ORIGINAL ARTICLE

Bottom boundary layer cooling and wind-driven upwelling enhance the catchability of spanner crab (*Ranina ranina*) in South-East Queensland, Australia

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Abstract

Species catchability is an important parameter used to help optimise stock assessment modelling and the economic efficiency of commercial fishing operations. Previous studies have shown several physical oceanographic parameters, including ambient temperature, waves and currents, affect the catchability of spanner crabs (*Ranina ranina*) throughout the Indo-Pacific. Most notably in the Australian fishery, where oceanographic processes vary over space and time, a positive relationship between bottom boundary layer temperature (BBLT) and catch rates was observed. Here, we aimed to better understand how localised oceanographic processes affected this relationship in the southernmost South-East Queensland (SEQ) sector of the Australian fishery at seasonal and short temporal scales. Our results show cooler BBLT, upwelling-favourable alongshore wind stress and increased catch rates occurred during mating season in austral spring. At the end of austral summer, BBLT began warming, downwelling-favourable winds were dominant, and catch rates declined around the post-moult period. Outputs from the generalised linear models (GLMs) that separated these effects in each season show that, at shorter temporal scales, daily catch rates also increased with episodic BBLT cooling and upwelling-favourable alongshore wind stress, but only during austral autumn and winter. These new findings suggest that region-specific, short-term and seasonal variability of oceanographic processes responsible from changes in BBLT play an important role in influencing the catchability of spanner crabs. We suggest that the effects of region-specific physical oceanographic processes must be considered in future work when investigating the catchability of commercially important fisheries species fished over large spatial domains.

1 | INTRODUCTION

Fisheries sustainability is a global issue requiring formalised controls for successful resource management (O'Neill, Campbell, Brown, & Johnstone, 2010). The Australian spanner crab fishery is the largest of the commercial fisheries for *Ranina ranina* across the Indo-Pacific region, which include Japan, Hawaii, Philippines and the Seychelles

(Kennelly & Scandol, 2002; Thomas, DiNardo, Lee, Piner, & Kahng, 2013). It was the first fishery in Queensland to implement stringent quota-regulated output controls using an empirical management procedure (O'Neill et al., 2010), resulting in an annual total allowable catch (TAC) with an individual transferable quota (ITQ) system (Dichmont & Brown, 2010).

Catchability is an important parameter for fisheries management and can be described as the interaction between species abundance and the efficiency of fishing gear (Arreguín-Sánchez, 1996). Commercial spanner crab fishers use highly size- and species-selective gear (tangle nets) which minimises the bycatch of undersize crabs and other biota (Brown, Dunning, Hansford, & Gwynne, 2001; Sumpton, Brown, & Kennelly, 1995). The adopted management controls for the Australian spanner crab fishery demonstrate promising progress towards a sustainable fishery, but our understanding of the environmental conditions influencing their catchability remains poorly resolved (Spencer, Brown, Lee, & Lemckert, 2017), limiting the predictive capacity of stock assessment models and the overall economics of commercial fishing operations.

Globally, various hydrographic (e.g., temperature) and hydrodynamic (e.g., currents and waves) processes have been linked to the catchability of spanner crabs (Brown et al., 2008; Craig & Kennelly, 1991; Hill & Wassenberg, 1999; Thomas et al., 2013). In the Australian fishery, a positive correlation between bottom temperature and commercial catch rates (CPUE) was found for the area between Noosa, Queensland (26.36°S, 152.97°E), and Ballina, New South Wales (28.84°S, 153.57°E; Brown et al., 2008). The positive effect temperature had on CPUE was assumed to be due to a temperature-mediated increase in metabolic activity, resulting in more frequent foraging and an increased likelihood of capture (Brown et al., 2008). Additionally, time of year (month) was found to have a strong statistically significant effect on catch rates (Brown et al., 2008). Spanner crabs are known to be more active in spring and summer, feeding and mating prior to their annual spawning and less active during their moult stage in autumn (Skinner & Hill, 1986, 1987) and, therefore, the effect of month may be related to their reproductive behaviour and moulting cycles.

