil)	

phytoflagellates	decrease	Sargian et al. (2007)	decrease	Patagonian crude oil - WSF	Smaller cells more sensitive
		Echeveste et al. (2010)	decrease	pyrene, phenanthrene	Smaller cells more sensitive
		Smith (1968)	decrease	*Torrey Canyon* (Kuwait crude oil)	Prasinophytes
		Harrison et al. (1986)	increase	Prudhoe Bay crude oil and Corexit® 9527	Mesocosm experiments; shift from diatoms to microflagellates
		Pérez et al. (2010)	decrease	naphthalene, phenanthrene, pyrene, fluoranthene	
		Nomura et al. (2007)	increase	Bunker A oil (and Corexit®)	
autotrophic ciliates	decrease	Ortmann et al. (2012)	decrease	Corexit® 9500A and MC252 dispersed oil	Mesocosm experiments
		Pérez et al. (2010)	decrease	naphthalene,	

				phenanthrene, pyrene, fluoranthene	
cryptomonads	decrease	Gilde and Pickney (2012)	decrease	South Louisiana crude	
cyanobacteria	increase	Gilde and Pickney (2012)	increase	South Louisiana crude	
euglenophytes	decrease	Gilde and Pickney (2012)	resistant	South Louisiana crude	
		Nomura et al. (2007)	resistant	Bunker A oil (and Corexit®)	
chlorophytes	decrease	Gilde and Pickney (2012)	resistant	South Louisiana crude	
heterotrophic flagellates	increase	Jung et al. (2012)	increase	Iranian heavy crude (and Hi-Clean dispersant)	Could have been stimulated by an increase in food (bacteria)
		Gertler et al. (2010)	increase		

heterotrophic	increase	Gertler et al. (2010)	increase	Ekofisk crude oil
ciliates		Dale (1987)	decrease	

Table 6. A comparison of the results of this study versus other studies conducted on phytoplankton and protozoan (species-level) exposures to crude oil and/or dispersant. For this study, a decrease refers to lower abundance in 2010 versus the baseline data (and vice versa for increase). For the other studies, a decrease indicates a lower abundance when exposed to oil (and/or dispersant) during a spill or in a mesocosm experiment. "Resistant" means the taxon was not affected by the oil. WAF = Water Accommodated Fraction; WSF = Water Soluble Fraction.

Taxa	This study	Other studies	Their results	Petroleum type
Diatoms				
Cerataulina pelagica	decrease	Varela et al. (2006)	decrease	*Prestige* (heavy fuel oil)
Chaetoceros compressus	decrease	Nomura et al. (2007)	resistant	Bunker A oil (and Corexit[®])
		Varela et al. (2006)	decrease	*Prestige* (heavy fuel oil)
Dactyliosolen fragilissimus	decrease	Nomura et al. (2007)	decrease	Bunker A oil (and Corexit[®])
Skeletonema costatum	decrease	Østgaard et al. (1984)	decrease	Ekofisk crude oil
Thalassionema nitzschioides	decrease	Nomura et al. (2007)	decrease	Bunker A oil (and Corexit[®])
		Varela et al. (2006)	increase	*Prestige* (heavy fuel oil)
		Jung et al. (2012)	increase	Iranian heavy crude (and Hi-Clean

				dispersant)
		González et al. (2009)	increase	*Prestige* - WAF
Guinardia delicatula	decrease	Nomura et al. (2007)	decrease	Bunker A oil (and Corexit[®])
		Jung et al. (2012)	increase	Iranian heavy crude (and Hi-Clean
				dispersant)
Guinardia striata	decrease	Varela et al. (2006)	decrease	*Prestige* (heavy fuel oil)
		Ozhan and Bargu (2014a)	decrease	South Louisiana crude
Leptocylindrus danicus	decrease	Ozhan and Bargu (2014a)	decrease	South Louisiana crude
Leptocylindrus minimus	decrease	Varela et al. (2006)	increase	*Prestige* (heavy fuel oil)
Dinoflagellates				
Heterocapsa niei	decrease	Varela et al. (2006)	decrease	*Prestige* (heavy fuel oil)
Karenia brevis	decrease	Ozhan and Bargu (2014b)	decrease	South Louisiana crude
Prorocentrum micans	decrease	Taş et al. (2011)	increase	*Volgoneft-248* (heavy fuel oil)
Prorocentrum minimum	decrease	Ozhan and Bargu (2014b)	decrease	South Louisiana crude
		Morales-Loo and Goutx (1990)	increase	Mexican crude (Isthmus Cactus – WSF)
		Okaichi (1983)	increase	Bunker C oil

| *Torodinium* spp. | decrease | Varela et al. (2006) | increase | *Prestige* (heavy fuel oil) |

Ciliates

| *Mesodinium rubrum* | decrease | Dale (1987) | decrease | Ekofisk crude oil |

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Fig. 1. Coastal Louisiana showing the location of C6* sampled in this study. C6* includes stations C6, C6A, C6B, and C6C.

