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Upwelling linked to warm summers and bleaching on the Great Barrier Reef

Ray Berkelmans,[a,b,*] Scarla J. Weeks,[b,c] and Craig R. Steinberg[a,b]

[a] Australian Institute of Marine Science, Townsville, Australia
[b] Reef and Rainforest Research Centre Ltd., Marine Tropical Science Research Facility, Cairns, Australia
[c] Global Change Institute, and Centre for Spatial Environmental Research, University of Queensland, Brisbane, Australia

Abstract

We investigate a range of indices to quantify upwelling on the central Great Barrier Reef (GBR), Australia, so that environmental and biological relationships associated with upwelling in this area can be explored. We show that "Upwelling days" (the number of days of upwelling) and diurnal variation in subsurface temperature (maximum–minimum, 20-m depth) are satisfactory metrics to describe the duration and intensity of upwelling events, respectively. We use these to examine key characteristics of shelf-break upwelling in the central GBR. Our results show, somewhat paradoxically, that although upwelling involves cold water being brought near to the surface, it is linked to positive thermal anomalies on the GBR, both locally and regionally. Summers (December to February) with strongest upwelling occurred during the GBR-wide bleaching events of 1997–1998 and 2001–2002. Upwelling in the GBR is enhanced during doldrums conditions that were a feature of these summers. During these conditions, the poleward-flowing East Australian Current flows faster, lifting the thermocline closer to the surface, spilling more sub-thermocline waters onto the shelf. Doldrums conditions also result in intense local heating, stratification of the water column, and, when severe, coral bleaching. Upwelling intrusions are spatially restricted (central GBR), generally remain subsurface, and are often intermittent, allowing GBR-wide bleaching to occur despite conditions resulting in enhanced upwelling. Intense upwelling events precede anomalous seasonal temperature maxima by up to 2 months and bleaching by 1–3 wk, leading to the prospect of using upwelling activity as a seasonal forecasting index of unusually warm summers and widespread bleaching.

Upwelling of cold, nutrient-rich, sub-thermocline waters to the sea surface is one of the most important oceanographic processes due to its vast influence on coastal ecological communities. The most intense coastal upwelling regions are associated with the four major eastern boundary current systems in the Atlantic and Pacific Oceans: the Peru–Humboldt, California, Benguela, and Canary Currents. These wind-driven coastal upwelling ecosystems are "hotspots" of marine primary production, accounting for up to 50% of the world's commercial fish production (Mann and Lazier 2006).

Upwelling along western boundary currents, especially in coral reef environments, is less well studied and its ecological effects consequently less well understood. Upwelling in these areas is often spatially restricted, less intense, more ephemeral, and ecosystem responses are less dramatic compared to upwelling ecosystems along eastern boundary currents. This is partly due to the trade winds that favor onshore transport of surface waters and suppress any surface expression of upwelling. Although upwelling was originally understood as the sustained surface expression of cold sub-thermocline water (Rochford 1991), we use the term to include all cold water uplifted to the surface layer regardless of whether it breaks the surface or not, because all uplifted cold water has the potential to influence reef communities. Ecosystem responses linked to upwelling in tropical reef environments include the formation and sustenance of extensive banks of calcareous algae (*Halimeda* sp.) behind narrow reef openings in the northern Great Barrier Reef (GBR) (Wolanski et al. 1988). An unusually strong Indian Ocean Dipole in 1997 caused intense upwelling resulting in plankton blooms that killed corals along a 4000-km stretch of coast from Bali to Sumatra (Van Woesik 2004). In the Arabian Gulf, upwelling is associated with high seasonal kelp and brown macroalgal growth, while the reduced temperatures associated with upwelling in this area are linked to suppression of reef development (Coles 1988). Reduced temperatures associated with upwelling have also been linked to decreased prevalence of coral disease off the northeast coast of Venezuela (Rodriguez and Croquer 2008). Cooler water associated with upwelling in coral reef areas off the Bahamas and South Africa has been suggested as having protected reefs from more severe bleaching during the 1998 global bleaching event (Riegl and Piller 2003). Coral reef bleaching is a stress response by stony corals and other organisms that are in obligate symbiosis with *Symbiodinium* algae. Severe or prolonged thermal stress results in the breakdown of this symbiotic relationship and can lead to mass mortality (Hughes et al. 2003; Hoegh-Guldberg et al. 2007). Upwelling regions in coral reef ecosystems have even been suggested to be refugia for coral during catastrophic climate change (Riegl and Piller 2003; Sheppard 2009). While these studies show a substantial influence of upwelling in coral reef environments, ongoing research is hampered by the difficulty in quantifying upwelling, and hence an ability to explore longer-term relationships between patterns and dynamics of upwelling and their effects on coral reefs.

The large-scale (hundreds to 1000 km) oceanography of Australia's GBR is well documented (reviewed by Steinberg 2007); however, many smaller-scale (tens to hundreds of

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[*] Corresponding author: r.berkelmans@aims.gov.au

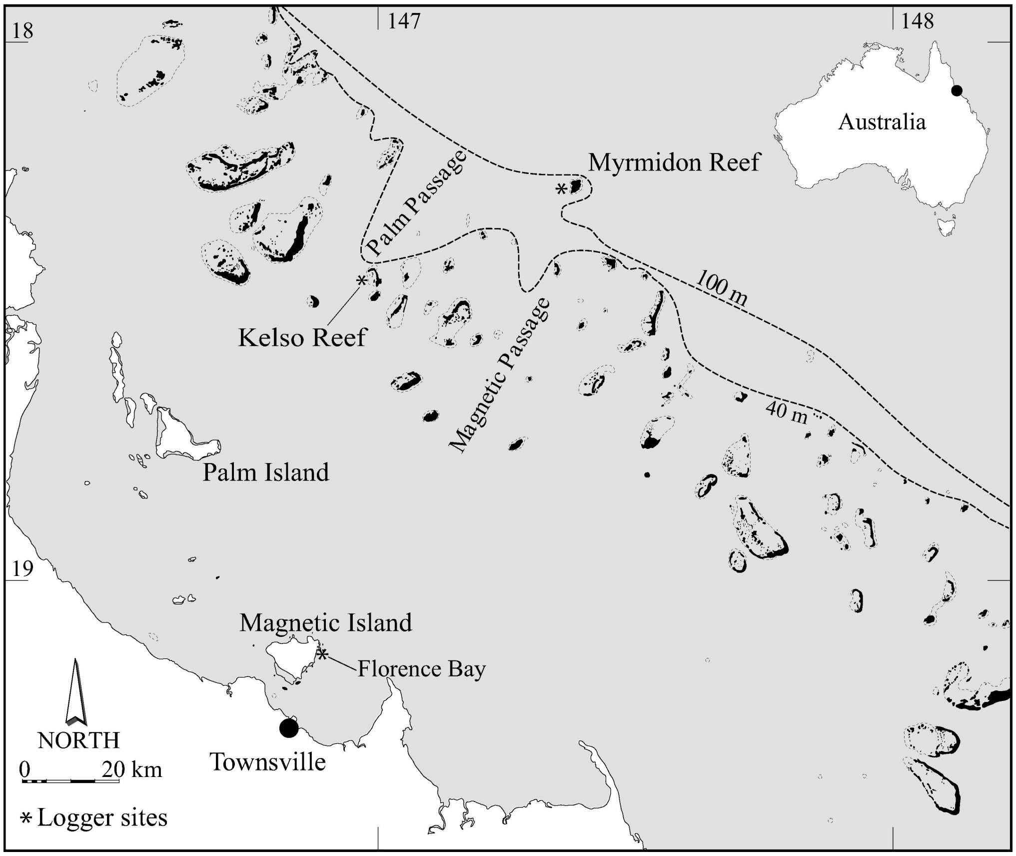

Fig. 1. Map of study sites at Myrmidon Reef, Kelso Reef, and Magnetic Island in the central Great Barrier Reef.

kilometers) phenomena remain poorly understood. While the GBR is not considered a major upwelling area due to its position along a western boundary current (East Australian Current), significant upwelling may occur at the continental shelf break (Bakun 1996). Upwelling in this region occurs when the strong poleward-flowing East Australian Current (EAC) creates frictional drag against the shallowing shelf edge leading, on a restricted scale, to bottom subgeostrophic flow as a consequence of an unbalanced onshore–offshore pressure gradient (Bakun 2006). This results in onshore transport of the bottom Ekman layer (Wolanski and Pickard 1983; Bakun 2006). Tidal pumping (Thompson and Golding 1981; Nof and Middleton 1989), cyclonic eddies (Szekielda 1971), and internal wave perturbations on the thermocline (e.g., caused by processes such as wind and tidal mixing) act in concert with the onshore transport of the bottom Ekman layer to draw sub-thermocline water to the surface layer (Wolanski and Bennett 1983; Griffin and Middleton 1986).