Similarly, a positive correlation was found between temperature and surveyed catch rates for the portunid crab *Scylla serrata* in estuarine waters of Queensland at both short- (day-to-day) and longer-term (month-to-month) temporal scales (Williams & Hill, 1982). The study concluded this may be related to the feeding activity of *S. serrata*, which markedly decreased at temperatures below 20°C (Hill, 1980). For other crab species, cooler ambient temperatures have been found to negatively affect their growth and survival (Green, Gardner, Hochmuth, & Linnane, 2014), osmoregulation and energy budget (Madeira, Narciso, Diniz, & Vinagre, 2014), emergence response time (Briffa, Bridger, & Biro, 2013), and drive shelf-wide shifts in populations (Kotwicki & Lauth, 2013). Considering ambient temperature is an important physical parameter affecting many crab species, a knowledge of the physical processes that drive temperature fluctuations in the bottom boundary layer (BBL; i.e., the crabs' habitat) over space and time is important for understanding changes in the species' behaviour.

While the large-scale gradients in bottom boundary layer temperature (BBLT) on the continental shelf are often related to latitudinal changes (Richaud, Kwon, Joyce, Fratantoni, & Lentz, 2016), spatiotemporal variations such as upwelling and downwelling are commonly associated with physical oceanographic processes that

influence cross-shelf transport. Upwelling drives cool, nutrient rich water onto the shelf from deep waters past the shelf break, which can result in short-term (<10 days) decreases in BBLT of up to 5°C (Roughan & Middleton, 2004) and, at times, cooler sea surface temperatures (SST; Suthers et al., 2011). Conversely, downwelling causes depression of the water column isotherms, which suppresses cool water from reaching the shelf (Roughan & Middleton, 2002). Across most of the Australian spanner crab fishery (25–29.5°S), downwelling is predominant during summer to mid-winter (January–August), while upwelling is more frequent during spring (September–November; Rossi et al., 2014). This is mostly governed by alongshore wind stress, which also changes seasonally (Brieva, Ribbe, & Lemckert, 2015; Cresswell, Peterson, & Pender, 2017), but various oceanographic processes also contribute to sporadic upwelling and downwelling. In the coastal area where the Australian spanner crab fishery operates, upwelling and downwelling are facilitated by alongshore wind stress as well as complex coastal topography, tides, eddies and the East Australian Current (EAC; Middleton et al., 1994; Oke & Middleton, 2000; Suthers et al., 2011).

The Australian spanner crab fishery extends from the southern Great Barrier Reef region in Queensland to northern New South Wales (23–29.43°S) on the east Australian continental shelf. In the wider shelf region of the southern Great Barrier Reef (23–25°S), there is evidence that the Capricorn Eddy drives upwelling and downwelling (Weeks, Bakun, Steinberg, Brinkman, & Hoegh-Guldberg, 2010) and upwelled waters can be transported towards the coast via flood tides through the Capricorn Channel (Middleton et al., 1994). At mid-latitudes of the fishery, south of Fraser Island (25–27°S), the shelf region is characterised by the downwelling-favourable cyclonic Fraser Gyre during autumn and winter (Ismail et al., 2017) and the “Southeast Fraser Island Upwelling System” in spring and summer (Brieva et al., 2015). Further south, the EAC has been found to intensify where the continental shelf narrows off the coast of northern New South Wales, resulting in current- and wind-driven upwelling (Cresswell et al., 2017; Oke & Middleton, 2000).

This suggests that localised and seasonal oceanographic processes may be important for variations in both BBLT and spanner crab catch rates in the Australian fishery. Our main objective for this study was to determine the seasonal and shorter-term effects of BBLT on spanner crab catch rates within a smaller region of South-East Queensland (SEQ) sector of the Australian fishery. We also investigated whether SST and alongshore wind stress, parameters that have been linked to upwelling and downwelling, explain fluctuations in both BBLT and spanner crab catch rates.

