An enigmatic decoupling between heat stress and coral bleaching on the Great Barrier Reef

Thomas DeCarlo [Corresp., 1, 2], Hugo B Harrison [3]

[1] Red Sea Research Center, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia

[2] Australian Research Council Centre of Excellence for Coral Reef Studies, University of Western Australia, Crawley, Australia

[3] Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Australia

Corresponding Author: Thomas DeCarlo
Email address: thomas.decarlo@kaust.edu.sa

Ocean warming threatens the functioning of coral reef ecosystems by inducing mass coral bleaching and mortality events. The link between temperature and coral bleaching is now well-established based on observations that mass bleaching events usually occur when seawater temperatures are anomalously high. However, times of high heat stress but without coral bleaching are equally important because they can inform an understanding of factors that mitigate temperature-induced bleaching. Here, we investigate the absence of mass coral bleaching on the Great Barrier Reef (GBR) during austral summer 2004. Using four gridded sea surface temperature (SST) data products, validated with *in situ* temperature loggers, we demonstrate that the summer of 2004 was among the warmest summers of the satellite era (1982-2017) on the GBR. At least half of the GBR experienced temperatures that were high enough to initiate bleaching in other years, yet mass bleaching was not reported during 2004. The absence of bleaching is not fully explained by wind speed or cloud cover. Rather, 2004 is clearly differentiated from bleaching years by the slow speed of the East Australian Current (EAC) offshore of the GBR. An anomalously slow EAC during summer 2004 may have dampened the upwelling of nutrient-rich waters onto the GBR shelf, potentially mitigating bleaching due to the lower susceptibility of corals to heat stress in low-nutrient conditions. Although other factors such as irradiance or acclimatization may have played a role in the absence of mass bleaching, 2004 remains a key case study for demonstrating the dynamic nature of coral responses to marine heatwaves.

1 An enigmatic decoupling between heat stress and coral bleaching on the Great Barrier Reef

3 Thomas M. DeCarlo[1,2]* and Hugo B. Harrison[3]

5 [1]Red Sea Research Center, Division of Biological and Environmental Science and Engineering,

6 King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia

7 [2]Australian Research Council Centre of Excellence for Coral Reef Studies, University of

8 Western Australia, Crawley, Australia

9 [3]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook

10 University, Townsville, Australia

12 *Corresponding author: Dr. Thomas M. DeCarlo

13 thomas.decarlo@kaust.edu.sa +966567272157

14 **Abstract**

15 Ocean warming threatens the functioning of coral reef ecosystems by inducing mass coral

16 bleaching and mortality events. The link between temperature and coral bleaching is now well-

17 established based on observations that mass bleaching events usually occur when seawater

18 temperatures are anomalously high. However, times of high heat stress but without coral

19 bleaching are equally important because they can inform an understanding of factors that

20 mitigate temperature-induced bleaching. Here, we investigate the absence of mass coral

21 bleaching on the Great Barrier Reef (GBR) during austral summer 2004. Using four gridded sea

22 surface temperature (SST) data products, validated with *in situ* temperature loggers, we

23 demonstrate that the summer of 2004 was among the warmest summers of the satellite era (1982-

24 2017) on the GBR. At least half of the GBR experienced temperatures that were high enough to

25 initiate bleaching in other years, yet mass bleaching was not reported during 2004. The absence

26 of bleaching is not fully explained by wind speed or cloud cover. Rather, 2004 is clearly

27 differentiated from bleaching years by the slow speed of the East Australian Current (EAC)

28 offshore of the GBR. An anomalously slow EAC during summer 2004 may have dampened the

29 upwelling of nutrient-rich waters onto the GBR shelf, potentially mitigating bleaching due to the

30 lower susceptibility of corals to heat stress in low-nutrient conditions. Although other factors

31 such as irradiance or acclimatization may have played a role in the absence of mass bleaching,

32 2004 remains a key case study for demonstrating the dynamic nature of coral responses to

33 marine heatwaves.

34 **Introduction**

35   Mass coral bleaching events have increased in frequency since the 1980s in concert with

36 rising sea surface temperature (SST) (Donner et al. 2017; Hughes et al. 2018a). Anomalously

37 high summertime temperatures disrupt the symbiosis between coral host and zooxanthellae

38 symbionts, leading to "bleaching" as the colorfully-pigmented symbionts are expelled and the

39 coral skeleton is revealed (Jokiel and Coles 1977; Glynn 1983; Gates et al. 1992). The

40 correspondence of mass bleaching events with anomalously high SST is often considered

41 indicative of a direct relationship between heat stress and coral bleaching (*e.g.* Glynn 1993;

42 Heron et al. 2016; Hughes et al. 2017, 2018a). However, the severity of mass bleaching events

43 varies in space and time, and a range of environmental factors besides temperature can affect the

44 bleaching sensitivity of corals. For example, changes in solar irradiance (Brown 1997; Dunne

45 and Brown 2001), and nutrient concentrations (Wooldridge 2009; Cunning and Baker 2012;

46 Wiedenmann et al. 2013; Vega Thurber et al. 2014) or ratios (Wiedenmann et al. 2013; Morris et

47 al. 2019), can either exacerbate or ameliorate temperature stress to determine the severity and

48 extent of bleaching.

49   Four mass bleaching events have been recorded on Australia's iconic Great Barrier Reef

50 (GBR) and all have been associated with anomalously high SST. The summer of 1997-1998 was,

51 at that time, the most extensive bleaching event observed on the GBR, with ~42% of reefs

52 showing signs of bleaching (Berkelmans and Oliver 1999). The GBR experienced another large-

53 scale bleaching event just four years later in 2002, which affected ~54% of reefs (Berkelmans et

54 al. 2004). In both cases, severe bleaching was predominantly observed on coastal reefs

55 (Berkelmans et al. 2004). The most severe and widespread bleaching on the GBR occurred in

56 2016, when comparative surveys suggest approximately 91% of reefs showed signs of bleaching,

57 with severe bleaching leading to widespread mortality in the northern third of the GBR (Hughes

58 et al. 2017). This was followed by the first recorded back-to-back bleaching in 2017, which

59 affected at least one third of the GBR and the remote atolls in the Coral Sea (Hughes and Kerry

60 2017; Harrison et al. 2018). In each case, the geographic footprint of bleaching on the GBR was

61 strongly correlated with the intensity and duration of SST anomalies (Hughes et al. 2017), a

62 pattern that mirrors the response of corals to SST anomalies globally (Hughes et al. 2018a). It is

63 also important to note that extensive bleaching and mortality was observed in 1982 at the

64 majority of reefs visited by researchers (Harriott 1985; Oliver 1985), yet these observations were

65 restricted to just 14 reefs in the central GBR and Lizard Island in the north, making it difficult to

66 distinguish whether 1982 was a minor or major bleaching event.

67   Observations of bleaching events have informed a strong causal link between SST

68 anomalies and the severity of bleaching (Glynn 1983; Bruno et al. 2001; Shuail et al. 2016;

69 Barkley et al. 2018; Hughes et al. 2018b), but heat stress has not always led to bleaching (Guest

70 et al. 2012; Pratchett et al. 2013). Assessments of coral bleaching sensitivities have typically

71 been retrospective; identifying the conditions that were necessary to trigger bleaching. This has

72 led to clearly defined temperature thresholds above which bleaching is expected (*e.g.* Glynn

73 1983; Shuail et al. 2016; Hughes et al. 2017). However, it is critical to consider periods when

74 these thresholds were crossed, but bleaching did not occur. Such cases are important because

75 they can inform our understanding of coral tolerance to heat stress, thereby assisting efforts to

76 predict when and where to find the most resilient coral reef ecosystems (Beyer et al. 2018;

77 Hoegh-Guldberg et al. 2018). Indeed, case studies documenting the absence of bleaching under

78 anomalously high summer SST have attributed the corals' tolerance to acclimatization (Guest et

79 al. 2012; Gintert et al. 2018), adaptation (Osman et al. 2018), high frequency temperature

80   variability (Safaie et al. 2018), night-time cooling (Richards et al. 2019), cloud cover (Skirving et

81   al. 2017), or unique environmental settings such as exposure to internal waves (Schmidt et al.

82   2016; DeCarlo et al. 2017; Green et al. 2019; Reid et al. 2019).

83   Despite the importance of times with high temperatures but not coral bleaching, such

84   events can be difficult to identify due to reporting bias. Bleaching databases that document the

85   occurrence of bleaching rather than absence thereof are of limited utility because they rarely

86   distinguish between the absence of bleaching and the absence of observations (Donner et al.

87   2017; Oliver et al. 2018). We are therefore limited to case studies where bleaching absence was

88   either directly reported (*e.g.,* Guest et al. 2012; Pratchett et al. 2013; DeCarlo et al. 2017; Gintert

89   et al. 2018) or to locations with continuous long-term monitoring programs such as the GBR.

90   Here, we investigate the conspicuous absence of severe coral bleaching on the GBR

91   during the austral summer of 2004. This was one of the warmer summers–and perhaps *the*

92   *warmest summer* – of the satellite era (1982-2017) on the GBR (Fig. 1), but widespread or severe

93   bleaching was not reported. We first use a suite of 52 *in situ* temperature loggers deployed across

94   the GBR in 2004 to validate satellite-derived SST for capturing reef-water temperatures, and to

95   identify which of four satellite SST products best represents 2004 GBR heat stress. We then

96   investigate potential reasons for the absence of bleaching reports during 2004, including the

97   possibility that widespread bleaching occurred but went unnoticed, that some environmental

98   factor mitigated heat stress, or that corals acclimatized following previous bleaching events in

99   1998 and 2002.

100

101   **Materials and Methods**

102   *Data sources of satellite-derived sea surface temperatures*

103   *In situ* temperature logger data were acquired from the Australian Institute of Marine

104   Science (AIMS 2018) for all available GBR and Coral Sea sites during the austral summer of

105   2004 (n = 52 loggers with continuous measurements throughout the summer). Additionally,

106   temperature data for mass bleaching events on the GBR (1998, 2002, 2016, 2017; see

107   Berkelmans and Oliver 1999; Berkelmans et al. 2004; Hughes et al. 2018a; Oliver et al. 2018)

108   were downloaded for all loggers deployed in both 2004 and at least one bleaching year.

109   Temporal resolutions typically ranged from 10 to 30 minutes, and nominal water depths varied

110   from 0 to 20 m. We note that nominal depths of 0 m indicate deployment within a few meters of

111   the surface, although the specific depth was not recorded (personal communications with AIMS

112   staff).

113   Gridded SST data were acquired for heat stress analyses from four sources: the National

114   Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch (CRW) "CoralTemp"

115   version 1.0 (NOAA Coral Reef Watch; Liu et al. 2014; Heron et al. 2016), Optimum

116   Interpolation SST (OI-SSTv1) (Reynolds et al. 2002), the higher-resolution OI-SSTv2 that is

117   based primarily on the Advanced Very High Resolution Radiometer (AVHRR) satellite

118   (Reynolds et al. 2007; Banzon et al. 2016), and the Canadian Meteorological Center (CMC,

119   2012). It is important to note that these SST products are not entirely independent because they

120   share some of the same data (*e.g.* Liu et al. 2014), but they nevertheless serve as alternative

121   estimates of SST that can be validated with *in situ* measurements. We refer to these as satellite-

122   SST products, although the OI products blend measurements from satellites, ships, and buoys

123   (Reynolds et al. 2002; Banzon et al. 2016). Both OI-SSTv1 and OI-SSTv2 cover the period

124   1982-2017, whereas CRW covers 1985-2017, and CMC covers 1993-2017. The temporal

125   resolution is daily for CRW, OI-SSTv2, and CMC, and weekly for OI-SSTv1. CRW has the

126   highest spatial resolution at 0.05° (approximately 5 km), OI-SSTv2 is at 0.25°, CMC is at 0.2°

127   and OI-SSTv1 is at 1° resolution. We re-gridded CMC, OI-SSTv1, and OI-SSTv2 to the same

128   0.05° grid used by CRW with simple linear interpolation. This enabled direct pixel-by-pixel

129   comparisons among the SST products, even though the true resolution of these products were

130   coarser than the 0.05° grid.

131   An additional analysis was conducted on SST data from the HadISST product (Rayner et

132   al. 2003). However, since HadISST is resolved only monthly, it is poorly suited for the

133   calculation of summertime heat stress, which often arises from anomalously warm days or

134   weeks. Nevertheless, HadISST allows a separate analysis of SST variability over time for

135   comparison to the four main SST products used in this study.

136

137   *Data sources of other environmental variables*

138   Outgoing longwave radiation (OLR) data were acquired from the National Center for

139   Atmospheric Research (NCAR) (Liebmann and Smith 1996). Surface wind data were acquired

140   from the National Center for Environmental Prediction (NCEP)/NCAR Reanalysis (Trenberth

141   and Olson 1988; Kalnay et al. 1996). Both OLR and wind datasets are of daily temporal

142   resolution and 2.5° spatial resolution, which is much coarser than the scale of individual coral

143   reefs. Photosynthetically active radiation (PAR) data (Frouin et al. 2002) were acquired from the

144   Moderate Resolution Imaging Spectroradiometer (MODIS) Terra (2002-2017) and SeaWiFS

145   (1998) satellites as 8-day composites at 9-km resolution.

146   Ocean currents and temperature, sea surface height (SSH), and surface wind stress were

147   acquired from the Simple Ocean Data Assimilation (SODA) version 3.3.1 at monthly temporal

148   resolution and 0.25° spatial resolution (Carton et al. 2018). SODA is a state-of-the-art ocean

149   modeling system constrained by observations when and where they are available, and it is well-

150   suited for quantifying temporal changes in sea level and ocean circulation in the Coral Sea and

151   along the Australian continent (Chepurin et al. 2014; Zhai et al. 2014).

152   Sub-daily, high-resolution (0.25°) wind speeds during austral summer 2004 were

153   acquired from QuikSCAT (Perry 2001). These data were used to assess the wind fields during

154   major cyclones near the GBR or Coral Sea.

155   We used the World Atlas of Coral Reefs for locations of the reefs of the GBR,

156   downloaded from ReefBase (Spalding et al. 2001).