Shelf-break upwelling on the GBR occurs in restricted areas such as the central GBR (Furnas and Mitchell 1996) and occurs annually between latitudes 18°S and 19°S (Fig. 1). In this area, the continental shelf changes orientation from predominately north–south to northwest–southeast, producing a component of on-shelf flow from the deflection of linear momentum due to curvature imposed on the flow (Bakun 2006). There are also large gaps with relatively deep channels between reefs along the shelf edge in this area, which allows Coral Sea water (surface and upwelled water) to periodically spill onto the shelf (Brinkman et al. 2002). The Palm and Magnetic Passages are the most prominent ingress points for upwelled water which then flows southeast through the GBR lagoon for up to 200 km (Andrews and Furnas 1986; Fig. 1). Shelf-edge upwelling occurs during the warmer months between October and April (Andrews and Gentien 1982; Andrews and Furnas 1986). Data from short-term (< 1 yr) current-meter deployments suggest that the seasonal component of these upwelling events coincides with cyclical wind-driven changes in the EAC (Andrews and Gentien 1982). However, long-term data on EAC dynamics and its influence on upwelling are still lacking. Within the warm season, upwelling events coincide with large fluctuations in the depth of the thermocline (from $>$ 100 m to within tens of meters of the surface). Most of the studies on upwelling on the GBR (reviewed by Steinberg 2007) to date have explored the short-term (< 1 yr) dynamics and causal factors associated with this phenomenon, while the longer-term (> 10 yr) dynamics of upwelling and its relationship to environmental variables, such as thermal anomalies and bleaching, remain unexplored.

In this study we analyze 13 yr (1995–2007) of data from temperature loggers in the central GBR to elucidate upwelling dynamics and its link to thermal anomalies. Specifically, we addressed the following questions: (1) Which are the best metrics with which to quantify

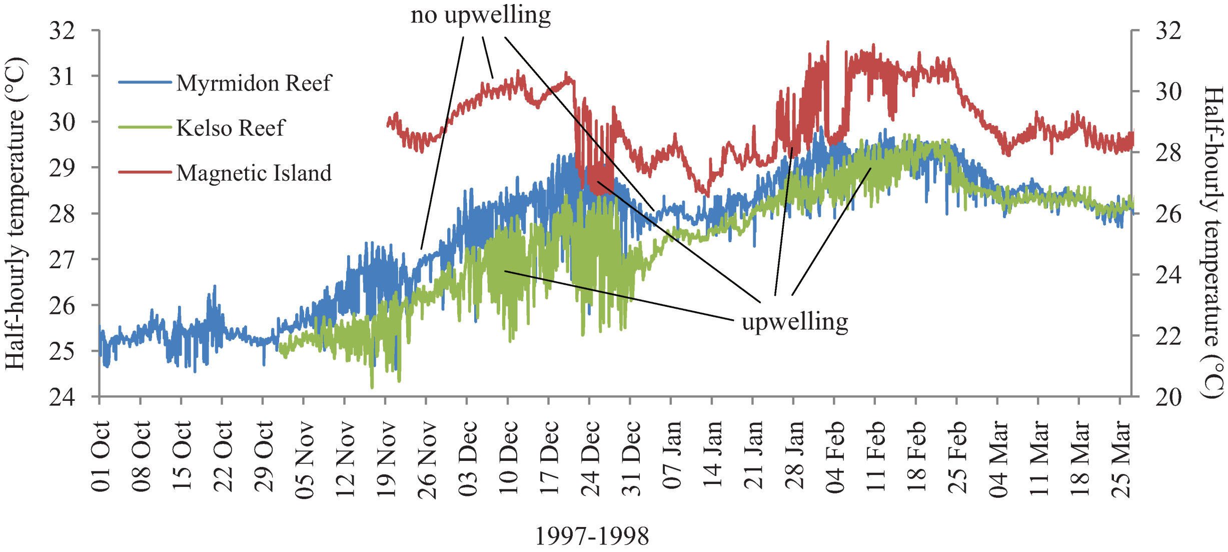

Fig. 2. Example of intense upwelling activity during the 1997–1998 summer as measured by temperature loggers at three locations in the central GBR: Myrmidon Reef (outer shelf, 20-m depth), Kelso Reef (mid-shelf, 20-m depth), and Magnetic Island (inshore, 9-m depth). Upwelling is typified by large negative temperature fluctuations that are highly variable in terms of their duration and magnitude. Examples of upwelling and non-upwelling periods indicated. Note: Magnetic Island data is drawn on a different scale for clarity (right *y*-axis).

upwelling? (2) What is the relationship between duration and intensity of upwelling? (3) Is there a relationship between upwelling duration and seasonal temperature? (4) Is there a relationship between the timing of upwelling and seasonal temperature?

We show that upwelling is linked to positive thermal anomalies on the GBR and that the most frequent and intense upwelling events occur during anomalously warm years, including the mass coral bleaching years of 1998 and 2002. Intense upwelling events precede anomalous seasonal maxima by up to 2 months and bleaching by 1–3 wk, leading to the prospect of using upwelling activity as a seasonal forecasting index of unusually warm summers and widespread bleaching.

Methods

Upwelling was inferred from temperature data obtained from loggers deployed on the lower reef slope at Myrmidon Reef (20-m depth) on the outer edge of the GBR, Kelso Reef in the middle of the Palm Passage (20-m depth), and Florence Bay on Magnetic Island (9-m depth; Fig. 1). Furnas and Mitchell (1996) showed that temperature is a satisfactory surrogate for upwelling on the GBR, with abrupt temperature plunges (spikes) correlating strongly with high-nutrient, upwelled water. As with upwelling in other regions, the duration and magnitude of these plunges varies with depth, location, and over time scales of $<$ 1 h to days. Temperature data from these sites were collected continuously at half-hourly measurement intervals and cover the period 1995 to 2006 for Myrmidon Reef, with a gap for the 1996–1997 and 1999–2000 summers; 1996 to 2007 for Kelso Reef, with a gap for the 2001–2002 summer; and 1995 to 2007 for Magnetic Island, with a gap for the 1996–1997 and 2004–2005 summers. Temperature loggers (Dataflow 392 and Odyssey, Dataflow Systems) have a measurement resolution of 0.02°C and were calibrated prior to each annual deployment to an accuracy of 0.1–0.2°C.