2 | MATERIALS AND METHODS

2.1 | Study region

Oceanographic, catch and fishing effort data used in this study were obtained from the shelf waters of SEQ, Australia, from 27.35°S to 28.25°S (Figure 1). The region is bounded by Moreton Island and North Stradbroke Island to the north and the Queensland and New

FIGURE 1 Map of study region, including an inset map illustrating the study region relative to the whole Australian spanner crab (SC) fishery and its locality within Australia. Orange “Crabbing zone” illustrates the 30–80 m depth range where most spanner crabs are caught. Markers, as identified in the legend, exhibit the locations of the metocean data sources for the SEQ study

South Wales border to the south. Spanner crabs in this region are typically taken from depths of 30–80 m (Dichmont & Brown, 2010) on a shelf width of approximately 40 km. Here, the benthic habitat consists primarily of uniform, medium-fine sandy substrata (Marshall & Oldham, 1980) with scattered, low-profile rocky reef (Richmond & Stevens, 2014). SEQ typically experiences cool, dry winters and warm, wet summers. Prevailing winds are from the south-east year-round with northerlies more frequent during spring (Brieva et al., 2015). To the east, the fishery is exposed to effects of the EAC

(Spencer et al., 2017), a major western boundary current flowing southward along the shelf break of Australia's eastern seaboard.

2.2 | Data collection and processing

2.2.1 | Field study

A preliminary study was conducted to (a) assess the effects of BBLT on catch rates and (b) ensure the Integrated Marine Observing

System (IMOS; imos.org.au) oceanographic mooring reference station located within the study region (Figure 1) was suitable for the more extensive SEQ study. This involved the collection of in situ measures of BBLT between May 2015 and April 2016 from various locations within our study region. Field measures of BBLT were obtained with the assistance of an individual commercial spanner crab fisher operating out of the Gold Coast Seaway, Queensland (Figure 1). Small temperature loggers (TidbiT™ or Sensus Ultra™) sampling at 1 Hz were attached to a single net on a setline of 15 nets. Three setlines, each containing one temperature logger, were deployed on the seabed for approximately 2 hr up to three times a day for a total of 64 days. Mean daily BBLTs were derived by averaging the temperature records from each setline on a given day. Corresponding catch and effort information was recorded on each day and included date, catch (total retained wet weight of legal-sized crabs in kilograms), total number of net lifts, and midday latitude and longitude. Catch and net lift data were skewed and therefore subjected to cube-root transformation (Campbell, O'Neil, & McGilvray, 2016).

Bottom boundary layer temperature recorded with the data loggers was compared with coincident data from the IMOS North Stradbroke Island National Reference Station (NRSNSI; Figure 1). Here, BBLT data were obtained from a Sea-bird™ CTD moored approximately 2 m above the seafloor in a total water depth of 65 m. Data were downloaded from the Australian Oceanographic Data Network portal (portal.aodn.org.au), and mean BBLT was derived from 15 min burst records between fishing hours conducted by the individual commercial fisher (5 a.m. to 5 p.m.).

2.2.2 | SEQ study

Building on the fieldwork results, we expanded the extent of our study region to include data from 2011 to 2014, using metocean measures of BBLT, SST and alongshore wind stress. Daily mean BBLT was obtained from the NRSNSI. Daily mean SST data were obtained by averaging 15 min records from the Brisbane Waverider buoy (<https://data.qld.gov.au>; Figure 1). Wind speed and direction data recorded at 3-hourly intervals were obtained from the Australian Bureau of Meteorology (BOM: <http://www.bom.gov.au>) Cape Moreton Lighthouse weather station (Figure 1). Wind data were converted into north-south (v) and east-west (u) components and vector averaged to provide estimates of the daily average alongshore wind stress (τ) using the formula (Smith, 1988):

$$\tau = C_D \rho v_{10}^2, \quad (1)$$

where ρ is density of air, 1.22 kg/m³, v_{10} is the alongshore (north-south) wind speed adjusted for the reference height at 10 m above sea level (Large & Pond, 1981), and C_D is the drag coefficient calculated using the formula (Large & Pond, 1981):

$$10^3 C_D = \begin{cases} 1.2, & 4 \leq v_{10} < 11 \text{ m/s} \\ 0.49 + 0.065 v_{10}, & 11 \leq v_{10} < 25 \text{ m/s} \end{cases} \quad (2)$$