157

158   *Calculation of degree heating weeks*

159   We calculated degree heating weeks (DHW) to assess heat stress using both *in situ*

160   loggers and satellite SST products. First, we calculated "Hotspots" as:

161   *Hotspots = temperature – MMM*   (1)

162   where temperature is the daily (CRW and OI-SSTv2), weekly (OI-SSTv1), or monthly

163   (HadISST) mean temperature and MMM is the maximum monthly mean. For consistency, we

164   used the MMM climatology from NOAA CRW CoralTemps when calculating Hotspots from all

165   temperature sources. We assessed whether this approach adds bias to OI-SSTv2 heat stress

166   metrics by comparing the climatologies calculated from CRW and OI-SSTv2 (Supplemental

167   Figs. S1 and S2). However, we found there was not a systematic offset between the two

168   climatologies, meaning that the OI-SSTv2 Hotspots calculated with the CRW climatology are

169   not substantially influenced by this approach (Supplemental Fig. S1). Furthermore, the

170   differences between the products vary strongly in time (Supplemental Fig. S2), which cannot

171   arise from the use of a single climatology. The MMM climatology is based on average monthly

172   temperatures during 1985-2012 using AVHRR data (Liu et al. 2006, 2014). Next, we calculated

173   DHW as:

174    $$DHW = \frac{\Sigma_1^{84\ days} Hotspots(if\ Hotspots > 1)}{7\ days}$$ (2)

175   where only Hotspots exceeding 1 °C above the MMM contribute to DHW, and the sum of

176   Hotspots during the previous 84 days (12 weeks) contribute to DHW.

177

178   *Comparison of in situ and satellite-derived SST*

179   We compared daily (or weekly for OI-SST) mean temperature between *in situ* loggers

180   and the four satellite SST products for the years 1998, 2002, 2004, 2016, and 2017. Initially, this

181   analysis included all available measurements of daily (or weekly) *in situ* temperature from

182   anywhere on the GBR or in the Coral Sea between October of the preceding year through June of

183   each year. We extracted SST from the satellite products for the grid cell encompassing each

184   logger, and temporally matched the *in situ* and satellite time series to enable direct comparisons.

185   From these spatially and temporally matched daily temperatures, we calculated root mean square

186   errors (RMSE) and biases (average of satellite – logger) for each year and each satellite product,

187   separately. We repeated these calculations for only Hotspot times because these are the only data

188   contributing to the DHW metric commonly used in coral bleaching assessments.

189   Additionally, we compared the heat stress calculated between loggers and satellite

190   products. For this analysis, we used only those loggers with continuous data from the start of

191   January through the end of March of each year. We calculated the mean number of hotspot days,

192   total hotspots, and maximum DHW for each logger and satellite product, separately for each

193   year.

194

195   *Assessment of other environmental variables*

196   We considered whether some other environmental factor besides temperature may have

197   played a role in bleaching susceptibility during 2004. OLR was used as a proxy measure of light

198   stress because OLR is affected by convective cloudiness (Reed 1976; Kessler et al. 2000), which

199   in turn is expected to influence the amount of sunlight reaching the sea surface. We recognize

200   that OLR is an imperfect proxy for irradiance reaching coral colonies because irradiance may

201   also be affected by turbidity, water depth, surface waves, and different types of clouds (Skirving

202   et al. 2017). Nevertheless, since OLR is available in a daily gridded product over the past several

203   decades, it is the most feasible way to compare irradiance on the GBR between years ranging

204   from 1998 to 2017. The PAR data were also used to assess radiative stress, although

205   measurements from the Terra satellite only began in 2000. Additionally, we assessed temporal

206   changes in wind speed because low-wind conditions could reduce wave heights and modulate the

207   transmission of solar irradiance across the sea surface (Payne 1972; Stramska and Dickey 1998).

208   For both the OLR and wind-speed datasets, we first calculated a weekly climatology (using a

209   base period of 1998-2016), and then compared the daily anomalies around this climatology

210   between 2004 and bleaching years. For PAR, we calculated March anomalies relative to the

211   2000-2017 March climatology because this is typically the month when the highest DHW occurs

212   on the GBR.

213   Furthermore, we assessed the oceanographic conditions surrounding the GBR during

214   1998, 2002, and 2004 using SODA (note that the years 2016 and 2017 are not included in the

215   most recent version of SODA). Specifically, we compared the velocity of the East Australian

216   Current (EAC), SSH, tilting of isotherms, and wind-driven upwelling between these three years.

217   The EAC is the poleward-flowing western boundary current extending southeastward from the

218   bifurcation point of the South Equatorial Current (SEC) colliding with the Australian continental

219   shelf at around 15° S, near the central to northern GBR. First, we calculated monthly anomalies

220   in near-surface velocity (0-25 m), SSH, and SST; and plotted maps of these anomalies during

221   austral summers (January, February, March; or "JFM"). We also calculated wind stress curl as:

222    $$curl = \nabla = \frac{\partial \tau_y}{\partial_x} - \frac{\partial \tau_x}{\partial_y}$$ (3)

223   where τ is wind stress at the sea surface, which is an output provided directly by SODA, and x

224   and y are eastward and northward, respectively. Ekman vertical transport (ω_E) was then

225   calculated from wind stress curl as:

226    $$\omega_E = \frac{\nabla}{\rho f}$$ (4)

227   where ρ is seawater density, f is the Coriolis frequency, and where positive (negative) ω_E

228   indicates upwelling (downwelling). Finally, we calculated and plotted maps of ω_E anomalies

229   during JFM of 1998, 2002, and 2004.

230

231   **Results**

232   *Satellite-derived heat stress on the Great Barrier Reef*

233   The level of heat stress (maximum annual DHW) on the GBR between 1998 and 2017

234   varies dramatically between the four SST products (Fig. 2). For example, in 1998, CRW implies

235   that DHWs across nearly the whole GBR did not exceed 2-3 °C-weeks, whereas OI-SSTv1

236   implies that large swaths of the southern and far northern GBR were exposed to 7-8 °C-weeks.

237   DHWs derived from CRW during both 2002 and 2004 were high in the Coral Sea but nearly the

238   entire GBR remained less than 3 °C-weeks. Conversely, OI-SSTv2 and CMC show that the high

239   DHWs in the Coral Sea during 2002 and 2004 extended all the way to the Australian coastline,

240   with most of the GBR experiencing 5-10 °C-weeks during these two years. OI-SSTv1 implies

241   even greater heat stress during 2002 and 2004, with sections of the southern and northern GBR

242   reaching 12-15 °C-weeks. The spatial patterns of DHW in 2016 and 2017 are very similar among

243   CRW, OI-SSTv2, and CMC, but CRW shows DHWs several °C-weeks higher than OI-SSTv2

244   throughout much of the central and northern GBR. Similar patterns exist in annual maximum

245   SST anomalies and in HadISST (Supplemental Figs. S3-S4).

246   Due to these differences in DHW histories, the year of maximum DHW varies immensely

247   between the four satellite SST products (Fig. 3). According to CRW, either 2016 or 2017 was the

248   year of greatest DHW on more than 60% of the reefs of the GBR, with only a portion of the far

249   southern GBR undergoing maximum DHW in 2002. In contrast, OI-SSTv1, OI-SSTv2, and

250   CMC imply that less than 35% of reefs experienced their maximum DHW in 2016 or 2017, and

251   instead that either 2002 or 2004 was the year of highest DHW on nearly the entire southern and

252   central sections of the GBR.

253

254   *Comparison of in situ temperature loggers and satellite-derived SST*

255   Scatterplots of temperature measured by *in situ* loggers and satellites are shown for each

256   year and each SST product in Figure 4, and metrics of comparison are listed in Tables 1 and 2. In

257   general, CRW and CMC were the most precise SST products (lowest RMSEs), and the precision

258   of each SST product increased over time. However, despite the relatively good precision of

259   CRW, it was not the most accurate (lowest bias) for 1998, 2002, and 2004. Rather, CRW

260   consistently underestimated *in situ* temperature during these three years, particularly during the

261   warmest days of the year (hotspot day biases of -0.74 to -0.42 °C). OI-SSTv2 was overall the

262   most accurate SST product during 1998, 2002, and 2004, and performed well at the highest

263   temperatures (hotspot day biases of -0.20 to 0.12 °C). While the bias of OI-SSTv2 remained

264   similar for 2016 and 2017 (hotspot day biases of -0.17 and -0.08 °C, respectively), CRW

265   improved substantially relative to previous years (2016 and 2017 hotspot day biases of -0.15 and

266   -0.08 °C, respectively).

267   Metrics of heat stress followed similar patterns to the biases in hotspot day temperatures

268   (Table 2). During 1998, 2002, and 2004, the total number of hotspot days, the total hotspots (°C),

269   and the maximum DHW recorded by *in situ* loggers most closely matched either OI-SSTv1 or

270   OI-SSTv2, with CRW underestimating each metric. Conversely, in 2016 and 2017, CRW most

271   closely matched the loggers for every metric except that total hotspots during 2016 were best

272   represented by CMC.

273   The agreement in maximum DHW between *in situ* loggers and satellite SST products

274   during 2004 varied spatially (Fig. 5). OI-SSTv2 best captured maximum DHW at Coringa-

275   Herald, the only logger site in the Coral Sea, which experienced among the highest DHWs

276   during 2004 (DHWs of 11, 9, and 5 °C-weeks in the logger, OI-SSTv2, and CRW, respectively).

277   Additionally, OI-SSTv2 performed best for most sites in the northern and north-central GBR,

278   and for most inshore reefs. However, maximum DHWs of a cluster of reefs in the central GBR

279   were best represented by CRW. Thus, while DHWs in OI-SSTv2 were higher than CRW for

280   nearly the entire GBR (Fig. 5), the reality was likely somewhere in between the two but closer

281   overall to OI-SSTv2 (*e.g.* metrics in Tables 1-2). There was a significant depth-dependence of

282   the difference in maximum annual DHW between OI-SSTv2 and loggers (p = 0.019), but it

283   explained relatively little variance (r^2 = 0.03) (Supplemental Fig. S5).

284

285   *Irradiance, winds, and currents*

286   Summertime (January – February – March, JFM) OLR anomalies were generally

287   positive, on average, for 2004 and bleaching years. Mean (± 1 standard deviation) JFM daily

288   OLR anomalies were 3 ± 23, 14 ± 19, 1 ± 24, 13 ± 28, and -1 ± 25 W m^{-2} for 1998, 2002, 2004,

289   2016, and 2017, respectively. Thus, while 2004 was characterized by lower OLR (and by

290   inference, lower irradiance) than 2002 and 2016, the large variance relative to the average

291   differences makes it difficult to conclude that there were meaningful disparities between these

292   years (Fig. 6; see also Supplement Figs. S9-11 for regional analyses). The 8-day PAR

293   composites shown in Figure 6 track the OLR anomalies closely, indicating that OLR is indeed a

294   reasonably effective proxy for cloud cover. However, it is also important to recognize that the

295   seasonal cycle of PAR (*e.g.* peaking at the solstice in December and declining through the

296   summer on the GBR) is not represented by OLR anomalies. March PAR anomalies were highest

297   overall in 2002 when almost the entire GBR was exposed to unusually high PAR, whereas 2004,

298   2016, and 2017 were characterized by a mixture of negative and positive anomalies (Fig. 7). The

299   spatial pattern of positive PAR anomalies during 2016 and 2017 were broadly similar to that of

300   bleaching, being mostly concentrated in the northern GBR. During 2004, similar or higher

301   numbers of reefs experienced positive PAR anomalies as 2016 and 2017, and the highest PAR

302   values were in the central to southern GBR, consistent with where the highest DHW occurred

303   (Fig. 2).

304   Wind speed anomalies tended to be negative during 2004 and bleaching years (Fig. 6).

305   Mean JFM daily wind speed anomalies were 0.5 ± 1.2, -0.3 ± 1.0, -0.5 ± 1.1, -0.4 ± 0.9, and -0.2

306   ± 1.2 m s^{-1} for 1998, 2002, 2004, 2016, and 2017, respectively.

307   The timing of maximum SST, and the temporal difference between SST and PAR

308   maxima, did not clearly distinguish 2004 from bleaching years. With the exception of 2002,

309   when SST maxima occurred relatively early in the season, the other years are generally

310   characterized by SST maxima between the 30th to 60th days of the year, which are usually 40 to

311   80 days after peak PAR (Fig. 8). We also do not find a clear pattern between the alignment of

312   temperature and PAR peaks and the onset of bleaching. For example, 1998 SST peaked in mid-

313   February, shortly after large OLR and PAR anomalies in early February (Fig. 6). However, 2002

314   SSTs were highest in early January, during a time of near-climatological OLR and PAR. The

315   late-January SST peak during 2004 occurred under slightly positive PAR anomalies, but was

316   followed by negative OLR and PAR excursions during early February (Fig. 6). This pattern was

317   broadly similar to 1998, when peak temperatures were followed a few days later with

318   anomalously low OLR. Additionally, there was a second SST peak during 2004 in mid- to late-

319   February that aligned closely with positive OLR and PAR anomalies (Fig. 6).

320   In contrast to the undetectable differences of OLR and wind conditions between 2004 and

321   bleaching years, the oceanographic setting in JFM of 2004 diverged clearly from bleaching years

322   (1998 and 2002, as SODA does not include 2016 and 2017). Both 1998 and 2002 were

323   characterized by an intensified East Australian Current (EAC) offshore of the central and

324   southern GBR, associated with anomalously high SSH in the Coral Sea and low SSH on the

325   GBR (Fig. 8). Conversely, the EAC was anomalously weak in 2004, and SSH in the Coral Sea

326   was anomalously low while SSH on the GBR was near average (Fig. 8). Linked to the EAC and

327   SSH fields, the depth-profile of isotherms during 1998 and 2002 tilted upwards from the Coral

328   Sea towards the GBR shelf, whereas the isotherms were nearly flat across the Coral Sea in 2004

329   (Fig. 8). "Moderate" bleaching also occurred during 1982 and 1987 on the central GBR (Hughes

330   et al. 2018a), and we find similar oceanographic settings during these two years as the severe

331   bleaching events of 1998 and 2002 (Supplemental Fig. S6).

332   The wind stress curl field in SODA displayed a broadly similar temporal pattern among

333   2004 and bleaching years as the oceanographic setting described above (Fig. 9). Wind stress curl

334   was consistent with positive vertical Ekman transport (upwelling-favorable) across most of the

335   GBR during JFM of 1998 and 2002. The opposite occurred during JFM of 2004, with winds

336   stress curl across most of the GBR consistent with negative vertical Ekman transport

337   (downwelling-favorable).

338

339   **Discussion**

340   *The history of heat stress on the GBR*

341   Satellite-derived SSTs suggest that the austral summer of 2004 was one of the warmest

342   on record across the GBR (Fig. 1). Yet, critically, the intensity and spatial distribution of heat

343   stress varies drastically among four different gridded SST products (Fig. 2 and Supplemental

344   Fig. S3). CRW, which is commonly used in assessments of GBR bleaching (Liu et al. 2003;

345   Hughes et al. 2018b), shows high DHWs offshore of the GBR and in the Coral Sea, but with the

346   GBR shelf representing a distinct boundary to these high DHWs such that only 12% of GBR

347   reefs experienced >4 °C-weeks during 2004 (Fig. 3). In stark contrast, OI-SSTv1, OI-SSTv2, and

348   CMC all suggest that high DHWs extended from the Coral Sea across the GBR shelf, with 81%,

349   67%, and 79% of reefs experiencing >4 °C-weeks, respectively (Fig. 3). This difference is

350   important because DHWs exceeding 4 °C-weeks have been observed to trigger a stress response

351   that leads to bleaching (Heron et al. 2016; Hughes et al. 2017, 2018b). Although the use of a

352   single MMM climatology for all our analyses could affect the absolute values of DHW, the most

353   important result is the comparison of 2004 to other years within each product. While CRW paints

354   2004 as a minor heat stress event compared to 2016-2017, OI-SSTv1, OI-SSTv2, and CMC all

355 indicate that heat stress in 2004 was sufficient to initiate widespread bleaching, and that similar

356 or greater numbers of reefs experienced >4 °C-weeks in 2004 compared to the severe bleaching

357 years of 1998, 2002, 2016, and 2017 (Fig. 3).