Exploring upwelling metrics—In order to explore upwelling dynamics, it is necessary to determine an appropriate measure with which to quantify upwelling. Negative temperature spikes associated with upwelling can be short- or long-lived ($<$ 1 hr to days) and the magnitude can range from almost undetectable ($<$ 0.5°C) to very large ($>$ 6°C). Typically, the pattern of variation during upwelling is erratic compared to non-upwelling periods at high temporal resolution (30 min; Fig 2). Ideally, a good metric to quantify upwelling would be reliably modeled using statistical techniques. For this study, we used a Classification Trees model as this produced more accurate results compared to binomial and multinomial logistic regression techniques in a training data set. Trees uses a hierarchical system of splits, each one resulting in more homogeneous groups (De'ath and Fabricius 2000). We used Trees to examine the effects of predictor metrics one at a time on the categorical response variable, upwelling.

Upwelling metrics were explored using high-temporal-resolution (half-hourly) temperature data from Myrmidon Reef. Three years were selected spanning the austral warm season (September to April), representing seasons of high (1995–1996), medium (2003–2004), and low (2002–2003) upwelling activity, based on preliminary visualization of the data. Periods of upwelling were flagged and classified in a time-series editing program (Wiski-TV, Kisters; www.kisters.de) based on sudden negative temperature spikes relative to preceding and following data. Data from a reef-flat (2 m) logger at each reef, which generally does not register upwelling, were used as an additional guide to discern upwelling-associated temperature spikes from normal diurnal temperature variation. A total of 26,209 temperature records were thus classified into four categories: (1) no upwelling: no negative temperature spikes evident; (2) low-intensity upwelling: negative temperature spikes of 0.5–1°C: (3) medium-intensity upwelling: negative temperature spikes of 1–2°C; (4) high-intensity upwelling: negative temperature spikes of > 2°C.

Model specifications were optimized to produce the most accurate prediction of upwelling (four categorical response levels) using rolling standard deviations of 3, 7, and 13 half-hourly temperatures. Data were then investigated for any predictive improvement gained by aggregating the upwelling observations to daily level using 24-h standard deviation and diurnal range (daily maximum–minimum [max.-min.]) as predictor metrics. Finally, data were investigated for further predictive improvement by collapsing the four categorical response variables into two (upwelling: yes or no). Analyses were performed using the statistical software SPSS V16.0 (SPSS Inc., Chicago, USA, www.spss.com).

Upwelling relationships—The best predictive metric for upwelling was a two-category variable (yes or no) based on data aggregated at daily level (*see* Results). On this basis, every half-hour record in the Myrmidon, Kelso, and Florence Bay data sets (spanning 13 yr, all months) were examined and manually flagged using the methods described above. Relationships between upwelling and seasonal temperature means, anomalies, seasonal start and end time of upwelling, and duration of upwelling season (derived from the temperature loggers) were explored using linear regression. To determine the robustness of the relationship to broad-scale regional sea surface temperature (SST) regimes, seasonal means and summer monthly maxima were generated from the National Oceanic and Atmospheric Administration (NOAA) Very High Resolution Radiometer (AVHRR) Pathfinder data set (Kilpatrick et al. 2001; NASA Jet Propulsion Laboratory 2009). The SST data, at 4-km resolution, were extracted for the region extending from 10.0°S to 30.0°S and 142.0°E to 158.0°E. Monthly mean SST files were generated for the austral summer months of December to February from 1995–1996 to 2006–2007, using only the highest-quality data (quality flag 7). Daytime and nighttime data were included. Three-monthly seasonal means (December–February) were also generated for each austral summer during this period. A mask was created for the GBR continental shelf area and subdivided at the latitudes of the Daintree (16.2°S) and Burdekin (19.7°S) Rivers, to represent the northern, central, and southern GBR shelf areas (Fig. 3). For each austral summer from 1995–1996 to 2006–2007, the mean and maximum spatiotemporal SST values were extracted for the whole GBR shelf area, and for each of the northern, central, and southern GBR shelf areas.

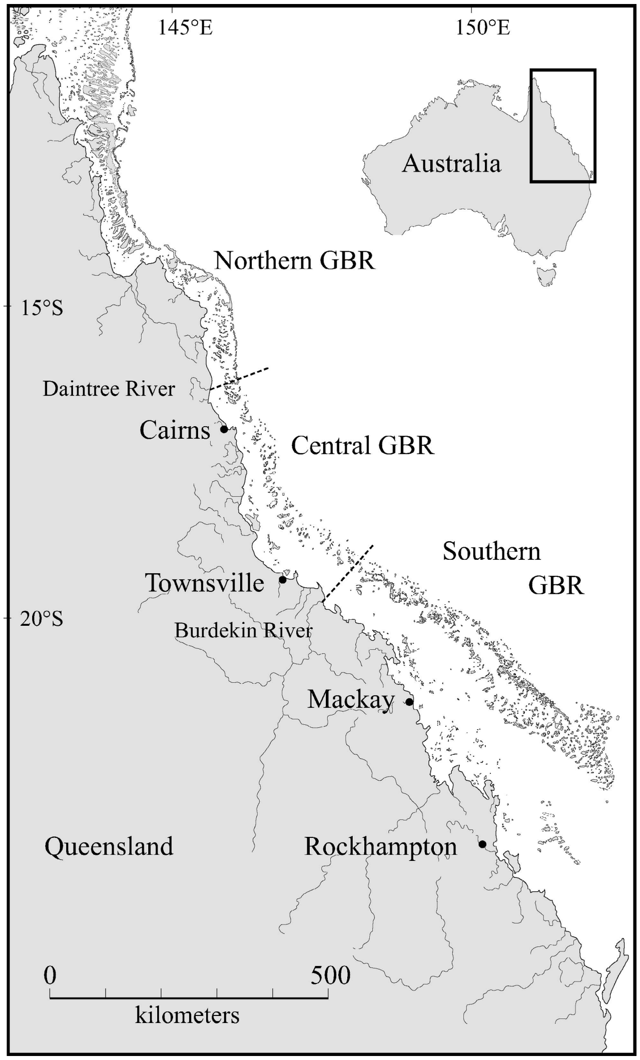

Fig. 3. Map of the Great Barrier Reef (GBR) and its subdivision into northern, central, and southern GBR.

Results

Exploring upwelling metrics—At half-hourly temporal resolution, 26,209 temperature logger records covered the three selected warm seasons (September to April) of upwelling at Myrmidon Reef on the outer shelf. Of these, 1892 records represented periods of upwelling with 726 manually scored as low-, 894 as medium-, and 272 as high-intensity upwelling events. At this level of temporal resolution and using four upwelling intensity categories, Classification Trees generally did a poor job of correctly predicting upwelling. Using a standard deviation of three half-hourly temperature measurements as the predictor variable, the model classification success was 91.2%; however, this was heavily weighted towards successful prediction of "no upwelling." None of the "low-intensity upwelling" records were correctly classified by the model and only $\sim$ 20% of medium- and high-intensity records were correctly classified (Table 1). Accuracy improved slightly by including a "misclassification cost" to incorrect classification of upwelling; however, this was at the expense of decreased accuracy in classifying no upwelling. Increasing the time period for the predictor variable from the standard deviation of 3 to 7, and 13 half-hourly temperatures decreased the accuracy of the model predictions.

Table 1. Classification results from a Classification Trees model using standard deviation of three half-hourly temperature values to predict upwelling events which were manually scored in four categories of intensity: no upwelling, low-intensity upwelling (0.5–1°C), medium-intensity upwelling (1–2°C), and high-intensity upwelling (> 2°C). Tree growing method = CRT, Risk = 1.

	Predicted				
Observed	No upwelling	Low	Medium	High	Percent correct (%)
No upwelling	23,555	0	128	54	99.2
Low	726	0	50	13	0
Medium	894	0	243	83	19.9
High	272	0	88	102	22.1
Overall percentage (%)	97.1	0	1.9	1.0	91.2

Decreasing the number of response categories from four to two (upwelling or no upwelling) improved model accuracy from ~ 20% to ~ 50% for upwelling, with a slight drop in accuracy of no upwelling (from 99% to 97%; Table 2A). None of the predictor metrics based on half-hourly temperature records were deemed acceptable.