Positive and negative values of τ correspond with southerly (downwelling-favourable) and northerly (upwelling-favourable) wind

stress, respectively. Considering a possible lag in upwelling and downwelling in response to the wind stress, daily average values of τ were low-pass filtered by applying a lagged running mean of the previous seven days (including the fishing day) to provide a weekly index of wind-driven upwelling or downwelling (τ_7).

Corresponding spanner crab logbook data were provided by the Queensland Department of Agriculture and Fisheries (DAF). Daily catch and effort information is compulsorily supplied by all spanner crab quota holders and includes fishing date, estimated total retained catch (kg), number of net lifts, quantity of gear (number of nets) permitted on-board, boat ID and fishing location (latitude and longitude). In total, the data set included 1,750 fishing trips for a total of 747 days. Boat ID and quantity of gear were considered as measures to account for the effect of different commercial fishermen (Campbell et al., 2016) but could not be included in our analyses due to an unbalanced number of fishing days across various licence holders. Catches were aggregated across the fleet within the study region, whereby the total sum of estimated retained catch and total net lifts on a given fishing day were derived. Daily aggregated catch and net lifts were normalised using a cube-root transformation for further statistical analyses (Campbell et al., 2016).

2.3 | Statistical analyses

The difference between the two BBLT data sets (loggers and NRSNSI) was analysed using a linear correlation model, and goodness-of-fit indicated by the coefficient of determination r^2 . Multiple linear regression models were used to determine whether variations in BBLT could be attributed to wind stress favouring upwelling or downwelling, and whether they can be identified from coastal SST signatures, after accounting for any similarities in seasonal variability. This was performed by modelling BBLT against τ_7 and month, and BBLT against SST and month, where month was modelled as a second order polynomial to account for seasonal cycles. Multiple r^2 (R^2) and p statistics were used to determine the strength of the models and significance of each variable, respectively. General linear correlation plots and r^2 values were then used to illustrate the strength of the relationships between BBLT and τ_7 , and between BBLT and SST. Prior to further statistical analyses, visual inspections of catch rates (kg/net lifts), BBLT, SST and τ_7 were made to identify specific seasonal trends in the broader SEQ study.

Generalised linear models (GLMs) were used to model the effect of BBLT on catch and effort data from both field and SEQ studies. For the SEQ study, SST and τ_7 were considered as explanatory variables in separate GLMs depending on their relationship with BBLT. Catch was modelled with Gaussian errors and an offset for the number of net lifts (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The offset allowed us to adjust for fishing effort and estimate catch rates. Considering time of year (month) had a strong statistically significant effect on catch rates (Brown et al., 2008), month was modelled as a numerical term using a second order polynomial to account for seasonal (cyclical) reproductive and moulting patterns (Skinner & Hill, 1986, 1987). For the extended SEQ study, year was included to

account for interannual variability. We used an a priori model selection process, which allowed for comparison between the two BBLT data sets in the field study, the use of SST or τ_7 in lieu of BBLT in the SEQ study, and the effect seasonal reproductive and moulting cycles had on catch rates in both studies. Goodness-of-fit of each model was compared by the difference in Akaike's information criterion (AIC) values (ΔAIC), where the best model was assigned a value of zero. Further investigation was carried out by assessing short-term effects of BBLT, SST and τ_7 within separate seasons (i.e., summer, autumn, winter and spring), whereby season was modelled as a parametric (factor) term (Zuur et al., 2009).