358   The key differences in heat stress histories among the satellite SST products demonstrate

359 the need for validation with *in situ* temperature loggers (*e.g.* Pan et al. 2017; Fiedler et al. 2019).

360 Using all available temperature loggers from the AIMS database (AIMS 2018), we show that OI-

361 SSTv2 provides the most accurate representation, on average, of reef-water temperatures (Table

362 1) and heat stress (Table 2) during austral summer 2004 on the GBR. While the accuracy of OI-

363 SSTv2 remained relatively consistent across bleaching years, CRW accuracy changed

364 substantially over time such that temperatures during 1998, 2002, and 2004 were underestimated

365 compared to 2016 and 2017. These findings have important ramifications for interpreting the

366 history of heat stress on the GBR. First, according to CRW, heat stress in 2016 and 2017 far

367 exceeded that of previous bleaching years and 2004. However, although CRW or CMC provided

368 the most accurate representation of temperatures in both 2016 and 2017, temperatures during

369 earlier years were likely underestimated by CRW, potentially due to less coverage and lower-

370 quality satellite data (Liu et al. 2014). In particular, either 2002 or 2004 was the year of highest

371 DHW on at least half of the GBR according to OI-SSTv2, which was the most accurate SST

372 product during these two years (Fig. 3). Second, our analysis indicates that 2004 heat stress

373 reached sufficient levels to spark mass coral bleaching (Fig. 3 histograms). This makes 2004

374 enigmatic because mass bleaching was not reported.

375   While OI-SSTv2 was overall the most accurate satellite SST product in austral summer

376 2004, it is important to recognize that substantial uncertainties remain. For instance, OI-SSTv2

377 performed best for capturing maximum annual DHW for the Coral Sea, northern GBR, and many

378   inshore reefs, but CRW performed best for a cluster of reefs in the central GBR (Fig. 5). Thus,

379   we cannot conclude that OI-SSTv2 is a true representation of 2004 temperatures across the entire

380   GBR, but rather that OI-SSTv2 provides a better representation of 2004 heat stress on average

381   across the GBR than CRW. Though CRW consistently underestimates temperatures and heat

382   stress during 2004 (Fig. 4 and Tables 1-2), OI-SSTv2 is an approximately even balance between

383   overestimation in some locations and underestimation in others (Figs. 4-5). Thus, while these

384   issues remain important, we can still conclude that temperatures on many reefs in 2004 reached

385   levels that were sufficient to cause severe coral bleaching in other years. In the following

386   sections, we explore potential reasons why widespread bleaching did not occur on the GBR in

387   2004. We place particular emphasis on the effects of environmental factors besides temperature

388   that can differentiate 2004 from mass bleaching events.

389

390   *Did bleaching occur but was not observed?*

391   Widespread bleaching on the GBR during 2004 is conspicuously absent from all existing

392   coral bleaching databases (Donner et al. 2017; Hughes et al. 2018a; Oliver et al. 2018). However,

393   it is critical to recognize that reporting bias can exist in such databases (Oliver et al. 2018), and

394   that an absence of bleaching reports should not necessarily be taken as an absence of bleaching.

395   Nevertheless, the GBR is one of the most closely monitored reef systems in the world. It is

396   regularly surveyed by government agencies and scientists, and visited by hundreds of thousands

397   of tourists every year. In 2004, the AIMS Long Term Monitoring Program (LTMP) reported

398   low-level bleaching (scattered bleaching of individual colonies with a maximum of 3% of corals

399   bleaching) between January and May on 20 of 80 reefs surveyed (Sweatman et al. 2005; AIMS

400   LTMP; see Supplementary Fig. S7). Additionally, analyses of density banding in coral skeletal

401   cores from the central and northern GBR captured the bleaching event in 2002 but did not show

402   evidence of mass bleaching in 2004 (Cantin and Lough 2014; DeCarlo et al. 2019). While it is

403   impossible to conclude with complete certainty that bleaching on the GBR was not more severe

404   in 2004, there is a low probability that sustained and widespread bleaching went unnoticed.

405   Meanwhile, benthic surveys of Lihou Reef in the central Coral Sea Marine Park reported

406   65% of hard corals were bleached in March 2004 (Oxley et al. 2004), commensurate with the

407   high levels of thermal stress (DHW of 13.1 °C-weeks) to which they were exposed (see point in

408   Fig. 2). Although the bleaching observations at Lihou, 300 km from the GBR, were the only

409   direct bleaching reports in the Coral Sea at that time, they suggest a strong disconnect from the

410   GBR, where many more direct observations are available but no extensive bleaching was

411   reported.

412   One consideration is that weather conditions could, at times, hamper monitoring efforts

413   and obscure detection of bleaching. Two major tropical cyclones affected the GBR and Coral

414   Sea region during summer 2004. The first, cyclone Fritz, impacted the far northern GBR in mid-

415   February (Supplementary Fig. S8), but this region was characterized by the lowest heat stress

416   during 2004, except for some of the outer-shelf reefs (Fig. 2). Thus, while cyclone Fritz may

417   have played a role in reducing heat stress in the far northern GBR, it is unlikely that the storm

418   prohibited detection of bleaching along the entire GBR. Tropical cyclone Grace formed in the

419   Coral Sea offshore of the central GBR on 20 March before moving southeast toward New

420   Caledonia (Supplementary Fig. S8). It passed directly over Lihou Reef three days after surveys

421   reported bleaching (Oxley et al. 2004), and while it may have prevented extensive coral

422   mortality, it clearly did not prevent bleaching. Although cyclone Grace never directly struck the

423   GBR, it is possible that this cyclone discouraged or prevented observers from visiting parts of the

424   reef at that time. However, the cyclone formed approximately two weeks after maximum DHWs

425   were reached in early-mid March and its core remained hundreds of kilometers away from the

426   GBR. Therefore, we find it possible, yet very unlikely, that widespread bleaching did occur but

427   was not observed.

428

429   *Did irradiance, winds, or currents mitigate bleaching?*

430   Coral bleaching susceptibility is known to depend on a variety of other factors besides

431   temperature, including light and nutrients (Brown 1997; Lesser 1997; Fitt et al. 2001;

432   Wooldridge 2009, 2016; Skirving et al. 2017). Therefore, it is possible that bleaching did not

433   occur in 2004 despite the high heat stress because of anomalous cloud cover, winds, or currents.

434   Cloudiness (as inferred from OLR), and wind speed were relatively low in austral summers of

435   2004 and bleaching years (Fig. 6). Likewise, PAR was high across the entire GBR in 2002, and

436   high in the warmest sections of the GBR in 2004 (central to southern), 2016 (northern), and 2017

437   (central to northern) (Fig. 7). The clear and calm conditions likely contributed, at least in part, to

438   the warm reef-waters during these years by enhancing air-sea heat flux (Schiller et al. 2009;

439   Davis et al. 2011; DeCarlo et al. 2017; Benthuysen et al. 2018). Beyond their influence on

440   temperature, cloud and wind conditions could enhance the light reaching corals, thereby

441   increasing their sensitivity to heat stress (Payne 1972; Stramska and Dickey 1998; Davis et al.

442   2011). In the Keppel Islands of the far southern GBR, the absence of bleaching despite

443   anomalously high temperatures in 2004 was attributed to relatively low light stress during that

444   summer (Skirving et al. 2017). Indeed, our analysis of MODIS PAR data shows the Keppel

445   Islands were exposed to PAR levels comparable to the climatological mean (Fig. 7). However,

446   north of the Keppel Islands, in much of the central to southern GBR, PAR anomalies were higher

447   at this time. Furthermore, in our analysis of OLR and wind-speed across the entire GBR, austral

448   summer 2004 was not detectably cloudier or windier than all bleaching years, making it unlikely

449   that differences in irradiance can explain the large-scale absence of bleaching in 2004. The

450   seasonal timing of maximum SST has also been considered as a factor affecting bleaching

451   sensitivity (Bahr et al. 2015). However, 2004 is not clearly differentiated from all bleaching

452   years based on the timing of maximum SST or the time difference between maximum SST and

453   maximum PAR (Fig. 8).

454   Nutrient levels can also modulate coral susceptibility to heat stress (Wooldridge 2009,

455   2016; Cunning and Baker 2012; Wiedenmann et al. 2013; D'Angelo and Wiedenmann 2014;

456   Vega Thurber et al. 2014; Baker et al. 2018; Wang et al. 2018). Excess nutrients increase the

457   concentrations of zooxanthellae within coral tissues (Marubini and Davies 1996; Wooldridge

458   2016), which can become detrimental when temperatures exceed normal summertime levels and

459   toxic levels of oxygen produced by the zooxanthellae lead to the breakdown of the symbiosis

460   (Lesser 1997; Fitt et al. 2001; Cunning and Baker 2012). A key process affecting nutrient levels

461   on the GBR is upwelling of Coral Sea water onto the shelf through passages, primarily located in

462   the central GBR (Andrews and Gentien 1982; Wolanski and Pickard 1983; Furnas and Mitchell

463   1996; Berkelmans et al. 2010; Benthuysen et al. 2016). The deeper waters that upwell onto the

464   shelf are nutrient-rich, and once they reach the shelf they are retained for weeks to months as

465   they spread for hundreds of kilometers within the GBR lagoon (Andutta et al. 2013; Benthuysen

466   et al. 2016). Although these waters rarely reach the sea surface directly, they can represent an

467   important source of nutrients into an otherwise largely oligotrophic system (Furnas and Mitchell

468   1996; Berkelmans et al. 2010). Upwelling through the reef passages and onto the shelf is

469   strongly influenced by the strength of the EAC offshore of the GBR (Steinberg 2007;

470   Berkelmans et al. 2010; Benthuysen et al. 2016). A faster-flowing EAC is generally associated

471   with an anomalously steep SSH gradient sloping downwards towards the shelf, and isotherms

472   tilting upwards towards the shelf (Steinberg 2007; Benthuysen et al. 2016). Our analysis of

473   SODA indicates that this was precisely the oceanographic setting during the 1998 and 2002

474   severe bleaching events (Fig. 9), and during the 1982 and 1987 moderate bleaching events (based

475   on definitions of Hughes et al., 2018a; although 1982 was arguably a severe event based on our

476   interpretation of Oliver, 1985) (see Supplemental Fig. S6). Indeed, detailed analysis of *in situ*

477   temperature logger data showed that upwelling occurred more frequently than normal during

478   summers 1998 and 2002 (Berkelmans et al. 2010), potentially contributing to widespread

479   bleaching by increasing nutrient levels along the GBR (Wooldridge 2009, 2016). Critically, the

480   opposite pattern persisted through the austral summer of 2004. The EAC was sluggish, SSH in

481   the Coral Sea was anomalously low, and isotherms remained nearly flat (Fig. 9), conditions

482   which inhibit upwelling onto the GBR shelf. Therefore, the slow EAC in 2004 may have played

483   a role in sparing the GBR from widespread bleaching.

484   The potential role of the EAC in modulating bleaching sensitivity on the GBR is distinct

485   from other current systems that may reduce surface temperatures. For example, the Equatorial

486   Undercurrent collides with coral reefs in the central Pacific Ocean, upwelling cold water to the

487   surface and directly mitigating thermal stress on resident corals (Gove et al. 2006; Karnauskas

488   and Cohen 2012; Barkley et al. 2018). Conversely, the EAC does not appear to mitigate

489   bleaching by reducing heat stress, but rather it can potentially enhance bleaching sensitivity by

490   adding nutrients into the GBR lagoon system without substantially affecting surface

491   temperatures (Berkelmans et al. 2010). Furthermore, the EAC typically only affects the central

492   and southern GBR, whereas the North Queensland Current (NQC) flows towards the equator

493   adjacent to the northern GBR (Schiller et al. 2009; Andutta et al. 2013). In fact, slowdowns in

494   the NQC can result in localized heating along the northern GBR, which likely contributed to the

495   bleaching in this region during 2016 (Wolanski et al. 2017). Critically, the geographic footprints

496   of >4 °C-weeks and the anomalously slow EAC mostly overlap across much of the central to

497   southern GBR during summer 2004 (Figs. 2 and 9), which were the areas most intensely

498   monitored at this time (Supplemental Fig. S7). Some of the outer-shelf reefs of the far northern

499   GBR also experienced >4 °C-weeks in the same area where the NQC was anomalously slow

500   (Figs. 2 and 9), although this area was not surveyed as extensively during the summer of 2004

501   (Supplemental Fig. S7). Thus, our interpretation of the EAC influencing the absence of bleaching

502   in 2004 applies primarily to the central and southern GBR, with the outer-shelf reefs of the far

503   northern sector being more likely to have experienced an unnoticed bleaching event.

504   Another related process capable of affecting upwelling is wind stress curl. Cyclonic

505   winds at the sea surface spread water laterally, in turn leading to upwelling of deeper waters (*e.g.*

506   Enriquez et al. 1995; Chelton et al. 2004). Most of the GBR was exposed to upwelling-favorable

507   wind stress curl in austral summers of both 1998 and 2002, but anomalous conditions that

508   favored downwelling during 2004 (Fig. 10). Thus, wind stress curl may have further enhanced

509   the upwelling that occurred during bleaching years while dampening upwelling during 2004,

510   when heat stress was high but bleaching did not occur.

511

512   *Did corals acclimatize after the 1998 and 2002 bleaching events?*

513   Acclimatization is the adjustment of an organism to variations in its environment, such

514   that it can tolerate a wider range or a different set of conditions. Corals exhibiting lower

515   bleaching susceptibility following previous exposure to heat stress is often taken as evidence of

516   acclimatization to higher temperature regimes (Berkelmans and Willis 1999; Guest et al. 2012;

517   Pratchett et al. 2013; Coles et al. 2018; Gintert et al. 2018; Palmer 2018; DeCarlo et al. 2019).

518   This can occur through a variety of processes such as hosting new zooxanthellae populations or

519   immune system responses (Buddemeier and Fautin 1993; Putnam et al. 2017; Palmer 2018).

520   Additionally, corals on some shallow reefs with relatively high daily temperature ranges may

521   gain tolerance to heat stress (Safaie et al. 2018). Coral communities may also become less

522   sensitive to heat stress if previous bleaching events eliminate the most susceptible species or

523   individuals (Vargas-Ángel et al. 2001; Harrison et al. 2018; Hughes et al. 2019). Nevertheless, if

524   we were to consider bleaching as solely a response to temperature, then the absence of bleaching

525   on the GBR in 2004 would be a strong indication of acclimatization because mass bleaching

526   occurred in 1998 and 2002 under similar or less heat stress. However, this logic may not hold if

527   other factors modulate the bleaching susceptibility to temperature. For instance, if lower nutrient

528   levels in 2004 reduced bleaching sensitivity, then acclimatization may not have been necessary.