Aggregating the temperature data, as described in the Methods, to a daily level produced 547 d of which 396 were no-upwelling days and 151 were upwelling days. At this temporal resolution and using two response categories, model classification accuracy improved markedly. Approximately 80% of upwelling days were correctly classified with the standard deviation of daily temperatures (48 records) as the predictor variable, while ~ 96% of non-upwelling days were correctly classified (Table 2B). This improved further when diurnal variation (daily max.–min.) was used as the predictor variable to ~ 93% for upwelling days with only a slight decline in accuracy of classifying no-upwelling days to 93% (Table 2B). Diurnal variation and upwelling days were thus considered the best predictor and response metrics, respectively, for quantifying upwelling.

Table 2. Classification results from a Classification Trees model for predicting upwelling (two response categories: no upwelling or upwelling) using: (A) half-hourly data and standard deviation of three half-hourly temperature values as the predictor; (B) daily aggregated data and standard deviation of 48 half-hourly temperature values as the predictor; and (C) daily aggregated data and diurnal variation (maximum–minimum) in temperatures as the predictor. Tree growing method = CRT, Misclassification cost = 1.

	Predicted		
Observed	No upwelling	Upwelling	Percent correct (%)
A			
No upwelling	23,113	624	97.4
Upwelling	1242	1229	49.7
Overall percentage (%)	92.9	7.1	92.9
B			
No upwelling	379	17	95.7
Upwelling	31	120	79.5
Overall percentage (%)	75.0	25.0	91.2
C			
No upwelling	370	26	93.4
Upwelling	10	141	93.4
Overall percentage (%)	69.5	30.5	93.4

Duration and intensity of upwelling—Upwelling activity, as measured by the number of days with upwelling, at the outer-shelf site of Myrmidon Reef in the central GBR between 1995 and 2006 has been highly variable, ranging from 35 d of upwelling in 2002–2003 to 133 d in 2001–2002 (Fig. 4A). Kelso Reef, in the middle of the Palm Passage, experiences a similar upwelling regime (Fig. 4B) to Myrmidon Reef, while at the inshore site of Magnetic Island, upwelling is detected less frequently and only in some seasons but not in others (Fig. 4C). The duration of upwelling is significantly and positively related to the intensity of upwelling. At all three reefs across the width of the GBR shelf, the summers with the most sustained upwelling activity, as measured by the number of upwelling days in each season, also coincided with intense upwelling as evident in the number of days where the diurnal range exceeded 2°C (Fig. 4A–C). This relationship was particularly strong at the nearshore site of Magnetic Island, where a linear regression of these variables explains almost 92% of the variation ($p = 0.00$, $F_{1,8} = 87.25$; Fig. 4C). While the correlation between upwelling duration and maximum summer diurnal range is weak at Myrmidon Reef, it is much stronger and statistically significant at Kelso Reef ($r^2 = 0.40$, $p = 0.05$, $F_{1,8} = 5.31$) and at Magnetic Island ($r^2 = 0.72$, $p = 0.00$, $F_{1,8} = 18.02$; Fig. 4D–F). Of particular note at Magnetic Island is that the bleaching summers of 1997–1998 and 2001–2002 (Berkelmans et al. 2004) stand out with > 25 d of upwelling compared to < 12 d during non-bleaching summers. These two summers also experienced > 15 d of high diurnal variation compared to < 5 d during non-bleaching summers and a maximum diurnal range of > 3.1°C compared to < 2.8°C during non-bleaching summers. The number of upwelling days and days with diurnal variation > 2°C were significantly different between bleaching summers and non-bleaching summers at the 0.05 significance level, but the maximum diurnal range was not (upwelling days: $p = 0.00$, $t_{0.05(2)} = 6.53$, df = 7; diurnal variation > 2°C: $p = 0.00$, $t_{0.05(2)} = 12.5$, df =

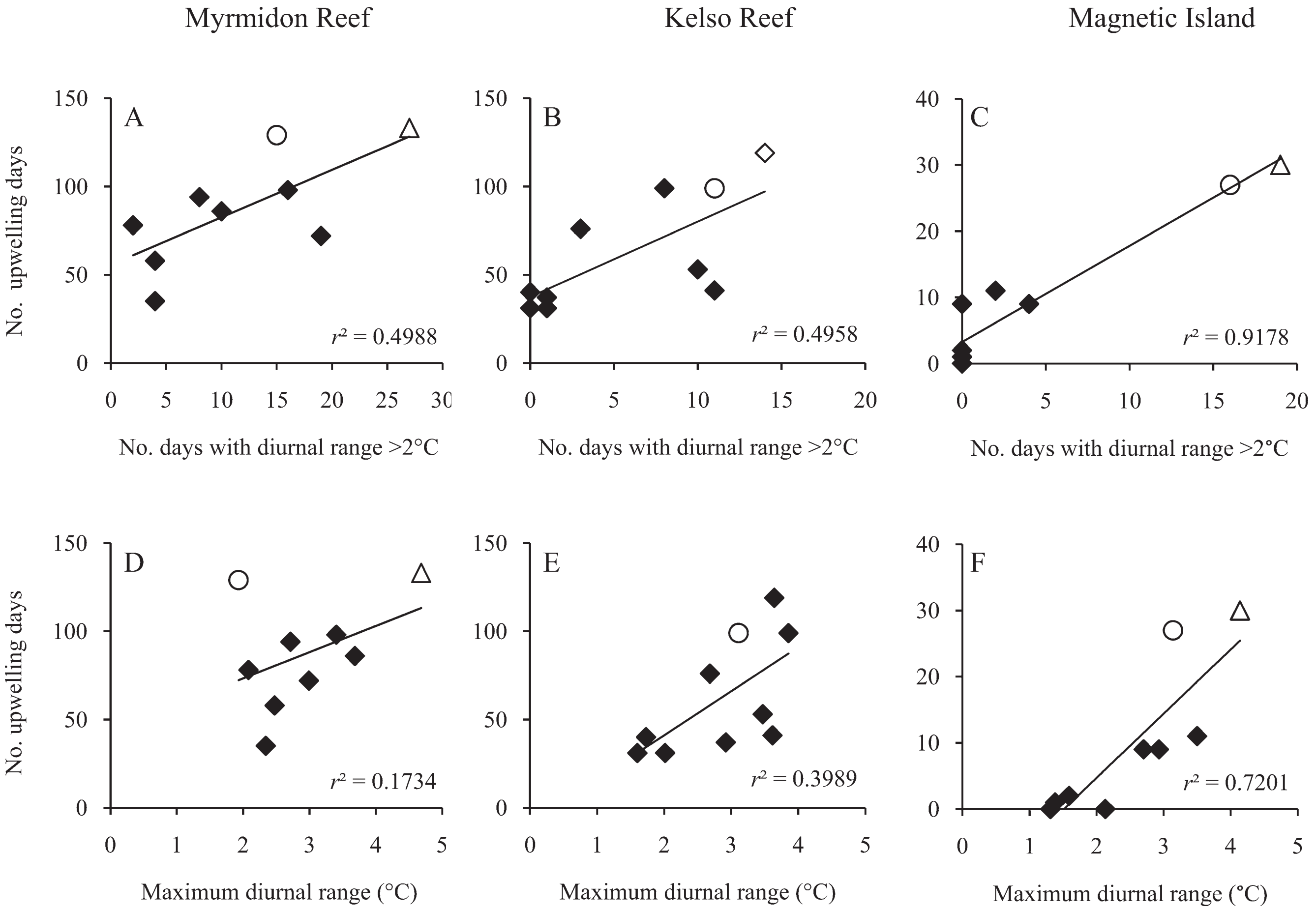

Fig. 4. Relationship between: (A–C) upwelling intensity (No. days with summer diurnal temperature variation $> 2°C$) and upwelling duration, and (D–F) maximum summer diurnal variation and upwelling duration (No. days of upwelling within a season) for three reefs in the central GBR. Note: *y*-axis for Magnetic Island is drawn on a different scale as upwelling is relatively infrequent. Non-bleaching summers (closed diamond); bleaching summer of 1997–1998 (open circle); bleaching summer of 2001–2002 (open triangle).