Explained deviance for each model was calculated using the following equation (Zuur et al., 2009):

$$ED = 100 \times \frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}}, \quad (3)$$

where the null and residual deviances are equivalent to the total sum of squares and the residual sum of squares, respectively (Zuur et al., 2009). The effect (i.e., positive or negative correlation) and significance of each variable were assessed by 95% confidence intervals (CI; du Prel, Hommel, Röhrig, & Blettner, 2009). All statistical analyses were performed using the statistical environment package, R (R Development Core Team, 2018).

3 | RESULTS

3.1 | Field study

BBLT data from the temperature loggers and mooring ranged from approximately 16 to 22.5°C (Figure 2), with warmest and coolest periods occurring around May–June and September–November, respectively. The two BBLT data sets showed good agreement ($r^2 = 0.65$) except for five days (7% of the records) on which

differences were greater than 2°C. Exclusion of the data from those days resulted in r^2 increasing to 0.79. The most variability across consecutive days occurred in November 2015, while the greatest difference between the two data sets on a given day occurred in March 2016 (3.2°C), when a warm event (24.2°C) was detected by the temperature loggers but not at the NRSNSI.

Results from the GLM analysing the effects of BBLT on catch rates showed temperature logger data had a lower AIC value compared to the model using NRSNSI data when seasonal effects (using month) were not modelled (Table 1). Both the small temperature loggers and NRSNSI BBLT data exhibited significant, inversely proportional relationships with catch rates (95% CI from –0.5 to –0.1 and –0.47 to –0.09, respectively). However, when seasonal effects were modelled (i.e., by including month), BBLT was no longer significant (95% CI from –0.29 to 0.05 for loggers and –0.33 to 0.02 for NRSNSI) but AIC decreased for each model. The GLM using month without either BBLT data set explained a similar amount of catch rate variability (ED = 31.1%; $\Delta AIC = 1$), which indicated the effect of BBLT could not be distinguished from the seasonal changes in BBLT and catch rates. For the GLMs modelled with month and BBLT, there was little difference when using either the NRSNSI or small temperature logger BBLT data (AIC = 174.4 and 175.4, respectively).

3.2 | SEQ study

The multiple linear regression model assessing the collective contribution of SST and month in explaining BBLT variability had an R^2 value of 0.14, whereas the model using τ_7 and month had a higher R^2 value of 0.31. BBLT and SST were not significantly correlated ($p > 0.05$), while significant relationships were observed between BBLT and τ_7 , and between BBLT and month ($p < 0.001$). Consistent with the multiple linear regression model results, the general linear correlation plots illustrated a weak correlation between SST and

FIGURE 2 Bottom boundary layer temperature data collected from the small temperature loggers and the NRSNSI mooring within the study region on 64 days for the period of May 2015 to April 2016 inclusive. Date labels on the x-axis represent the middle of each month (day 15). Lines connecting each data point were used to better illustrate how each data set agreed over the time series. Each point represents daily average temperature during fishing hours

TABLE 1 The effects NRSNSI BBLT data, small temperature logger (Loggers) BBLT data and month had on catch rates in the field study (May 2015–April 2016)

GLM	AIC	Δ AIC	ED (%)
NRSNSI + month ^a + offset (net lifts)	174.4	0	34.3
Loggers + month ^a + offset (net lifts)	175.4	1	33.2
Month ^a + offset (net lifts)	175.4	1	31.1
Loggers + offset (net lifts)	188.1	12.7	15.7
NRSNSI + offset (net lifts)	191	15.6	11.8
Offset (net lifts)	196.9	21.5	0

Notes. AIC: Akaike's information criterion; Δ AIC: difference in AIC value from best model; ED (%): percentage of explained deviance.

^aFitted with 2nd order polynomial to model cyclical (seasonal) effects. Net lifts were modelled using an offset to estimate catch rates.

BBLT ($r^2 = 0.03$, Figure 3a), whereas the τ_7 and BBLT model exhibited a better fit ($r^2 = 0.26$, Figure 3b).