529   Rather, conditions during 2004 may simply have been less stressful if nutrient levels were lower,

530   even though temperatures were exceptionally high. Therefore, acclimatization remains a

531   potential factor in contributing to the absence of bleaching in 2004, but we cannot conclude with

532   certainty that it occurred to a meaningful extent.

533

534   *Conclusion*

535   The austral summer of 2004 on the GBR is enigmatic because it was one of the warmest

536   summers on record, yet only very low levels (< 3%) of bleaching were recorded. Our analyses of

537   satellite SST products, validated against a suite of *in situ* temperature loggers, indicates that

538   temperatures were sufficiently high in 2004 to trigger widespread coral bleaching, based on

539   observed bleaching thresholds in other years. Ocean currents–but not winds, cloud cover, or

540   temperature–differentiate 2004 from bleaching years. Specifically, a slowdown of the EAC

541   during austral summer 2004 established conditions unfavorable for upwelling of nutrient-rich

542   water on the GBR shelf. We infer that nutrient levels may play a role in modulating coral

543   bleaching susceptibility on the GBR, and that changes in the strength of the EAC can potentially

544   either mitigate or enhance bleaching. Since 1980, the EAC has accelerated (see also Hill et al.

545   2008; Suthers et al. 2011) and the NQC has decelerated (Fig. 11). If the strength of the EAC

546   continues to increase as expected due to the 'spin-up' of the SEC (Oliver and Holbrook 2014;

547   Roemmich et al. 2016), the GBR could become even more prone to mass bleaching events as

548   global warming drives more frequent marine heatwaves.

549   Understanding the role of oceanography and environmental variables in corals' responses to

550   heat stress requires additional testing in laboratory and natural settings, as well as long-term *in*

551   *situ* measurements of irradiance, winds, currents, and nutrients. We suggest that continuous

552   monitoring of a greater suite of environmental variables in coral reef ecosystems is necessary to

553   better quantify bleaching thresholds and corals' adaptive capacity in an era of rapid

554   environmental change. Nevertheless, our findings clearly highlight the dynamic nature of coral

555   bleaching thresholds during marine heatwaves. Other examples of an absence of coral bleaching

556   despite high temperature stress exist in well-monitored areas, for example during 1968 in

557   Hawai'i (Bahr et al. 2015), and investigating such case studies can advance our understanding of

558   coral heat tolerance.

559

560   **Data accessibility**

561   Raw data and code are available at: https://codeocean.com/capsule/8487532/

562

Acknowledgements:

We thank the Australian Institute of Marine Science for providing bleaching reports from the Long Term Monitoring Program. We are grateful to the organizations that made the climate data used in this study publicly available, and to Kris Karnauskas (University of Colorado Boulder), Jessica Benthuysen (AIMS), and Mike Emslie (AIMS) for insightful discussions. We thank Dr. Keisha Bahr and an anonymous reviewer for their constructive comments.

569

Conflict of interest: On behalf of all authors, the corresponding author states that there is no conflict of interest.

572

References:

Andrews JC, Gentien P (1982) Upwelling as a Source of Nutrients for the Great Barrier Reef Ecosystems: A Solution to Darwin's Question? Mar Ecol Prog Ser 8:257–269

Andutta FP, Ridd P V., Wolanski E (2013) The age and the flushing time of the Great Barrier Reef waters. Cont Shelf Res 53:11–19

Australian Institute of Marine Science (2018) Sea Temperatures. https://www.aims.gov.au/docs/research/climate-change/climate-monitoring/sst.html

Bahr KD, Jokiel PL, Rodgers KS (2015) The 2014 coral bleaching and freshwater flood events in Kāne'ohe Bay, Hawai'i. PeerJ 3:e1136

Baker DM, Freeman CJ, Wong JCY, Fogel ML, Knowlton N (2018) Climate change promotes parasitism in a coral symbiosis. ISME J 12:921–930

Banzon V, Smith TM, Chin TM, Liu C, Hankins W (2016) A long-term record of blended

585   satellite and in situ sea-surface temperature for climate monitoring, modeling and

586   environmental studies. Earth Syst Sci Data 8:165–176

587   Barkley H, Cohen A, Mollica N, Brainard R, Rivera H, DeCarlo T, Lohmann G, Drenkard E,

588   Alpert A, Young C, Vargas-Angel B, Lino K, Oliver T, Pietro K, Luu V (2018) Repeat

589   bleaching of a central Pacific coral reef over the past six decades (1960-2016). Commun

590   Biol 1:177

591   Benthuysen JA, Oliver ECJ, Feng M, Marshall AG (2018) Extreme Marine Warming Across

592   Tropical Australia During Austral Summer 2015-2016. J Geophys Res Ocean 123:1301–

593   1326

594   Benthuysen JA, Tonin H, Brinkman R, Herzfeld M, Steinberg C (2016) Intrusive upwelling in

595   the Central Great Barrier Reef. J Geophys Res Ocean 121:8395–8416

596   Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and

597   2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and

598   predictions. Coral Reefs 23:74–83

599   Berkelmans R, Oliver JK (1999) Large-scale bleaching of corals on the Great Barrier Reef. Coral

600   Reefs 18:55–60

601   Berkelmans R, Weeks SJ, Steinberga CR (2010) Upwelling linked to warm summers and

602   bleaching on the Great Barrier Reef. Limnol Oceanogr 55:2634–2644

603   Berkelmans R, Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of

604   corals on the inshore Central Great Barrier Reef. Coral Reefs 18:219–228

605   Beyer HL, Kennedy E V., Beger M, Chen CA, Cinner JE, Darling ES, Eakin CM, Gates RD,

606   Heron SF, Knowlton N, Obura DO, Palumbi SR, Possingham HP, Puotinen M, Runting

607   RK, Skirving WJ, Spalding M, Wilson KA, Wood S, Veron JE, Hoegh-Guldberg O (2018)

608   Risk-sensitive planning for conserving coral reefs under rapid climate change. Conserv Lett

609   e12587

610 Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:129–138

611 Bruno J, Siddon C, Witman J, Colin P, Toscano M (2001) El Nino related coral bleaching in

612   Palau, western Caroline Islands. Coral Reefs 20:127–136

613 Buddemeier R, Fautin D (1993) Coral bleaching as an adaptive mechanism: A testable

614   hypothesis.

615 Cantin NE, Lough JM (2014) Surviving Coral Bleaching Events: Porites Growth Anomalies on

616   the Great Barrier Reef. PLoS One 9:e88720

617 Carton JA, Chepurin GA, Chen L, Carton JA, Chepurin GA, Chen L (2018) SODA3: A New

618   Ocean Climate Reanalysis. J Clim 31:6967–6983

619 Center CM (2012) GHRSST Level 4 CMC0.2deg Global Foundation Sea Surface Temperature

620   Analysis (GDS version 2).

621 Chelton DB, Schlax MG, Freilich MH, Milliff RF (2004) Satellite measurements reveal

622   persistent small-scale features in ocean winds. Science 303:978–83

623 Chepurin GA, Carton JA, Leuliette E (2014) Sea level in ocean reanalyses and tide gauges. J

624   Geophys Res Ocean 119:147–155

625 Coles SL, Bahr KD, Rodgers KS, May SL, McGowan AE, Tsang A, Bumgarner J, Han JH

626   (2018) Evidence of acclimatization or adaptation in Hawaiian corals to higher ocean

627   temperatures. PeerJ 6:e5347

628 Cunning R, Baker AC (2012) Excess algal symbionts increase the susceptibility of reef corals to

629   bleaching. Nat Clim Chang 3:259–262

630 D'Angelo C, Wiedenmann J (2014) Impacts of nutrient enrichment on coral reefs: new

631   perspectives and implications for coastal management and reef survival. Curr Opin Environ

632   Sustain 7:82–93

633 Davis KA, Lentz SJ, Pineda J, Farrar JT, Starczak VR, Churchill JH (2011) Observations of the

634   thermal environment on Red Sea platform reefs: a heat budget analysis. Coral Reefs 30:25–

635   36

636 DeCarlo TM, Cohen AL, Wong GTF, Davis KA, Lohmann P, Soong K (2017) Mass coral

637   mortality under local amplification of 2 °C ocean warming. Sci Rep 7:44586

638 DeCarlo TM, Harrison HB, Gajdzik L, Alaguarda D, Rodolfo-Metalpa R, D'Olivo J, Liu G,

639   Patalwala D, McCulloch MT (2019) Acclimatization of massive reef-building corals to

640   consecutive heatwaves. Proc R Soc B Biol Sci 286:20190235

641 Donner SD, Rickbeil GJM, Heron SF, Triebold C, DuBois E, Henss J (2017) A new, high-

642   resolution global mass coral bleaching database. PLoS One 12:e0175490

643 Dunne R, Brown B (2001) The influence of solar radiation on bleaching of shallow water reef

644   corals in the Andaman Sea, 1993–1998. Coral Reefs 20:201–210

645 Enriquez AG, Friehe CA, Enriquez AG, Friehe CA (1995) Effects of Wind Stress and Wind

646   Stress Curl Variability on Coastal Upwelling. J Phys Oceanogr 25:1651–1671

647 Fiedler EK, McLaren A, Banzon V, Brasnett B, Ishizaki S, Kennedy J, Rayner N, Roberts-Jones

648   J, Corlett G, Merchant CJ, Donlon C (2019) Intercomparison of long-term sea surface

649   temperature analyses using the GHRSST Multi-Product Ensemble (GMPE) system. Remote

650   Sens Environ 222:18–33

651 Fitt WK, Brown BE, Warner ME, Dunne RP (2001) Coral bleaching: interpretation of thermal

652   tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20:51–65

653 Frouin R, Franz B, Werdell P (2002) The SeaWiFS PAR product. In: Hooker S., Firestone E.

654  (eds) Algorithm Updates for the Fourth SeaWiFS Data Reprocessing. NASA Technical

655  Memorandum, pp 46–50

656 Furnas MJ, Mitchell AW (1996) Nutrient inputs into the central Great Barrier Reef (Australia)

657  from subsurface intrusions of Coral Sea waters: a two-dimensional displacement model.

658  Cont Shelf Res 16:1127–1148

659 Gates RD, Baghdasarian G, Muscatine L (1992) Temperature Stress Causes Host Cell

660  Detachment in Symbiotic Cnidarians: Implications for Coral Bleaching. Biol Bull 182:324–

661  332

662 Gintert BE, Manzello DP, Enochs IC, Kolodziej G, Carlton R, Gleason ACR, Gracias N (2018)

663  Marked annual coral bleaching resilience of an inshore patch reef in the Florida Keys: A

664  nugget of hope, aberrance, or last man standing? Coral Reefs 37:533–547

665 Glynn PW (1983) Extensive 'bleaching' and death of reef corals on the Pacific coast of Panama.

666  Environ Conserv 10:149–154

667 Glynn PW (1993) Coral reef bleaching: ecological perspectives. Coral Reefs 12:1–17

668 Gove JM, Merrifield MA, Brainard RE (2006) Temporal variability of current-driven upwelling

669  at Jarvis Island. J Geophys Res Ocean 111:

670 Green RH, Lowe RJ, Buckley ML, Foster T, Gilmour JP (2019) Physical mechanisms

671  influencing localized patterns of temperature variability and coral bleaching within a system

672  of reef atolls. Coral Reefs 1–13

673 Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi

674  YA, Chou LM (2012) Contrasting Patterns of Coral Bleaching Susceptibility in 2010

675  Suggest an Adaptive Response to Thermal Stress. PLoS One 7:e33353

676 Harriott VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching

677   event. Mar Ecol Prog Ser 21:81–88

678 Harrison HB, Álvarez-Noriega M, Baird AH, Heron SF, MacDonald C, Hughes TP (2018) Back-

679   to-back coral bleaching events on isolated atolls in the Coral Sea. Coral Reefs 1–7

680 Heron S, Johnston L, Liu G, Geiger E, Maynard J, De La Cour J, Johnson S, Okano R,

681   Benavente D, Burgess T, Iguel J, Perez D, Skirving W, Strong A, Tirak K, Eakin C (2016)

682   Validation of Reef-Scale Thermal Stress Satellite Products for Coral Bleaching Monitoring.

683   Remote Sens 8:59

684 Hill KL, Rintoul SR, Coleman R, Ridgway KR (2008) Wind forced low frequency variability of

685   the East Australia Current. Geophys Res Lett 35:L08602

686 Hobday A, Oliver E, Sen Gupta A, Benthuysen J, Burrows M, Donat M, Holbrook N, Moore P,

687   Thomsen M, Wernberg T, Smale D (2018) Categorizing and Naming Marine Heatwaves.

688   Oceanography 31:

689 Hoegh-Guldberg O, Kennedy E V., Beyer HL, McClennen C, Possingham HP (2018) Securing a

690   Long-term Future for Coral Reefs. Trends Ecol Evol 0:

691 Hughes T, Kerry J (2017) Back-to-back bleaching has now hit two-thirds of the Great Barrier

692   Reef.

693 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK,

694   Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H,

695   Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett

696   M, Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass

697   bleaching of corals in the Anthropocene. Science (80-) 359:80–83

698 Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH,

699   Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M,

700   Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM,

701   Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom

702   MO, Kennedy E V., Kuo C, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA,

703   McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ,

704   Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and

705   recurrent mass bleaching of corals. Nature 543:373–377

706 Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS,

707   Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS,

708   Torda G (2018b) Global warming transforms coral reef assemblages. Nature 556:492–496

709 Hughes TP, Kerry JT, Connolly SR, Baird AH, Eakin CM, Heron SF, Hoey AS, Hoogenboom

710   MO, Jacobson M, Liu G, Pratchett MS, Skirving W, Torda G (2019) Ecological memory

711   modifies the cumulative impact of recurrent climate extremes. Nat Clim Chang 9:40–43

712 Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef

713   corals. Mar Biol 43:201–208

714 Kalnay E, Kanamitsu M, Kistler R, Collins W, Deaven D, Gandin L, Iredell M, Saha S, White G,

715   Woollen J, Zhu Y, Leetmaa A, Reynolds R, Chelliah M, Ebisuzaki W, Higgins W,

716   Janowiak J, Mo KC, Ropelewski C, Wang J, Jenne R, Joseph D (1996) The NCEP/NCAR

717   40-Year Reanalysis Project. Bull Am Meteorol Soc 77:437–471

718 Karnauskas KB, Cohen AL (2012) Equatorial refuge amid tropical warming. Nat Clim Chang

719   2:530–534

720 Kessler WS, Kleeman R, Kessler WS, Kleeman R (2000) Rectification of the Madden–Julian

721   Oscillation into the ENSO Cycle. J Clim 13:3560–3575

722 Lesser MP (1997) Oxidative stress causes coral bleaching during exposure to elevated

723   temperatures. Coral Reefs 16:187–192

724   Liebmann B, Smith CA (1996) Description of a Complete (Interpolated) Outgoing Longwave

725   Radiation Dataset. Bull Am Meteorol Soc 77:1275–1277

726   Liu G, Heron S, Eakin C, Muller-Karger F, Vega-Rodriguez M, Guild L, De La Cour J, Geiger

727   E, Skirving W, Burgess T, Strong A, Harris A, Maturi E, Ignatov A, Sapper J, Li J, Lynds S

728   (2014) Reef-Scale Thermal Stress Monitoring of Coral Ecosystems: New 5-km Global