7; maximum diurnal range: $p = 0.07$, $t_{0.05(2)} = 1.94$, df = 7). Thus, strong and sustained upwelling episodes at the outer edge of the GBR result in an inshore upwelling signal that is markedly different between bleaching and non-bleaching years.

Seasonal temperatures and upwelling—Austral summer (December, January, and February [DJF]) temperatures are significantly and positively correlated with upwelling activity. At the upwelling sites, temperature logger data from the reef flat show that mean summer temperatures explain 72% of the variation in upwelling days at Myrmidon Reef ($p = 0.00$, $F_{1,7} = 17.89$), 62% at Kelso Reef ($p = 0.01$, $F_{1,8} = 13.10$), and 29% at Magnetic Island ($p = 0.16$, $F_{1,8} = 2.35$; Fig. 5A–C). The correlation between upwelling activity and the number of anomalous summer days (days with daily means $> 0.5°C$ above the long-term [13 yr] summer mean) is also strong, with 57% of the variation explained at Myrmidon Reef ($p = 0.02$, $F_{1,7} = 9.13$, long-term summer [DJF] mean: 28.6°C), 57% at Kelso Reef ($p = 0.03$, $F_{1,8} = 7.4$, long-term summer [DJF] mean: 28.1°C), and 72% at Magnetic Island ($p = 0.00$, $F_{1,8} = 18.23$, long-term summer mean: 28.9°C; Fig 5D–F). At Magnetic Island, the warmest summers were the bleaching summers of 1997–1998 and 2001–2002, which coincided with almost three times the number of upwelling days compared to non-bleaching summers (Fig. 5F). Bleaching summers at Myrmidon also stand out strongly from non-bleaching summers, but not at Kelso Reef (Fig. 5D,E).

The relationship between upwelling activity and temperature remains strong over larger spatial scales. Derived from Pathfinder AVHRR data, summer (DJF) temporal mean SSTs averaged spatially over the GBR explain 48% of the variation in upwelling activity at Myrmidon Reef with strong and statistically significant correlations in the central ($r^2 = 0.45$, $p = 0.04$, $F_{1,7} = 5.71$) and southern GBR ($r^2 = 0.47$, $p = 0.04$, $F_{1,7} = 6.14$), but not in the northern GBR ($r^2 = 0.22$, $p = 0.20$, $F_{1,7} = 1.97$; Fig. 6A,C,E,G). Maximum monthly summer SSTs explain even more of the variation in upwelling activity averaged over the GBR ($r^2 = 0.63$, $p = 0.01$, $F_{1,7} = 11.99$), mostly due to a very strong correlation in the southern GBR ($r^2 = 0.75$, $p = 0.00$, $F_{1,7} = 20.68$; Fig. 6F,H), although substantially, and nonsignificantly, less in the northern and central GBR (Fig. 6B,D).

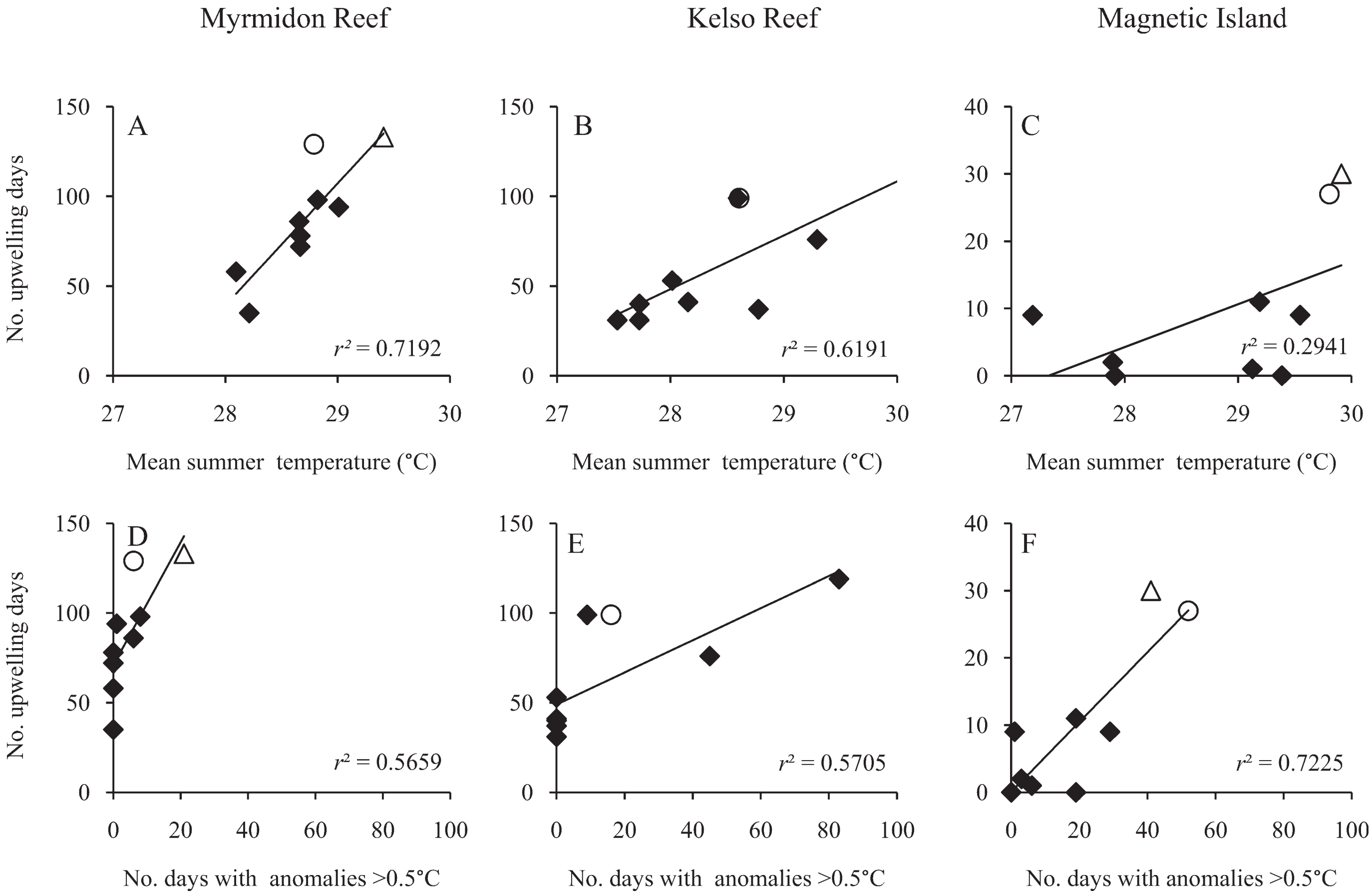

Fig. 5. Relationship between local in situ mean summer (DJF) temperature (reef flat) and (A–C) upwelling activity; and (D–F) unusually warm summers (No. days with anomalies $> 0.5°C$ above the long-term summer mean) and upwelling activity for three reefs in the central GBR. Note: *y*-axis for Magnetic Island is drawn on a different scale as upwelling is relatively infrequent. Non-bleaching summers (closed diamond); bleaching summer of 1997–1998 (open circle); bleaching summer of 2001–2002 (open triangle).