Time series plots of SST, BBLT, τ_7 and catch rates illustrate clear seasonal cycles (Figure 4). SST exhibited less short-term variability compared to the variations observed in BBLT, τ_7 and catch rates. During spring (September–November), catch rates were consistently much higher, northerly τ_7 (upwelling-favourable) were more frequent, and BBLT was generally cooler than other seasons (Figure 4, blue shaded area). Catch rates then decrease around the end of summer and start of autumn (February–March) and, at the same time, southerly τ_7 (downwelling-favourable) became dominant and BBLT typically started to increase (Figure 4, orange shaded area). The Australian spanner crab fishery closure occurs annually from 20 November to 20 December, and immediately following this period, catch rates were consistently high across all years. SST was excluded from further analyses with catch rates due to the weak correlation with BBLT.

The GLM analyses for the SEQ study (Table 2) illustrate τ_7 and BBLT had a similar effect on daily catch rates but the model using BBLT had a lower AIC value and higher explained deviance. Without modelling seasonal effects, both τ_7 and BBLT had a significant, inversely proportional effect on catch rates (95% CI from -9.8 to -4.6

and -0.28 to -0.18 , respectively). Δ AIC values indicate that month was the most important parameter, explaining 14.9% of catch rate variability alone, which highlights a strong seasonal (cyclical) effect as observed in the field study (Table 1). Even when seasonal variability (month) was incorporated in the GLM, τ_7 and BBLT returned a significant inversely proportional relationship with catch rates (95% CI from -5.3 to -0.03 and -0.19 to -0.08 , respectively), though their effects were weaker. The weaker, but still significant, effects suggest both BBLT and τ_7 explain some short-term variation in catch rates beyond that explained by the confounding seasonal variability of BBLT, τ_7 and catch rates. The BBLT and τ_7 GLMs modelled with month and year had explained deviances of 18.4% and 16.0%, respectively (Table 2). The model of best fit was the GLM that included BBLT, month and year (Δ AIC = 0).

By separating each season, further analyses of the short-term effects BBLT and τ_7 had on catch rates showed significance only during autumn and winter months (Table 3). Explained deviances indicate that far more of the variability in catch rates was accounted for by BBLT (28%) than by τ_7 (10%). This suggests that episodic BBLT cooling and less frequent upwelling-favourable τ_7 improve catch rates but only during seasons that generally experience warmer BBLT and downwelling-favourable τ_7 (Figure 4).

4 | DISCUSSION

Our main objective of this work was to investigate the effect of BBLT on spanner crab catch rates in the southern part of SEQ, Australia. The field study showed that BBLT had a significant effect on catch rates; however due to limited data, the GLMs using month highlighted a spurious relationship between BBLT, season and catch rates for the field study. This caused both BBLT data (loggers and NRSNSI) to lose significance. This may be due to the field study being limited by data from a single fisherman and an unbalanced number of observations across various months.

Subsequent investigation of the effect of BBLT on catch rates over larger spatiotemporal scale for the SEQ study region involved

FIGURE 3 General linear models showing the relationship between BBLT and SST (a) and BBLT and τ_7 (b) for the 747 fishing days during 2011 and 2014. Goodness-of-fit is described using the coefficient of determination (r^2)

FIGURE 4 Daily SST, τ_7 , BBLT and catch rate data from the 747 days from 2011 to 2014. Daily mean catch rate represents standardised catch (total retained weight [kg]) by the measure of effort (total net lifts) across all spanner crab fishermen operating on each day. Positive and negative alongshore wind stress represents southerlies and northerlies, respectively. Date ticks correspond with the middle of the labelled month (day 15). Blue shaded areas highlight the period spanner crabs become more active which corresponds with seasonal upwelling and the orange shaded areas highlight the period when spanner crabs start becoming less active during post-moult

TABLE 2 GLM models used to analyse the various effects of BBLT, τ_7 , month and year on catch rates in the SEQ study (2011–2014)

GLM	AIC	Δ AIC	ED (%)
BBLT + month ^a + year + offset (net lifts)	2229.4	0	18.4
BBLT + month ^a + offset (net lifts)	2233.6	4.2	17.7
τ_7 + month ^a + year + offset (net lifts)	2250.6	21.2	16.0
τ_7 + month ^a + offset (net lifts)	2255.2	25.8	15.3
Month ^a + offset (net lifts)	2257.1	27.7	14.9
BBLT + offset (net lifts)	2305.6	76.2	9.1
τ_7 + offset (net lifts)	2348.9	119.5	3.7
Offset (net lifts)	2375.3	145.9	0

Notes. AIC: Akaike's information criterion; Δ AIC: difference in AIC value from best model; ED (%): percentage of explained deviance.