729   Products from NOAA Coral Reef Watch. Remote Sens 6:11579–11606

730   Liu G, Strong A, Skirving W, Arzayus L (2006) Overview of NOAA coral reef watch program's

731   near-real time satellite global coral bleaching monitoring activities. Proc 10th Int coral reef

732   Symp Okinawa

733   Liu G, Strong AE, Skirving W (2003) Remote sensing of sea surface temperatures during 2002

734   Barrier Reef coral bleaching. Eos, Trans Am Geophys Union 84:137–141

735   Marubini F, Davies PS (1996) Nitrate increases zooxanthellae population density and reduces

736   skeletogenesis in corals. Mar Biol 127:319–328

737   Morris LA, Voolstra CR, Quigley KM, Bourne DG, Bay LK (2019) Nutrient Availability and

738   Metabolism Affect the Stability of Coral–Symbiodiniaceae Symbioses. Trends Microbiol

739   NOAA Coral Reef Watch NOAA Coral Reef Watch Daily Global 5-km Satellite Coral

740   Bleaching Degree Heating Week Product.

741   Oliver ECJ, Holbrook NJ (2014) Extending our understanding of South Pacific gyre "'spin-up'":

742   Modeling the East Australian Current in a future climate. J Geophys Res 119:2788–2805

743   Oliver J (1985) Recurrent seasonal bleaching and mortality of corals on the Great Barrier Reef.

744   Oliver JK, Berkelmans R, Eakin CM (2018) Coral Bleaching in Space and Time. In: van Oppen

745   M.J.H., Lough J.M. (eds) Coral Bleaching. Springer, Cham, pp 27–49

746   Osman EO, Smith DJ, Ziegler M, Kürten B, Conrad C, El-Haddad KM, Voolstra CR, Suggett DJ

747   (2018) Thermal refugia against coral bleaching throughout the northern Red Sea. Glob

748   Chang Biol 24:e474–e484

749   Oxley W, Emslie M, Muir P, Thompson A (2004) Marine Surveys undertaken in the Lihou Reef

750   National Nature Reserve, March 2004.Produced for Department of the Environment and

751   Heritage.

752   Palmer C V. (2018) Immunity and the coral crisis. Commun Biol 1:91

753   Pan X, Wong GTF, DeCarlo TM, Tai J-H, Cohen AL (2017) Validation of the remotely sensed

754   nighttime sea surface temperature in the shallow waters at the Dongsha Atoll. Terr Atmos

755   Ocean Sci 28:517

756   Payne RE (1972) Albedo of the Sea Surface. J Atmos Sci 29:959–970

757   Perry KL (2001) SeaWinds on QuikSCAT Level 3 Daily, Gridded Ocean Wind Vectors (JPL

758   SeaWinds Project) Version 1.1.

759   Pratchett MS, McCowan D, Maynard JA, Heron SF (2013) Changes in Bleaching Susceptibility

760   among Corals Subject to Ocean Warming and Recurrent Bleaching in Moorea, French

761   Polynesia. PLoS One 8:e70443

762   Putnam HM, Barott KL, Ainsworth TD, Gates RD (2017) The Vulnerability and Resilience of

763   Reef-Building Corals. Curr Biol 27:R528–R540

764   Rayner NA, Parker DE, Horton EB, Folland CK, Alexander L V., Rowell DP, Kent EC, Kaplan

765   A (2003) Global analyses of sea surface temperature, sea ice, and night marine air

766   temperature since the late nineteenth century. J Geophys Res 108:4407

767   Reed RK (1976) On estimation of net long-wave radiation from the oceans. J Geophys Res

768   81:5793–5794

769   Reid EC, DeCarlo TM, Cohen AL, Wong GTF, Lentz SJ, Safaie A, Hall A, Davis KA (2019)

770   Internal waves influence the thermal and nutrient environment on a shallow coral reef.

771   Limnol Oceanogr lno.11162

772   Reynolds RW, Rayner NA, Smith TM, Stokes DC, Wang W (2002) An Improved In Situ and

773   Satellite SST Analysis for Climate. J Clim 15:1609–1625

774   Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily High-

775   Resolution-Blended Analyses for Sea Surface Temperature. J Clim 20:5473–5496

776   Richards ZT, Garcia R, Moore G, Fromont J, Kirkendale L, Bryce M, Bryce C, Hara A, Ritchie

777   J, Gomez O, Whisson C, Allen M, Wilson NG (2019) A tropical Australian refuge for

778   photosymbiotic benthic fauna. Coral Reefs 1–8

779   Roemmich D, Gilson J, Sutton P, Zilberman N, Roemmich D, Gilson J, Sutton P, Zilberman N

780   (2016) Multidecadal Change of the South Pacific Gyre Circulation. J Phys Oceanogr

781   46:1871–1883

782   Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams

783   GJ, Davis KA (2018) High frequency temperature variability reduces the risk of coral

784   bleaching. Nat Commun 9:1671

785   Schiller A, Ridgway KR, Steinberg CR, Oke PR (2009) Dynamics of three anomalous SST

786   events in the Coral Sea. Geophys Res Lett 36:L06606

787   Schmidt GM, Wall M, Taylor M, Jantzen C, Richter C (2016) Large-amplitude internal waves

788   sustain coral health during thermal stress. Coral Reefs 1–13

789   Shuail D, Wiedenmann J, D'Angelo C, Baird AH, Pratchett MS, Riegl B, Petrov P, Amos C

790   (2016) Local bleaching thresholds established by remote sensing techniques vary among

791   reefs with deviating bleaching patterns during the 2012 event in the Arabian/Persian Gulf.

792   Mar Pollut Bull 105:654–659

793   Skirving W, Enríquez S, Hedley J, Dove S, Eakin C, Mason R, De La Cour J, Liu G, Hoegh-

794   Guldberg O, Strong A, Mumby P, Iglesias-Prieto R, Skirving W, Enríquez S, Hedley JD,

795   Dove S, Eakin CM, Mason RAB, De La Cour JL, Liu G, Hoegh-Guldberg O, Strong AE,

796   Mumby PJ, Iglesias-Prieto R (2017) Remote Sensing of Coral Bleaching Using

797   Temperature and Light: Progress towards an Operational Algorithm. Remote Sens 10:18

798   Spalding M, Ravilious C, Green EP (Edmund P (2001) World atlas of coral reefs. University of

799   California Press,

800   Steinberg C (2007) Impacts of climate change on the physical oceanography of the Great Barrier

801   Reef. Climate Change and the Great Barrier Reef: A Vulnerability Assessment. Great

802   Barrier Reef Marine Park Authority, pp 818

803   Stramska M, Dickey TD (1998) Short-term variability of the underwater light field in the

804   oligotrophic ocean in response to surface waves and clouds. Deep Sea Res Part I Oceanogr

805   Res Pap 45:1393–1410

806   Suthers IM, Young JW, Baird ME, Everett JD, Brassington GB, Byrne M, Condie SA, Hartog

807   JR, Hassler CS, Hobday AJ, Holbrook NJ, Malcolm HA, Oke PR, Thompson PA (2011)

808   The strengthening East Australian Current, its eddies and biological effects — an

809   introduction and overview. Deep Sea Res Part II Top Stud Oceanogr 58:538–546

810   Sweatman H, Burgess S, Cheal A, Coleman G, Delean S, Emslie M, McDonald A, Miller I,

811   Osborne K, Thompson A (2005) Long-term monitoring of the Great Barrier Reef. Status

812   Report Number 7.

813   Trenberth E, Olson G (1988) Evaluation of NMC Global Analyses: 1979-1987.

814   Vargas-Ángel B, Zapata FA, Hernández H, Jiménez JM (2001) Coral and coral reef responses to

815   the 1997–98 El Niño event on the Pacific coast of Colombia. Bull Mar Sci 69:111–132

816 Vega Thurber RL, Burkepile DE, Fuchs C, Shantz AA, McMinds R, Zaneveld JR (2014)

817   Chronic nutrient enrichment increases prevalence and severity of coral disease and

818   bleaching. Glob Chang Biol 20:544–554

819 Wang L, Shantz AA, Payet JP, Sharpton TJ, Foster A, Burkepile DE, Vega Thurber R (2018)

820   Corals and Their Microbiomes Are Differentially Affected by Exposure to Elevated

821   Nutrients and a Natural Thermal Anomaly. Front Mar Sci 5:101

822 Wiedenmann J, D'Angelo C, Smith EG, Hunt AN, Legiret F-E, Postle AD, Achterberg EP

823   (2013) Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nat

824   Clim Chang 3:160–164

825 Wolanski E, Andutta F, Deleersnijder E, Li Y, Thomas CJ (2017) The Gulf of Carpentaria

826   heated Torres Strait and the Northern Great Barrier Reef during the 2016 mass coral

827   bleaching event. Estuar Coast Shelf Sci 194:172–181

828 Wolanski E, Pickard G (1983) Upwelling by internal tides and kelvin waves at the continental

829   shelf break on the Great Barrier Reef. Mar Freshw Res 34:65

830 Wooldridge SA (2009) Water quality and coral bleaching thresholds: Formalising the linkage for

831   the inshore reefs of the Great Barrier Reef, Australia. Mar Pollut Bull 58:745–751

832 Wooldridge SA (2016) Excess seawater nutrients, enlarged algal symbiont densities and

833   bleaching sensitive reef locations: 1. Identifying thresholds of concern for the Great Barrier

834   Reef, Australia. Mar Pollut Bull

835 Zhai F, Hu D, Wang Q, Wang F (2014) Long-term trend of Pacific South Equatorial Current

836   bifurcation over 1950-2010. Geophys Res Lett 41:3172–3180

837

838 **Figure captions:**

839

840 Figure 1. Sea surface temperature (SST) time series of the Great Barrier Reef (GBR). The middle

841 and bottom panels show the average SST of all grid boxes in the weekly NOAA OI-SSTv1 or

842 monthly HadISST dataset covering the entire GBR from 1982 to 2017. The vertical axes are

843 restricted to >27.5 °C to highlight summertime temperatures. Red background coloring indicates

844 the years of severe mass coral bleaching reported in the GBR (1998, 2002, 2016, and 2017). The

845 horizontal blue dashed lines indicate the maximum GBR-wide SST in each dataset. On average

846 across the GBR, the highest temperatures of the satellite era were reached in 2004 (note that this

847 does not mean 2004 was the warmest summer everywhere on the GBR; see spatial analyses

848 below). The right axis and top panel show the summertime Marine Heatwave (MHW) index as

849 defined by Hobday et al. (2018). Category 2 ("Strong") heatwaves occurred GBR-wide in 1998,

850 2002, and 2004.

851

852 Figure 2: Heat stress on the GBR during austral summers of 2004 and years when mass coral

853 bleaching was observed. Rows correspond to different satellite-SST products and columns show

854 the key years assessed in this study. Colors represent the maximum DHW per 5-km pixel during

855 each year. White triangles indicate the locations of *in situ* temperature loggers used each year in

856 the validation of satellite-derived SST. Black dots represent the reefs of the GBR and Coral Sea.

857 The white circle in 2004 maps indicates Lihou Reef, where 65% bleaching was observed.

858

859 Figure 3. Year of maximum DHW (1998-2017). In A, D, G, J, colors indicate the year with

860 highest DHW. Locations where the highest DHW occurred in any year other than 1998, 2002,

861   2004, 2016, or 2017 are colored white. Histograms show the proportion of reefs on the GBR

862   experiencing their highest DHW in each year (B, E, H, K), and the proportion of reefs with

863   DHW exceeding 4 °C-weeks (C, F, I, L).

864

865   Figure 4. Satellite-logger temperature validations per year (rows) and per SST product

866   (columns). The data are daily for CRW, OI-SSTv2, and CMC, and weekly for OI-SSTv1. Gray

867   points are non-hotspot times, blue points are hotspot times only in loggers, red points are hotspot

868   times only in satellite products, and black points are hotspot times in both the loggers and

869   satellites. The dashed black lines indicate 1:1 relationships.

870

871   Figure 5. Comparison of DHW derived from CRW and OI-SSTv2 during 2004. Colors show the

872   difference in maximum DHW, where red indicates that OI-SSTv2 estimates higher DHW than

873   CRW. Circles show were temperature loggers best matched maximum DHW in CRW (dark

874   gray) or OI-SSTv2 (light gray).

875

876   Figure 6. Outgoing longwave radiation (OLR and photosynthetically active radiation (PAR; A-

877   E), surface wind speed (F-J), and SST (OI-SSTv2; K-O) time series during January, February

878   and March of 2004 and years when bleaching was observed. Red indicates anomalously high and

879   blues indicate anomalously low OLR or winds relative to the weekly climatology. Only grid

880   boxes covering GBR reefs were included in the analysis. The SST panels also indicate marine

881   heatwave categories, as defined by Hobday et al., (2018).

882

883   Figure 7. Photosynthetically active radiation (PAR) March anomalies during 1998, 2002, 2004,

884   2016, and 2017 (A-E). Histograms (F-J) show the proportions of GBR reefs with positive (red)

885   and negative (blue) PAR anomalies in March of each year. The black circle in the 2004 map

886   indicates the location of the Keppel Islands, where Skirving et al. (2017) assessed PAR and heat

887   stress.

888

889   Figure 8. Seasonal timing of SST maxima and their difference from PAR maxima. A-E show the

890   year day of maximum SST during 2004 and bleaching years (negative days indicate December of

891   the preceding year), using OI-SSTv2 data. Histograms (F-J) with black bars show the proportion

892   of GBR reefs with SST maximum occurring at various year days. K-O maps show the difference

893   in days between maximum SST and maximum PAR, and the histograms in P-T show the

894   corresponding proportions of GBR reefs. Red (blue) indicates that maximum SST occurred after

895   (before) maximum PAR. SST maxima occurred relatively early in 2002, but the timing of

896   maximum SST during 2004 is broadly similar to that of 1998, 2016, and 2017.

897

898   Figure 9. Sea surface currents, height, and temperature anomalies for January, February, and

899   March of bleaching years (1998, 2002, 2004) included in SODA. In the velocity plots (A-C),

900   arrows indicate the absolute current velocity, and colors represent the anomaly of absolute

901   current velocity relative to the climatological mean (1982-2015). In the SSH (D-F) and SST (G-

902   I) plots, colors likewise indicate anomalies relative to the climatological mean. Green lines

903   indicate the location of the temperature and SSH cross-sections shown in J-L (location of cross-

904   section corresponds to the main upwelling intrusion passages; see Benthuysen et al. 2016). Inset

905   image in the 1998 velocity maps shows the general location of each current, although the

906   location of the bifurcation point varies over time. EAC: East Australian Current, NQC: North

907   Queensland Current, SEC: South Equatorial Current.

908

909   Figure 10. Ekman vertical transport anomalies for January, February, and March of bleaching

910   years (1998, 2002, 2004) included in SODA. Red (blue) indicate anomalously upwelling

911   (downwelling) favorable wind stress curl.