Fig. 2. Group average cluster analysis of the environmental data (by year) displaying SIMPROF groupings (dashed lines connect statistically similar years). Euclidean distances were used for the cluster analysis. The cluster grouping containing 2010 and similar years is delineated by the box encompassing the respective years on the x-axis.

Fig. 3. Group average cluster analysis of the phytoplankton data (by year) displaying SIMPROF groupings (dashed lines connect statistically similar years). Bray-Curtis similarity values were used for the cluster analysis.
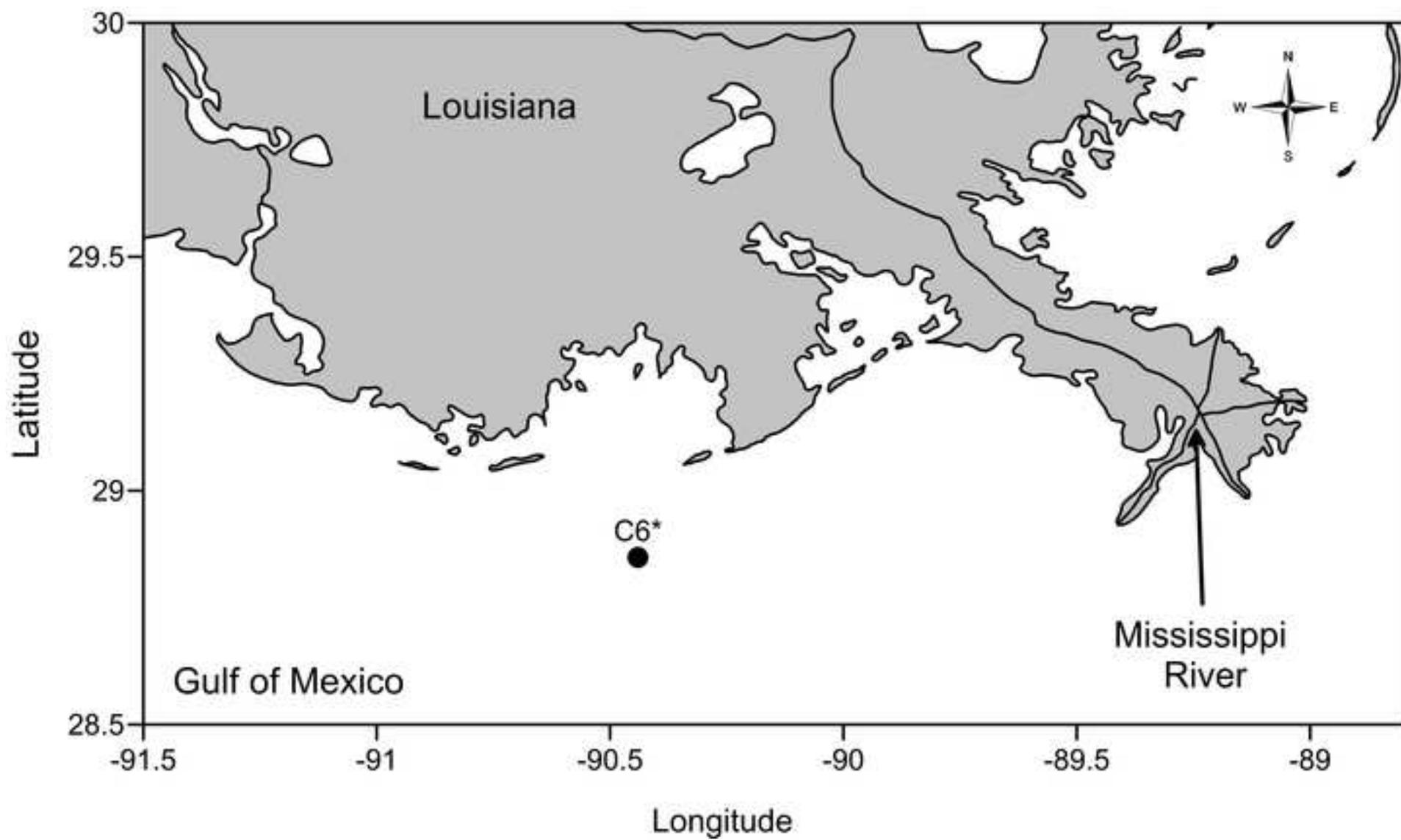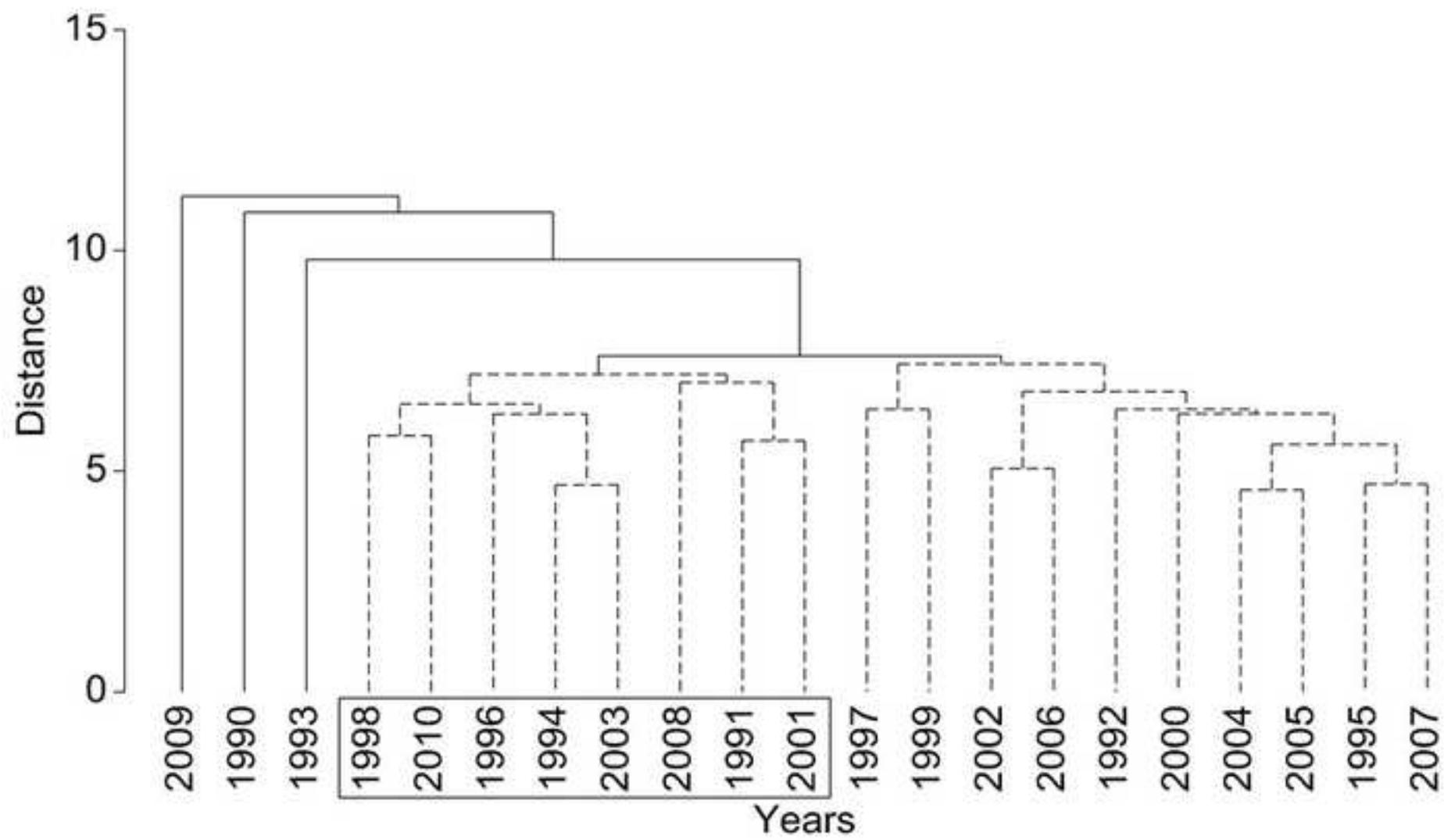
Figure 1

Figure 2

Figure 3