^aFitted with 2nd order polynomial to model cyclical (seasonal) effects. Net lifts were modelled using an offset to estimate catch rates.

TABLE 3 Short-term effects BBLT and τ_7 have on catch rates within each season

GLM	Season	CI (2.5%)	CI (97.5%)	ED (%)
BBLT: season + offset (net lifts)	Summer	−0.10	0.01	28
	Autumn ^a	−0.15	−0.03	
	Winter ^a	−0.15	−0.05	
	Spring	−0.09	0.03	
τ_7 : season + offset (net lifts)	Summer	−3.37	5.04	10
	Autumn ^a	−18.57	−9.78	
	Winter ^a	−21.69	−12.6	
	Spring	−4.37	6.53	

Notes. CI (2.5%) and CI (97.5%): lower and upper confidence limits, respectively; ED (%): percentage of explained deviance.

^aNegatively correlated and significant within 95% confidence intervals. Net lifts were modelled using an offset to estimate catch rates.

the use of catch and effort data from a number of vessels in the fishing fleet. Firstly, we demonstrated that the NRSNSI oceanographic mooring was a suitable source of long-term BBLT data for our study region. With the exception of 5 out of 64 days, when the difference between the loggers and the NRSNSI exceeded 2°C, the two data sets exhibited a strong correlation. Given the complex nature of the BBL on the continental shelf (Grant & Madsen, 1986), these anomalies observed on the five days may be associated with a lag between oceanographic processes such as eddies, internal waves and internal tides passing through the region (Griffin & Middleton, 1992; Halliwell & Mooers, 1979; Huthnance, 1995; Oke & Middleton, 2000; Pineda, 1994; Ribbe & Brieva, 2016; Schaeffer, Gramouille, Roughan, & Mantovanelli, 2017). The GLMs using month, however, showed that both BBLT data sets yielded similar results.

Findings from the SEQ study were consistent with the field study, though BBLT remained statistically significant even after modelling seasonal effects, which suggested there was a relationship between BBLT and catch rates at both seasonal and short-term temporal scales. This difference between the field and SEQ studies may be related to the SEQ study having been based on a much larger data set and therefore able to include several short-term fluctuations in both catch rates and BBLT. GLM results also demonstrated τ_7 and BBLT share a similar, significant effect on daily catch rates. Even though τ_7 only explains a small amount of BBLT variability, our results highlight there is still a significant relationship with catch rates, suggesting that wind-driven upwelling and downwelling play a role for the catchability of spanner crab. BBLT, however, consistently performed better than τ_7 in all models tested, which suggests processes other than wind-driven upwelling responsible for short-term decreases in BBLT also increase their catchability.

Our results differ from the positive relationship between BBLT and CPUE found in the previous study (Brown et al., 2008). Similar to our field study, the study of Brown et al. (2008) also had large data gaps between days, seasons and even years, which may partly explain the difference in findings. However, these differences may also be related to higher catch rates taken from a region that generally experiences warmer BBLT. For example, off the Gold Coast the BBLT range was approximately 3–4°C cooler and the mean CPUE was approximately 30% less than that measured off the Sunshine Coast. Latitude was not incorporated into the original GLM analyses (Brown et al., 2008) to account for such meridional spatial variability. Thus, the difference in temperature ranges and catch rates may be due to latitudinal differences in spanner crab populations and/or oceanographic processes, such as the seasonally reoccurring Fraser Gyre (Ismail et al., 2017) which influences the Sunshine Coast but not the Gold Coast.