912

913   Figure 11. Trends in near-surface (0-25 m) velocity during January, February and March in

914   SODA (1980-2015). Colors indicate the rate of velocity change, and arrows indicate the

915   climatological mean velocity field.

916

Comparison of satellite-derived SST and *in situ* temperature measurements on the GBR and in the Coral Sea.

CRW and OI-SSTv2 data are daily, and OI-SSTv1 is weekly. RMSE indicates the root mean square error between daily or weekly satellite and logger temperature data (°C). Bias indicates the mean difference between satellite and logger temperature data (°C). Hotspots refers to the days (or weeks for OI-SST) with temperature >1 °C above the maximum monthly mean (MMM), and thus contribute to degree heating weeks (DHW). For each metric and each year, the best performing satellite product is in bold and underlined.

2 Table 1. Comparison of satellite-derived SST and *in situ* temperature measurements on the GBR

3 and in the Coral Sea. CRW and OI-SSTv2 data are daily, and OI-SSTv1 is weekly. RMSE

4 indicates the root mean square error between daily or weekly satellite and logger temperature

5 data (°C). Bias indicates the mean difference between satellite and logger temperature data (°C).

6 Hotspots refers to the days (or weeks for OI-SST) with temperature >1 °C above the maximum

7 monthly mean (MMM), and thus contribute to degree heating weeks (DHW). For each metric

8 and each year, the best performing satellite product is in bold and underlined.

	1998				2002				2004			
	CRW	OISSTv2	OISSTv1	CMC	CRW	OISSTv2	OISSTv1	CMC	CRW	OISSTv2	OISSTv1	CMC
RMSE	0.63	0.71	0.80	**0.61**	0.71	0.74	0.79	**0.63**	**0.46**	0.57	0.63	0.48
Bias	-0.10	**0.06**	0.31	0.23	-0.27	**0.09**	0.23	0.21	-0.09	**0.04**	0.25	0.14
RMSE (hotspots)	1.12	1.00	1.03	**0.80**	1.16	0.96	0.97	**0.84**	0.75	0.80	1.11	**0.74**
Bias (hotspots)	-0.74	-0.20	**-0.02**	-0.30	-0.73	**-0.05**	0.07	0.07	-0.42	**0.12**	0.40	0.25

	2016				2017			
	CRW	OISSTv2	OISSTv1	CMC	CRW	OISSTv2	OISSTv1	CMC
RMSE	**0.40**	0.46	0.53	**0.40**	**0.30**	0.43	0.54	0.34
Bias	**0.03**	-0.06	0.11	0.08	**-0.01**	0.02	**0.01**	**0.01**
RMSE (hotspots)	0.61	0.75	0.74	**0.57**	**0.36**	0.54	0.68	0.37
Bias (hotspots)	-0.15	-0.17	0.20	**0.08**	-0.08	-0.08	-0.23	**-0.04**

Comparison of satellite-derived and *in situ* logger estimates of heat stress metrics.

Hotspot days are the total number of days with temperature >1 °C above the maximum monthly mean (MMM). Total hotspots are the number of hotspot days multiplied by average anomaly relative to the MMM for those days. Degree heating weeks (DHW) are defined in the text, and integrate both the magnitude and duration of temperatures anomalies exceeding the MMM. All three metrics are presented as the average among available loggers (and the grid boxes covering those logger sites). For each metric and each year, the best performing satellite product is in bold and underlined. Note that the loggers do not represent a random sampling of GBR locations, and the locations of loggers was not the same across years, meaning that the absolute values of heat stress metrics presented here should be compared within each year but not between years.

1   Table 2. Comparison of satellite-derived and *in situ* logger estimates of heat stress metrics.

2   Hotspot days are the total number of days with temperature >1 °C above the maximum monthly

3   mean (MMM). Total hotspots are the number of hotspot days multiplied by average anomaly

4   relative to the MMM for those days. Degree heating weeks (DHW) are defined in the text, and

5   integrate both the magnitude and duration of temperatures anomalies exceeding the MMM. All

6   three metrics are presented as the average among available loggers (and the grid boxes covering

7   those logger sites). For each metric and each year, the best performing satellite product is in bold

8   and underlined. Note that the loggers do not represent a random sampling of GBR locations, and

9   the locations of loggers was not the same across years, meaning that the absolute values of heat

10 stress metrics presented here should be compared within each year but not between years.

	1998					2002					2004				
	CRW	OISST v2	OISST v1	CMC	Loggers	CRW	OISST v2	OISST v1	CMC	Loggers	CRW	OISST v2	OISST v1	CMC	Loggers
Hotspot days	10.5	**20.8**	25.1	20.0	21.2	14.7	41.7	**40.1**	46.5	38.5	13.1	**31.4**	31.6	37.7	23.1
Total Hotspots	14.3	31.2	**31.7**	27.4	35.1	18.6	**61.2**	53.3	68.7	62.7	16.4	**42.4**	43.4	50.3	33.5
Maximum DHW	2.0	4.4	**4.5**	3.8	4.9	2.4	7.8	**7.6**	8.9	7.6	2.2	**5.5**	6.2	6.7	4.5

	2016					2017				
Hotspot days	**14.4**	12.8	24.7	22.0	17.5	**40.4**	35.0	21.7	33.5	42.0
Total Hotspots	18.7	16.7	31.0	**28.3**	23.9	**51.0**	46.9	25.4	42.1	55.4
Maximum DHW	**2.7**	2.4	4.4	4.0	3.3	**7.3**	6.5	3.6	6.0	7.5

Figure 1

Sea surface temperature (SST) time series of the Great Barrier Reef (GBR).

The middle and bottom panels show the average SST of all grid boxes in the weekly NOAA OI-SSTv1 or monthly HadISST dataset covering the entire GBR from 1982 to 2017. The vertical axes are restricted to >27.5 °C to highlight summertime temperatures. Red background coloring indicates the years of severe mass coral bleaching reported in the GBR (1998, 2002, 2016, and 2017). The horizontal blue dashed lines indicate the maximum GBR-wide SST in each dataset. On average across the GBR, the highest temperatures of the satellite era were reached in 2004 (note that this does not mean 2004 was the warmest summer everywhere on the GBR; see spatial analyses below). The right axis and top panel show the summertime Marine Heatwave (MHW) index as defined by Hobday et al. (2018) . Category 2 ("Strong") heatwaves occurred GBR-wide in 1998, 2002, and 2004.
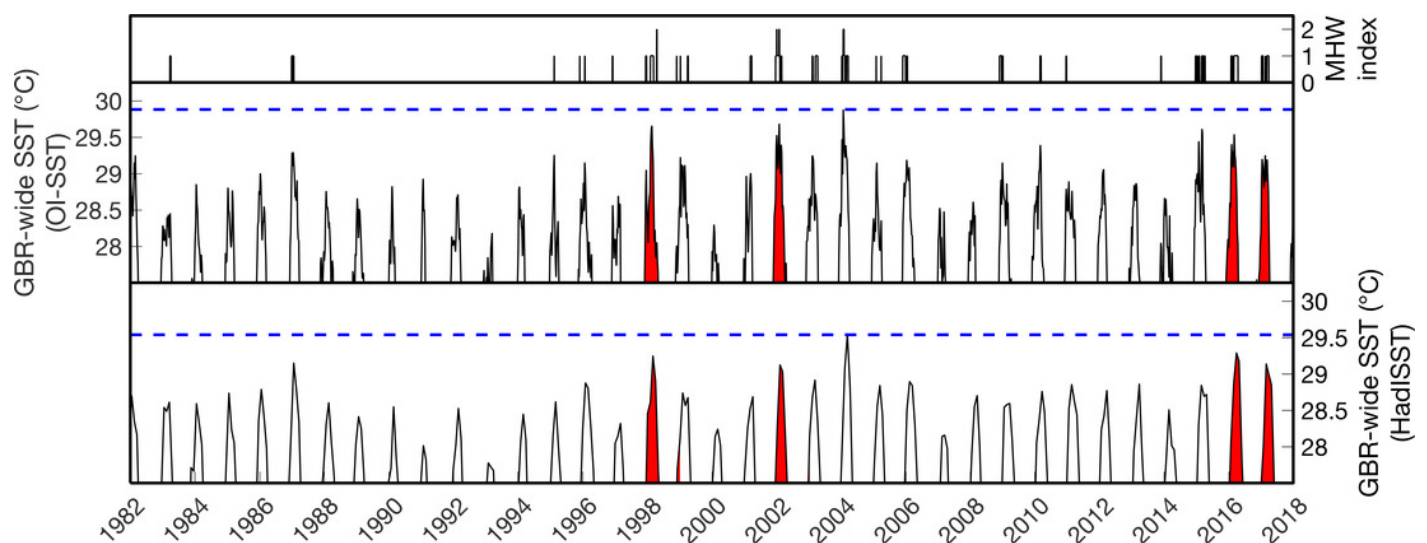
Figure 2

Heat stress on the GBR during austral summers of 2004 and years when mass coral bleaching was observed.

Rows correspond to different satellite-SST products and columns show the key years assessed in this study. Colors represent the maximum DHW per 5-km pixel during each year. White triangles indicate the locations of *in situ* temperature loggers used each year in the validation of satellite-derived SST. Black dots represent the reefs of the GBR and Coral Sea. The white circle in 2004 maps indicates Lihou Reef, where 65% bleaching was observed.
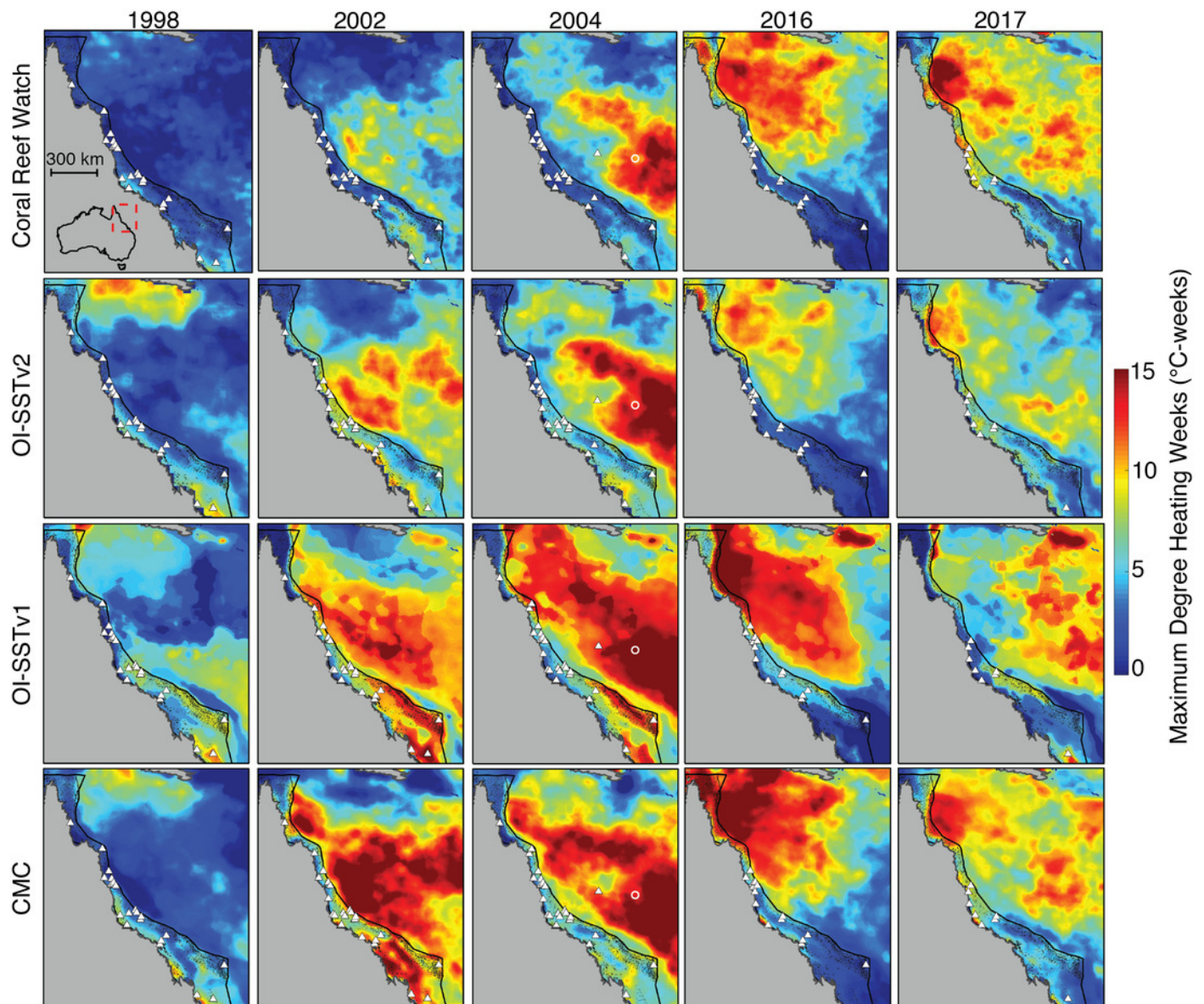
Figure 3

Year of maximum DHW (1998-2017).