Timing of upwelling—While summer (DJF) temperatures correlate strongly with upwelling activity, upwelling on the mid- and outer shelf of the central GBR can start anywhere between mid-September and early November and can continue sporadically throughout the summer. In summer and autumn, upwelling can cease anywhere between the end of January and early April. However, despite the high variability in timing, early starts or late ends to the upwelling season are not related to unusual upwelling activity. Upwelling showed a poor correlation with start and end times during the upwelling season at Myrmidon Reef (spring $r^2 = 0.08$, autumn $r^2 = 0.08$) and at Kelso Reef (spring $r^2 = 0.22$, autumn $r^2 = 0.18$; data not shown).

Similarly, there is no clear relationship between the timing of upwelling and warm summers. Warm summers, as indicated by the number of days with anomalies $> 0.5°C$ above the long-term mean, were poorly correlated with spring start time or autumn end time of the upwelling season (spring $r^2 = 0.04$–0.39, autumn $r^2 = 0.00$–0.08). Upwelling in the lead-up to the 1997–1998 and 2001–2002 bleaching summers commenced in late September and mid-October, respectively, at Myrmidon Reef and ceased in the first week of March on both occasions, well within the time range of non-bleaching years.

Discussion

Water upwelled from below the thermocline to the surface layer is characteristically cold, nutrient rich, and saline (Rochford 1975; Furnas and Mitchell 1996; Bograd et al. 2001). Yet paradoxically, our study shows that on the GBR most upwelling activity occurs during anomalously warm summers. This was most pronounced at the inshore site of Magnetic Island where the anomalously warm bleaching summers of 1997–1998 and 2001–2002 (Berkelmans et al. 2004) coincided with three times the number of upwelling days compared to non-bleaching summers. The reason(s) for the link between upwelling activity and anomalously warm summers are unclear. However, it is likely to be related to the dominant driver of shelf-edge upwelling on the GBR, which is different from that of the major upwelling ecosystems along eastern boundary currents such as the California and Peru–Humboldt Currents. Eastern boundary upwelling systems are wind driven, whereas the EAC, which flanks the GBR, flows in the opposite direction (southward) to the dominant trade winds (from the southeast). Shelf-edge upwelling on the central GBR is a result of seasonal strengthening of the poleward-flowing current when the opposing trade winds

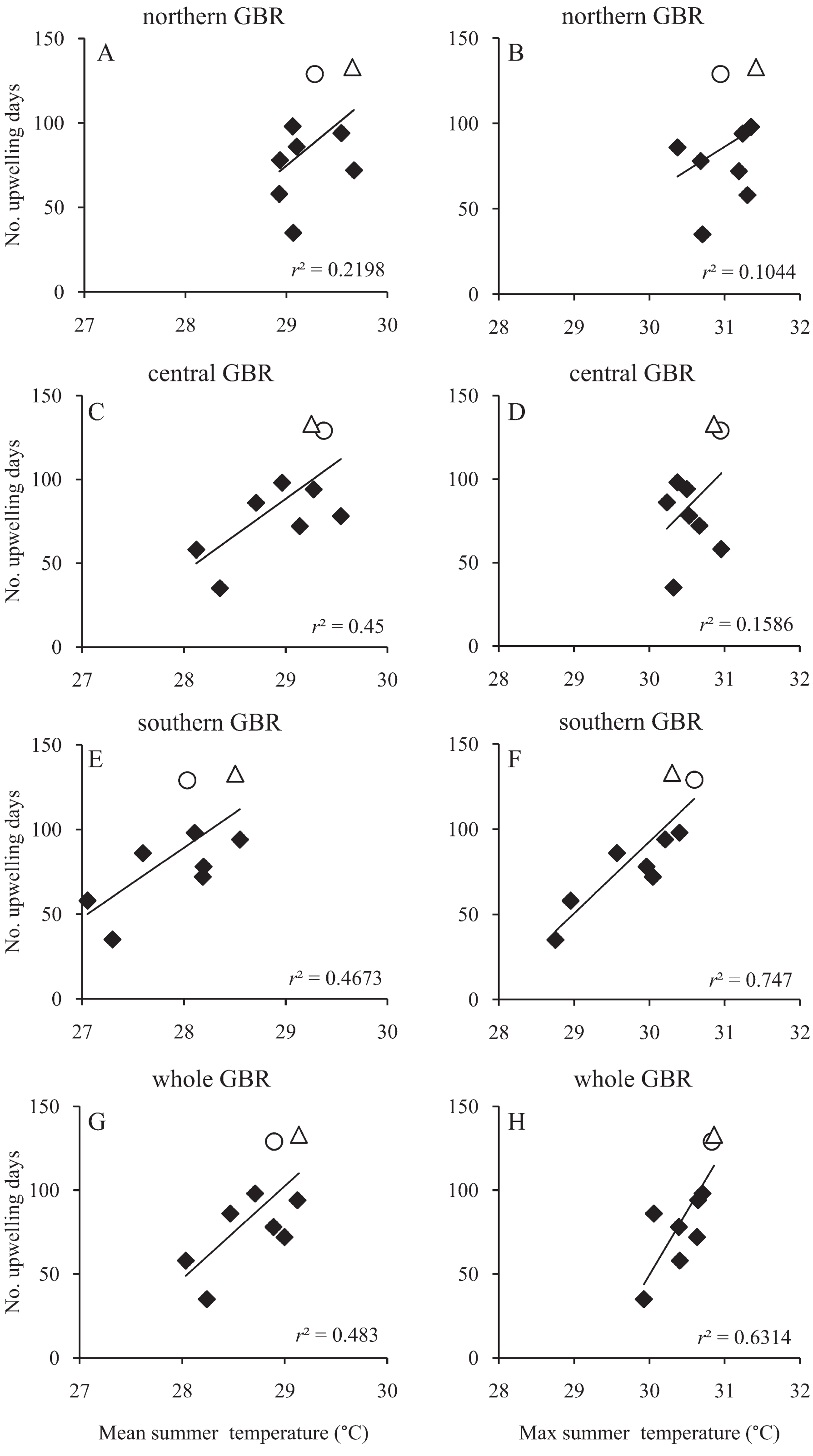

Fig. 6. Relationship between regional Pathfinder summer mean (DJF) and maximum SSTs and upwelling activity at Myrmidon Reef for the (A,B) northern, (C,D) central, (E,F) southern, and (G,H) whole GBR. Non-bleaching summers (closed diamond); bleaching summer of 1997–1998 (open circle); bleaching summer of 2001–2002 (open triangle).

subside in the austral spring and summer (Andrews and Furnas 1986; Burrage et al. 1994). A faster-flowing EAC will produce a significant rise in thermocline level over the continental slope, through the effects of baroclinic adjustment. This effect, combined with the enhanced frictional drag of the flow against the shelf edge, will lead to onshore transport of the bottom Ekman layer, further raising the thermocline. Long periods of doldrums conditions are therefore conducive to upwelling. These same conditions also cause greatly enhanced local heating and stratification, the primary causal factors behind bleaching. In addition, doldrums conditions enhance settlement of particulate matter, increasing light penetration (visible and ultraviolet; Zepp et al. 2008), which in turn accelerates bleaching in heat-impaired corals (Jones et al. 1998, 2000). Doldrums conditions also provide the potential for a positive feedback. Surface waters trap the majority of the heat, which is enhanced by reduced vertical mixing due to low wind speeds and intense surface heating, thus further amplifying warming of the surface layer.