The effect of seasonal reproductive and moulting behaviour on catch rates (Skinner & Hill, 1986, 1987) appears to be reflected in our data (Figure 4 and Table 2). Coincidentally, similar seasonal trends were apparent in τ_7 and BBLT. Most notably, catch rates were highest during the period of seasonal upwelling in austral spring and declined as BBLT warmed and downwelling-favourable winds began to dominate. The exception to these trends occurred in December (immediately following the fishery closure) and may be related to an

increased abundance (and availability) of spanner crab after an intermittent period of no fishing effort. The increase in catch rates following the onset of seasonal, upwelling-favourable alongshore winds may be a useful guide for commercial fishermen and assist with the transition to more ecologically based stock assessments. Additionally, off-season (autumn-winter) episodic BBLT cooling, occasionally attributed to wind-driven upwelling, can be useful in helping explain short-term fluctuations in catch rates.

These results raise questions as to why spanner crabs are responding favourably to cooler BBLT and upwelling-favourable winds. A possibility may be that there is a spurious relationship between seasonal changes in BBLT (as seen in the field study), due to wind-driven upwelling and downwelling, and seasonal changes in catch rates as a result of increased feeding during mating season (spring) and decreased feeding during their post-moult period (starting at the end of summer). However, this possibility lacks explanation as to why episodic BBLT and wind-driven upwelling increase catch rates during austral autumn and winter. Alternatively, there may be a phenological relationship between spanner crab movements and changes in BBLT, whereby seasonal upwelling and downwelling are used as a biological or ecological “cue.”

Crustaceans have been observed to use multiple environmental cues for foraging (Zimmer-Faust, 1987), migration (Rebach, 1981) and reproduction (Skov et al., 2005). For example, hermit crabs have been observed to migrate when water temperatures fall below 10°C (Rebach, 1981). Temperature can also affect the timing of seasonal reproductive behaviour for some crab species, as seen with fiddler crabs (*Uca terpsichores*) where courtship occurred earlier at locations where the sediment temperature declines seasonally than at locations where temperatures remained elevated throughout the year (Kerr et al., 2014). Spanner crabs may exhibit similar behavioural traits by using cooler BBLT and upwelling as a cue for seasonal mating. While upwelling and catch rates were consistently higher during austral spring, spanner crab mating activity may be stimulated by off-season episodic BBLT cooling, making them more active in the fishery during autumn and winter. Warming BBLT at the end of summer may encourage spanner crabs to moult, which could benefit both larvae (Minagawa, 1990) and adult growth and survival (Green et al., 2014) during these particularly vulnerable periods of their lifecycle. During their post-moult stage, spanner crabs can spend up to 52 days buried (Skinner & Hill, 1987), reducing their availability (and catchability) to the fishery.

5 | CONCLUSION

Using two independent data sets, we have shown a significant inversely proportional relationship between BBLT and spanner crab catch rates in the southernmost part of the SEQ sector of the Australian fishery. This finding appears to be related to seasonal fluctuations in catch rates for both studies and short-term changes in catch rates during autumn and winter months for the SEQ study, where cooler BBLT and upwelling-favourable wind stress significantly improve daily spanner crab catch rates. Consequently, BBLT should be

considered in future stock assessment models. In lieu of BBLT, τ_7 may also be a useful indicator of upwelling, which could help anticipate seasonal and short-term variations in catch rates and improve the overall economics of commercial fishing operations. Future field studies would benefit from understanding the specific mechanisms driving BBLT fluctuations, including a more precise quantification of wind-driven upwelling and downwelling. Our results also emphasise that any study attempting to examine the relationship between catchability and oceanographic parameters must consider the spatiotemporal variability of physical oceanographic processes. Future laboratory studies would benefit from investigations into the spanner crabs' response to changes in temperature at different times of the year, which could help determine whether the crabs use temperature as a cue for mating and moulting. The Australian spanner crab fishery could benefit greatly from the development of numerical hydrodynamic and biogeochemical models capable of predicting BBLT fluctuations.

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CONFLICT OF INTEREST

None.

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