In A, D, G, J, colors indicate the year with highest DHW. Locations where the highest DHW occurred in any year other than 1998, 2002, 2004, 2016, or 2017 are colored white. Histograms show the proportion of reefs on the GBR experiencing their highest DHW in each year (B, E, H, K), and the proportion of reefs with DHW exceeding 4 °C-weeks (C, F, I, L).
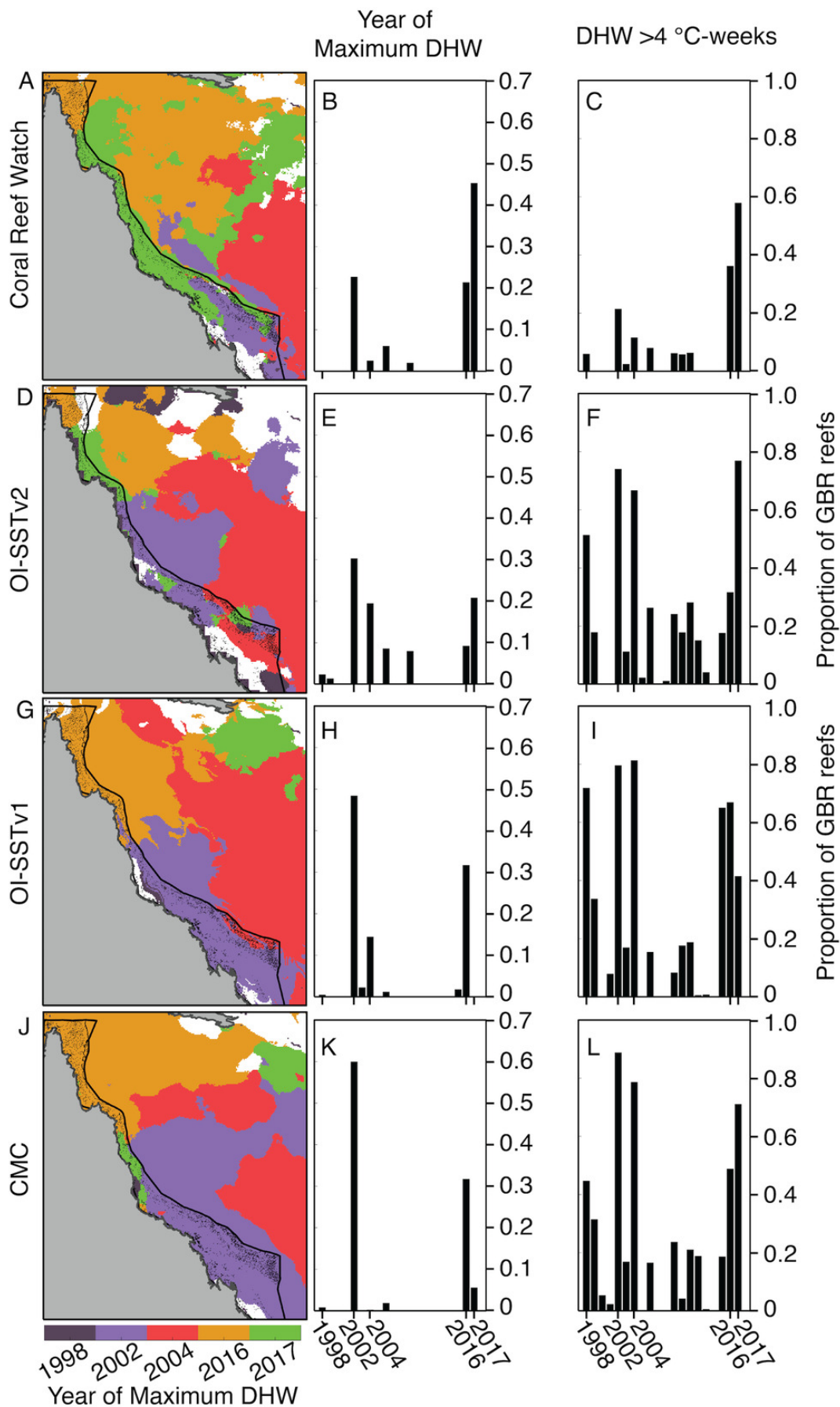
Figure 4

Satellite-logger temperature validations per year and per SST product.

The data are daily for CRW, OI-SSTv2, and CMC, and weekly for OI-SSTv1. Gray points are non-hotspot times, blue points are hotspot times only in loggers, red points are hotspot times only in satellite products, and black points are hotspot times in both the loggers and satellites. The dashed black lines indicate 1:1 relationships.
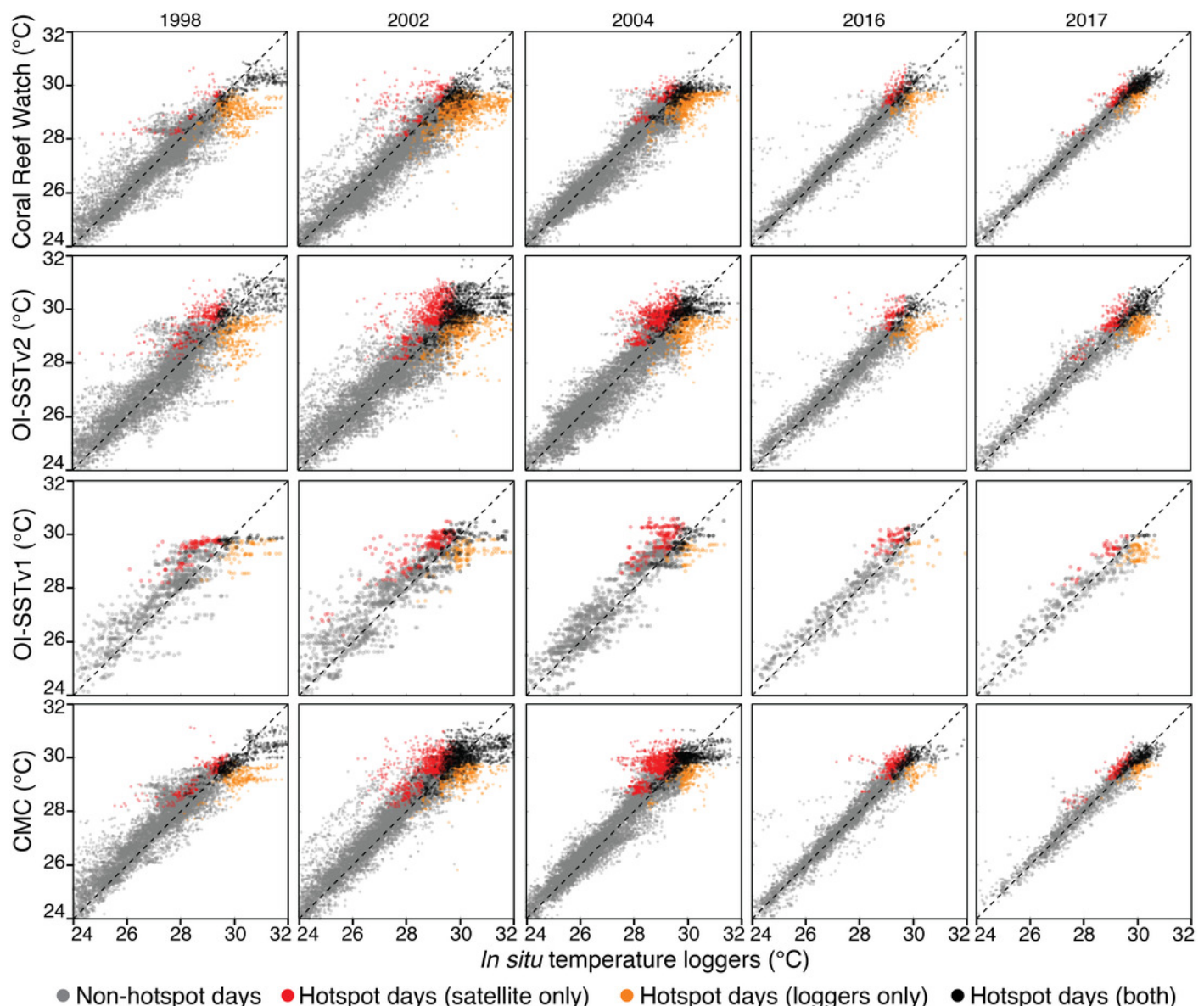
Figure 5

Comparison of DHW derived from CRW and OI-SSTv2 during 2004.

Colors show the difference in maximum DHW, where red indicates that OI-SSTv2 estimates higher DHW than CRW. Circles show were temperature loggers best matched maximum DHW in CRW (dark gray) or OI-SSTv2 (light gray).
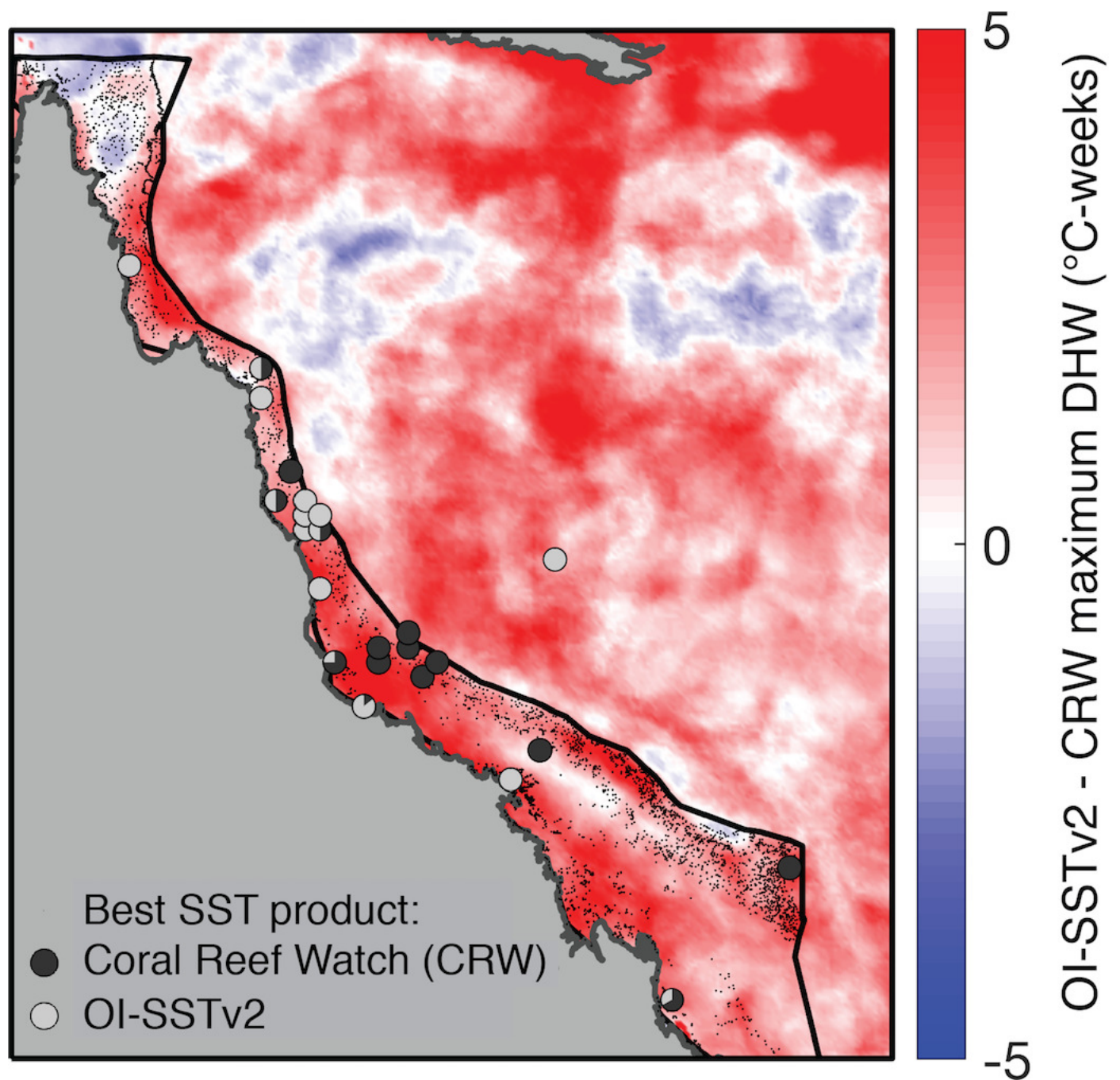
Figure 6

Outgoing longwave radiation (OLR and photosynthetically active radiation (PAR; A-E), surface wind speed (F-J), and SST (OI-SSTv2; K-O) time series during January, February and March of 2004 and years when bleaching was observed.

Red indicates anomalously high and blues indicate anomalously low OLR or winds relative to the weekly climatology. Only grid boxes covering GBR reefs were included in the analysis. The SST panels also indicate marine heatwave categories, as defined by Hobday et al., (2018).
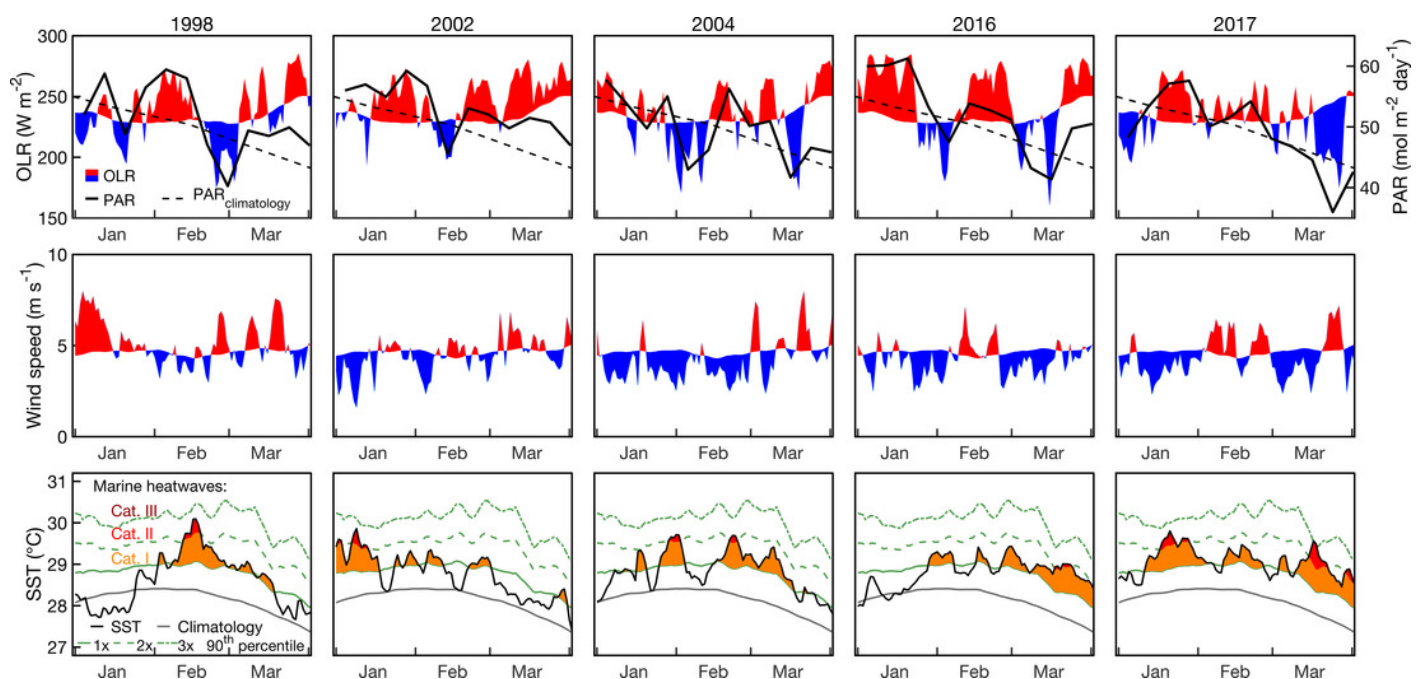
Figure 7

Photosynthetically active radiation (PAR) March anomalies during 1998, 2002, 2004, 2016, and 2017 (A-E).