Upwelling activity at the inshore site of Magnetic Island is substantially different from the offshore sites at Kelso Reef and Myrmidon Reef. The fringing reef on the southeast corner of the island, Florence Bay, is shallow (< 10 m) and ~ 120 km from the edge of the continental shelf. The slope and distance from the shelf edge ensure that only intense and sustained pulses of upwelled water reach this site. These factors therefore effectively act as a filter for significant upwelling activity. The strong correlation between high upwelling activity and warm summer temperatures (especially in the central and southern GBR) and the fact that upwelling commences well before summer maxima (which usually occur in February) also means that upwelling at Magnetic Island may be a useful predictor of an anomalously warm summer ahead. Early warning of an anomalously warm summer enables researchers and managers to coordinate and mobilize monitoring and research efforts, as well as coordinate the dissemination of timely information on an unfolding ecological disturbance (Marshall and Schuttenberg 2006). The four warmest summers in the central GBR since the mid-1990s (1995–1996, 1997–1998, 2001–2002, and 2003–2004) were also preceded and accompanied by the most significant upwelling activity. Two of these (1997–1998 and 2001–2002) saw widespread coral bleaching on the GBR (Berkelmans and Oliver 1999; Berkelmans et al. 2004), while the summers of 1995–1996 and 2003–2004 also saw mild and more local-scale bleaching (Michalek-Wagner 2001; R. Berkelmans unpubl. data). If 5 d of upwelling with a diurnal range of $> 2°C$ were used as a threshold between large-scale bleaching years and non-bleaching years, bleaching in 1997–1998 could have been predicted 4 wk ahead of the first observed report of bleaching on 23 January 1998 (Berkelmans and Oliver 1999). This upwelling threshold was also exceeded 6 wk before the eventual summer maximum daily mean temperature, which occurred on 04 February 1998. Bleaching in the 2001–2002 summer commenced early at Magnetic Island due to an acute spike in temperatures in early January 2002 (first bleaching report received 07 January 2002; Berkelmans et al. 2004), yet despite this, bleaching was predictable at least 1 wk earlier. The upwelling threshold was also exceeded 5 wk before the eventual summer maximum daily mean temperature, which was reached on 12 February 2002. This period of temperature anomalies was also sustained over much of the rest of the GBR, with reports of widespread bleaching commencing in mid-February. Thus, upwelling activity at Magnetic Island may be used as a seasonal forecasting tool of an upcoming anomalously warm summer where intense and sustained upwelling can indicate the likelihood of widespread bleaching, especially over the central and southern GBR. Future work may involve exploring anomalies in the speed of the EAC and the processes that influence it (including local and regional southeast trade winds, equatorial monsoon winds, and the complex contribution of the South Equatorial Current to the EAC) with a view to extending the predictions to longer ranges and wider spatial scales.

Quantification of upwelling has been used in numerous studies to examine the effects of ocean variability on biotic responses (Sydeman and Allen 1999; Parrish et al. 2000; Weeks et al. 2006). The Coastal Upwelling Index for the California and Peru–Humboldt boundary currents (Bakun 1973; Schwing et al. 1996) in the eastern Pacific is a classic example and is provided by the NOAA, Environmental Research Division to researchers and environmental managers in 6-h time steps, updated monthly (NOAA 2009). A similar index was developed for coastal upwelling in Lake Michigan (Plattner et al. 2006). Indices such as these work because upwelling in these systems is a result of predictable offshore Ekman transport driven by geostrophic wind stress. However, not all regions that experience upwelling are as well understood as these. This is especially the case for the GBR where upwelling is not driven directly by wind stress, but by a complex interaction of tides, internal waves, local wind variability, topography, and the speed of a poleward-flowing western boundary current, which responds to the competing effects of local and remote wind fields. In such systems, other ways of enumerating upwelling are needed. We show that the number of upwelling days is a suitable metric for quantifying the duration of upwelling, and diurnal range (max.-min.) for the intensity of upwelling, based on in situ temperature loggers. While these metrics are retrospectively derived, real-time temperature monitoring can provide the opportunity for an early warning system. The diurnal range metric is site and depth specific, and therefore requires interpreting in the context of local (site and depth) conditions. Nevertheless, these metrics provide a useful framework with which to advance studies on the relationship between upwelling events and the biological response in ecosystems such as the GBR.

Our results also indicate that the effects of shelf-break upwelling may influence a far greater extent of the GBR than previously believed. Until this study, cold water upwelling at the shelf break was understood to enter the shelf via the Palm and Magnetic passages in the central GBR and remain in the central GBR lagoon (Andrews and Furnas 1986; Brinkman et al. 2002). We show that cold, nutrient-rich water from intense upwelling intrusions can span the entire width of the continental shelf. Cold-water intrusions influence reef communities at 20-m depth on the mid- and outer-shelf reefs in the vicinity of the Palm and Magnetic Passages in the central GBR. Loggers on the reef slope at 6–9-m depth also record cold-water pulses but to a lesser extent; however, reef-flat loggers at 1–3-m depth do so rarely (data not shown). These observations imply that current nutrient budgets for the GBR may substantially underestimate the influx of nutrients onto the GBR, especially during warm years (Furnas 2003). Increasingly warm summers resulting from climate change may also have an unexpected side effect in boosting annual nutrient influxes in some areas of the GBR, with possible flow on effects in biological production. In addition, any increase in the strength of the EAC (Cai et al. 2005) will increase the potential of across-shelf intrusions due to the shallowing of the thermocline above the shelf break. A larger sphere of influence of cool upwelled water (both horizontally and vertically) may also increase the scope of potential refuges for reef communities during coral bleaching episodes.

In conclusion, this study demonstrates a strong link between upwelling activity and anomalously warm summers on the GBR, especially those that coincide with widespread coral bleaching. Cool, upwelled water is spatially restricted (central GBR), remains subsurface, and can coexist with warm, stratified surface waters. However, during strong upwelling periods it can precede bleaching by up to 1–3 wk, which may have application as an early warning system for bleaching. The detection of cool, upwelled water on inshore fringing reefs > 100 km from the shelf edge implies that nutrient budgets for the GBR may be underestimated during warm summers and that localized refugia for corals from excessively warm water may not be restricted to shelf-edge passages through the GBR.

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References

Andrews, J. C., and M. J. Furnas. 1986. Subsurface intrusions of Coral Sea water into the central Great Barrier Reef—I. Structures and shelf-scale dynamics. Continent. Shelf Res. **6:** 491–514, doi:10.1016/0278-4343(86)90020-8

———, and P. Gentien. 1982. Upwelling as a source of nutrients for the Great Barrier Reef ecosystems: A solution to Darwin's question? Mar. Ecol. Progr. Ser. **8:** 257–269, doi:10.3354/meps008257

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–1971. U.S. Department of Commerce, NOAA Technical Report NMFS SSRF-693.

———. 1996. Patterns in the ocean: Ocean processes and marine population dynamics. University of California Sea Grant in cooperation with Centro de Investigaciones Biológicas de Noroeste.

———. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: Opportunity, adaptive response and competitive advantage. Sci. Mar. **70:** 105–122, doi:10.3989/scimar.2006.70s2105

Berkelmans, R., G. De'ath, S. Kininmonth, and W. J. Skirving. 2004. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: Spatial correlation, patterns and predictions. Coral Reefs **23:** 74–83, doi:10.1007/s00338-003-0353-y

———, and J. K. Oliver. 1999. Large scale bleaching of corals on the Great Barrier Reef. Coral Reefs **18:** 55–60, doi:10.1007/s003380050154

Bograd, S. J., T. K. Chereskin, and D. Roemmich. 2001. Transport of mass, heat, salt, and nutrients in the southern California Current System: Annual cycle and interannual variability. J. Geophys. Res. C Oceans **106:** 9255–9275, doi:10.1029/1999JC000165

Brinkman, R., E. Wolanski, E. Deleersnijder, F. McAllister, and W. Skirving. 2002. Oceanic inflow from the Coral Sea into the Great Barrier Reef. Estuar. Coast. Shelf Sci. **54:** 655–668, doi:10.1006/ecss.2001.0850

Burrage, D., K. Black, and K. Ness. 1994. Long-term current prediction in the central Great Barrier Reef. Continent. Shelf Res. **14:** 803–829, doi:10.1016/0278-4343(94)90074-4

Cai, W., G. Shi, T. Cowan, D. Bi, and J. Ribbe. 2005. The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. Geophys. Res. Lett. **32:** 4.

Coles, S. L. 1988. Limitations on reef coral development in the Arabian Gulf: Temperature or algal competition? Proc. 6th Int. Coral Reef Symp. **3:** 211–216.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology **81:** 3178–3192, doi:10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

Furnas, M. [Ed.]. 2003. Catchment and corals: Terrestrial runoff to the Great Barrier Reef. Australian Institute of Marine Science.

Furnas, M. J., and A. W. Mitchell. 1996. Nutrient inputs into the central Great Barrier Reef (Australia) from subsurface intrusions of Coral Sea waters: A two dimensional displacement model. Continent. Shelf Res. **19:** 1127–1148, doi:10.1016/0278-4343(95)00060-7

Griffin, D. A., and J. H. Middleton. 1986. Coastal trapped waves behind a large continental shelf island, southern Great Barrier Reef. J. Phys. Oceanogr. **16:** 1651–1664, doi:10.1175/1520-0485(1986)016<1651:CTWBAL>2.0.CO;2

Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. A. Munthiga, R. H. Bradbury, A. Dubi, and M. E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acidification. Science **318:** 1737–1742, doi:10.1126/science.1152509

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. Science **301:** 929–933, doi:10.1126/science.1085046

Jones, R. J., O. Hoegh-Guldberg, A. W. D. Larcum, and U. Schreiber. 1998. Temperature-induced beaching of corals begins with impairment of the CO_2 fixation mechanism in zooxanthellae. Plant Cell Environ. **21:** 1219–1230, doi:10.1046/j.1365-3040.1998.00345.x

———, S. Ward, A. Yang Amri, and O. Hoegh-Guldberg. 2000. Changes in quantum efficiency of Photosystem II of symbiotic dinoflagellates of corals after heat stress, and of bleached corals sampled after the 1998 Great Barrier Reef mass bleaching event. Mar. Freshwat. Res. **51:** 63–71, doi:10.1071/MF99100

Kilpatrick, K. A., G. P. Podesta, and R. Evans. 2001. Overview of the NOAA/NASA advanced very high resolution radiometer Pathfinder algorithm for sea surface temperature and associated matchup database. J. Geophys. Res. C Oceans **106:** 9179–9197, doi:10.1029/1999JC000065

Mann, K. H., and J. R. N. Lazier. 2006. Dynamics of marine ecosystems: Biological–physical interactions in the oceans, 3rd ed. Wiley-Blackwell.

Marshall, P., and H. Schuttenberg [eds.]. 2006. A reef managers guide to coral bleaching. Great Barrier Reef Marine Park Authority.

Michalek-Wagner, K. 2001. Seasonal and sex-specific variations in the levels of photo-protecting mycosporine-like amino acids (MAAs) in soft corals. Mar. Biol. **139:** 651–660.

NASA Jet Propulsion Laboratory. 2009. Physical Oceanography Distributed Active Archive (PO.DAAC). Pasadena, California; 2009 July 27 Accessed. Available from http://podaac@podaac.jpl.nasa.gov.

NOAA. 2009. Upwelling Indices. Pacific Grove, California. NOAA Pacific Research Division; 2009 August 15 Accessed. Available from http://pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html.

Nof, D., and J. Middleton. 1989. Geostrophic pumping inflows and upwelling in barrier reefs. J. Phys. Oceanogr. **19:** 874–889, doi:10.1175/1520-0485(1989)019<0874:GPIAUI>2.0.CO;2

Parrish, R. H., F. B. Schwing, and R. Mendelssohn. 2000. Mid-latitude wind stress: The energy source for climatic shifts in the North Pacific Ocean. Fish. Oceanogr. **9:** 224–238, doi:10.1046/j.1365-2419.2000.00136.x

Plattner, S., D. M. Mason, G. A. Leshkevich, D. J. Schwab, and E. S. Rutherford. 2006. Classifying and forecasting coastal upwellings in Lake Michigan using satellite derived temperature images and buoy data. J. Great Lakes Res. **32:** 63–76, doi:10.3394/0380-1330(2006)32[63:CAFCUI]2.0.CO;2

Riegl, B., and W. E. Piller. 2003. Possible refugia for reefs in times of environmental stress. Int. J. Earth Sci. **92:** 520–531, doi:10.1007/s00531-003-0328-9

Rochford, D. J. 1975. Nutrient enrichment of East Australian coastal waters. II. Laurieton upwelling. Aust. J. Mar. Freshwater Res. **26:** 233–243, doi:10.1071/MF9750233

———. 1991. "Upwelling": Does it need a stricter definition? Aust. J. Mar. Freshwater Res. **42:** 45–46, doi:10.1071/MF9910045

Rodriguez, S., and A. Croquer. 2008. Dynamics of Black Band Disease in a *Diploria strigosa* population subjected to annual upwelling on the northeastern coast of Venezuela. Coral Reefs **27:** 381–388, doi:10.1007/s00338-007-0341-8

Schwing, F. B., M. O'Farrell, J. M. Steger, and K. Batlz. 1996. Coastal upwelling indices West Coast of North America 1946–95. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-231.

Sheppard, C. 2009. Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: Comparison with satellite data and relevance to coral refuges. Coral Reefs **28:** 399–403, doi:10.1007/s00338-009-0476-x

Steinberg, C. R. 2007. Impacts of climate change on the physical oceanography of the Great Barrier Reef, p. 52–74. *In* J. E. Johnson and P. A. Marshall [eds.], Climate change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office.

Sydeman, W. J., and S. G. Allen. 1999. Pinniped population dynamics in central California: Correlations with sea surface temperature and upwelling indices. Mar. Mamm. Sci. **15:** 446–461, doi:10.1111/j.1748-7692.1999.tb00812.x

Szekielda, K.-H. 1971. Anticyclonic and cyclonic eddies near the Somali Coast. Ocean Dynam. **24:** 26–29.

Thompson, R.O.R.Y., and T. J. Golding. 1981. Tidally induced 'upwelling' by the Great Barrier. J. Geophys. Res. **86:** 6517–6521, doi:10.1029/JC086iC07p06517

van Woesik, R. 2004. Comment on "Coral reef death during the 1997 Indian Ocean Dipole linked to Indonesian wildfires." Science **303:** 5662, doi:10.1126/science.1091983

Weeks, S. J., R. Barlow, C. Roy, and F. A. Shillington. 2006. Remotely sensed variability of temperature and chlorophyll in the southern Benguela: Upwelling frequency and phytoplankton response. Afr. J. Mar. Sci. **28:** 493–509.

Wolanski, E., and A. F. Bennett. 1983. Continental shelf waves and their influence on the circulation around the Great Barrier Reef. Aust. J. Mar. Freshwater Res. **34:** 23–47, doi:10.1071/MF9830023

———, E. Drew, K. Able, and J. O'Brien. 1988. Tidal jets, nutrient upwelling and their influence on the productivity of the alga *Halimeda* in the Ribbon Reefs, Great Barrier Reef. Estuar. Coast. Shelf Sci. **26:** 169–201, doi:10.1016/0272-7714(88)90049-2

———, and G. L. Pickard. 1983. Upwelling by internal tides and Kelvin waves at the continental shelf break on the Great Barrier Reef. Aust. J. Mar. Freshwater Res. **34:** 65–80, doi:10.1071/MF9830065

Zepp, R. G., G. C. Shank, E. Stabenau, K. W. Patterson, M. Cyterski, W. Fisher, E. Bartels, and S. L. Anderson. 2008. Spatial and temporal variability of solar ultraviolet exposure of coral assemblages in the Florida Keys: Importance of colored dissolved organic matter. Limnol. Oceanogr. **53:** 1909–1922.

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