Histograms (F-J) show the proportions of GBR reefs with positive (red) and negative (blue) PAR anomalies in March of each year. The black circle in the 2004 map indicates the location of the Keppel Islands, where Skirving et al. (2017) assessed PAR and heat stress.
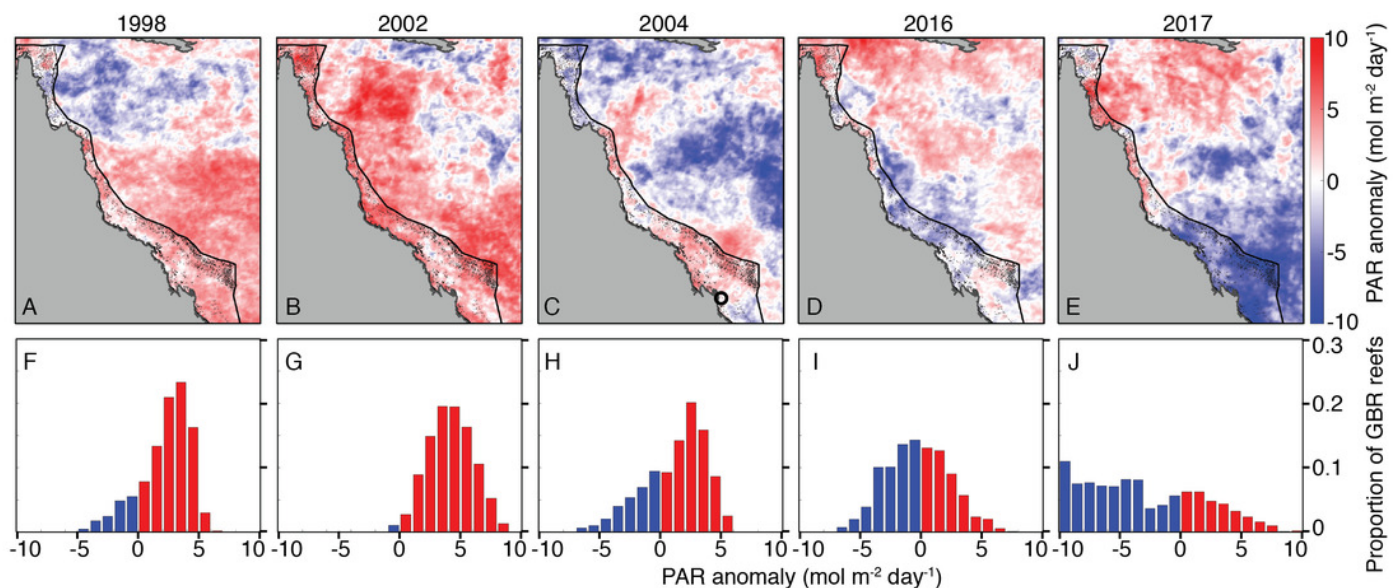
Figure 8

Seasonal timing of SST maxima and their difference from PAR maxima.

A-E show the year day of maximum SST during 2004 and bleaching years (negative days indicate December of the preceding year), using OI-SSTv2 data. Histograms (F-J) with black bars show the proportion of GBR reefs with SST maximum occurring at various year days. K-O maps show the difference in days between maximum SST and maximum PAR, and the histograms in P-T show the corresponding proportions of GBR reefs. Red (blue) indicates that maximum SST occurred after (before) maximum PAR. SST maxima occurred relatively early in 2002, but the timing of maximum SST during 2004 is broadly similar to that of 1998, 2016, and 2017.
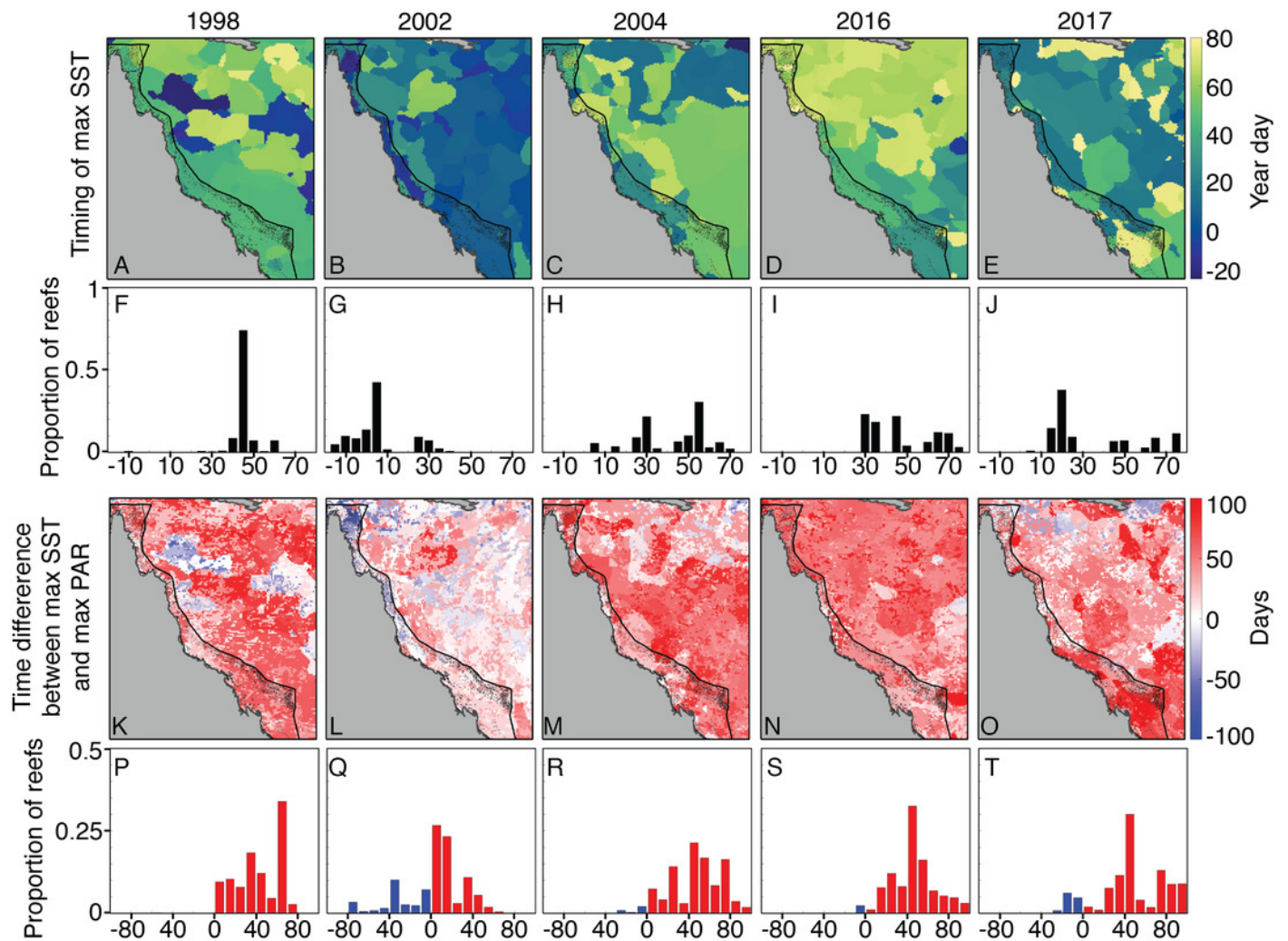
Figure 9

Sea surface currents, height, and temperature anomalies for January, February, and March of bleaching years (1998, 2002, 2004) included in SODA.

In the velocity plots (A-C), arrows indicate the absolute current velocity, and colors represent the anomaly of absolute current velocity relative to the climatological mean (1982-2015). In the SSH (D-F) and SST (G-I) plots, colors likewise indicate anomalies relative to the climatological mean. Green lines indicate the location of the temperature and SSH cross-sections shown in J-L (location of cross-section corresponds to the main upwelling intrusion passages; see Benthuysen et al. 2016) . Inset image in the 1998 velocity maps shows the general location of each current, although the location of the bifurcation point varies over time. EAC: East Australian Current, NQC: North Queensland Current, SEC: South Equatorial Current.
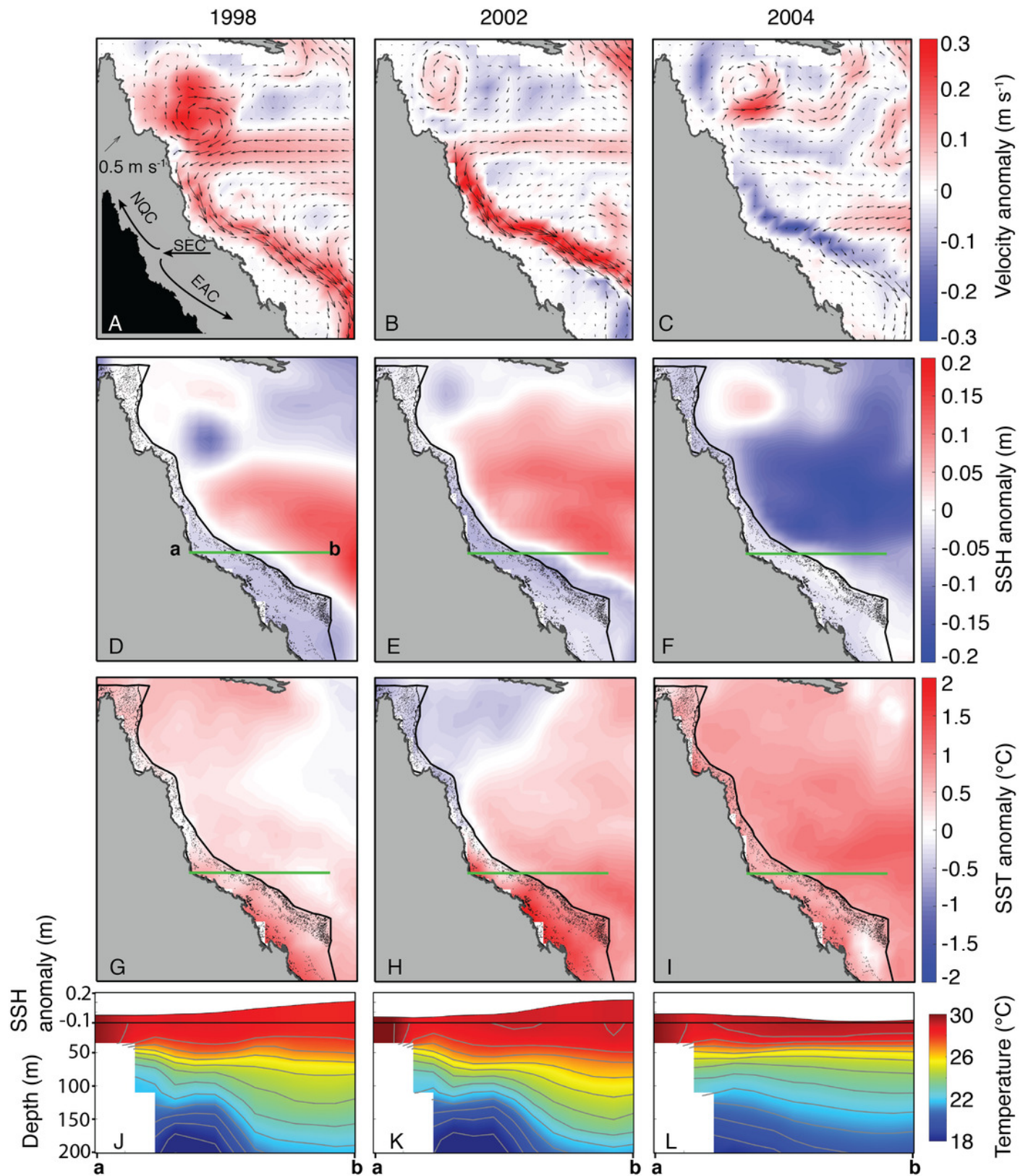
Figure 10

Ekman vertical transport anomalies for January, February, and March of bleaching years (1998, 2002, 2004) included in SODA.

Red (blue) indicate anomalously upwelling (downwelling) favorable wind stress curl.
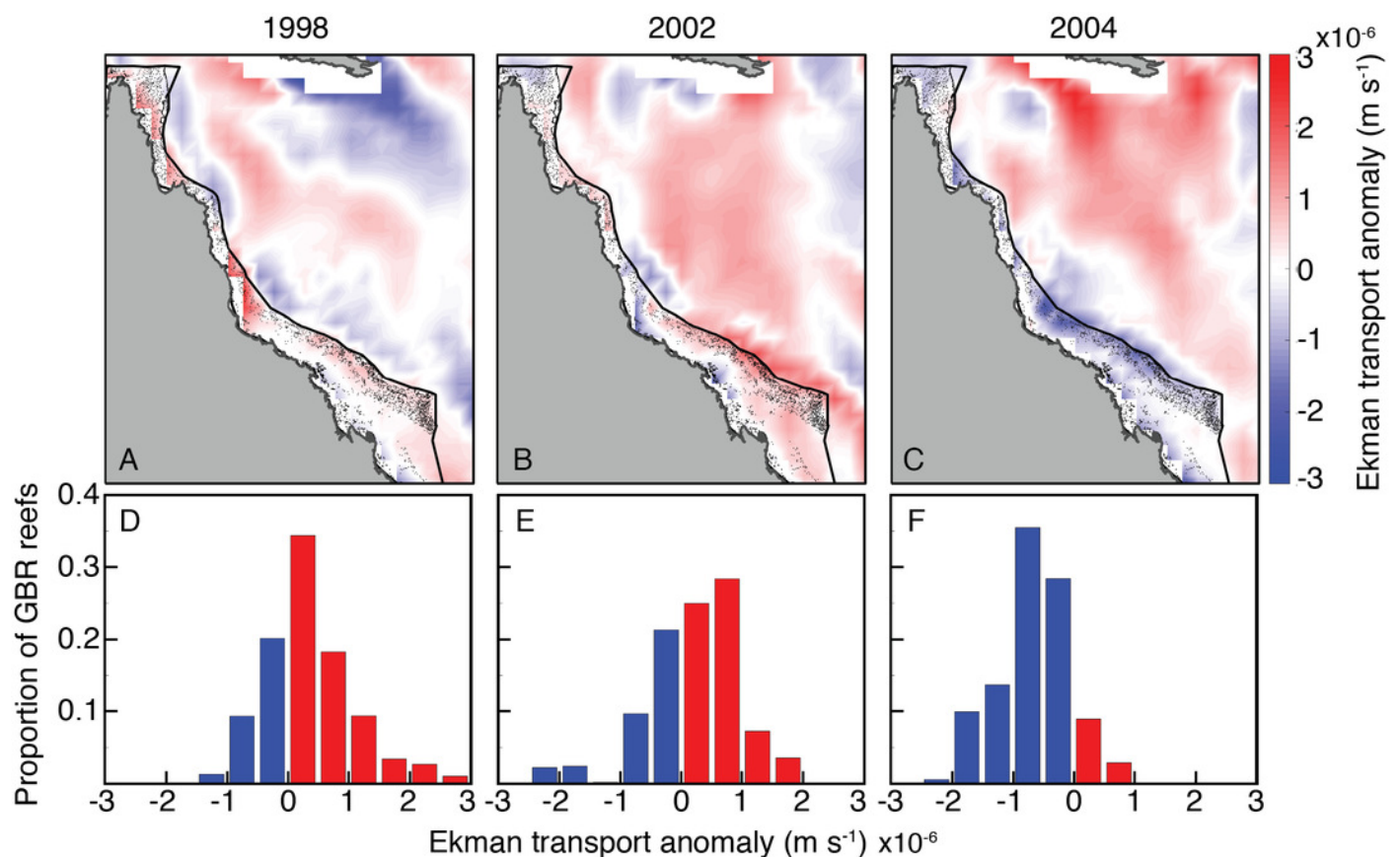
Figure 11

Trends in near-surface (0-25 m) velocity during January, February and March in SODA (1980-2015).

Colors indicate the rate of velocity change, and arrows indicate the climatological mean velocity field.