Coastal winds drive a recruitment mechanism for estuarine fisheries

Hayden T. Schilling[1,2]*, Charles Hinchliffe[2], Jonathan P. Gillson[3], Anthony Miskiewicz[2,4], Iain M. Suthers[1,2]

1. Sydney Institute of Marine Science, Chowder Bay Road, Mosman, 2088, Australia
2. Centre for Marine Science & Innovation, UNSW Australia, 2052 Australia
3. The Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, NR33 0HT, United Kingdom
4. Australian Museum, College St., Sydney 2000, Australia

*Corresponding author: h.schilling@unsw.edu.au

Running title: Coastal wind driven recruitment

Abstract

Coastal winds transport larval fish onshore or offshore which may contribute to estuarine recruitment, yet our understanding of the mechanism underlying this relationship is limited. Here, we show that larval abundance of coastally spawned species increased with weak to moderate upwelling favourable winds 14 days prior to sampling, reflecting increased nutrient and plankton availability for larval fish. A strong decline in larval abundance was observed following strong upwelling favourable winds while abundance increased with onshore (downwelling favourable) winds, in relation to offshore and onshore wind-driven transport. Subsequently, we show that effects of wind during the spawning period can be detected in lagged estuarine commercial fisheries catch rates of coastally spawned species (lagged by 2 – 8 years depending on species' growth rates), representing the same mechanism proposed for larval fish. Upwelling favourable winds in the southeast Australian region have increased since 1850 while onshore winds have decreased, which may reduce larval recruitment to estuaries. Coastal winds are likely an important factor for estuarine recruitment in the east Australian region and future research on the estuarine recruitment of fish should incorporate coastal winds. As global winds are changing, it is important to investigate if this mechanism is applicable to other regions around the world where coastal winds are a key driver of upwelling.

Keywords: larval fish, retention, wind driven upwelling, fisheries production, Harald Dannevig, downwelling, estuarine recruitment

Introduction

For most marine species, the transition from larva to juvenile is often characterised by high mortality (Houde, 2008), and a shift in habitat from open water to more protected habitats such as estuarine nursery areas (Schilling *et al.*, 2018). Some environmental conditions such as downwelling are often favourable for larval transport or advection towards juvenile habitat (Wenner *et al.*, 1998; Reichert *et al.*, 2010). By increasing the proportion of larvae reaching suitable juvenile habitat, it is likely that mortality within a cohort is decreased (Garvine *et al.*, 1997; Helbig and Pepin, 1998; Pepin, 2016), producing a strong year class when this cohort is eventually harvested by fisheries.

Previous studies have linked strong year classes with many abiotic and biotic factors during the larval period, including the high abundance of zooplankton prey (McFarlane and Beamish, 1992), low abundance of predators (Van der Veer *et al.*, 2000) and favourable oceanic and climatic conditions (Harris *et al.*, 1988; Schroeder *et al.*, 2019). Onshore winds were first recognised as affecting nearshore retention and potentially driving fluctuations in commercial catches in eastern Australian estuaries in the early 20th century (Dannevig, 1907). Dannevig (1907) hypothesised that onshore winds reduced unfavourable advection of fish eggs and larvae, retaining them nearer the coast and therefore increasing recruitment to estuarine fisheries. A positive correlation between estuarine commercial catch rates and onshore winds lagged by three or four years has been observed (Dannevig, 1907; Suthers *et al.*, 2020).

Since then, many studies have shown relationships between wind and juvenile recruitment. Both positive relationships with onshore or downwelling favourable winds (Caputi *et al.*, 2001; Perry *et al.*, 2003; Queiroga, 2003) and negative relationships with offshore or upwelling favourable winds (Nelson *et al.*, 1977; Parrish *et al.*, 1981; Nakata *et al.*, 2000; Takeshige *et al.*, 2013) were associated with settlement and recruitment. Onshore winds increase larval retention near suitable juvenile habitat, while offshore winds advect larvae away from favourable nursery areas (Janzen and Wong, 2002). An idealised scenario has been proposed as a combination of moderate upwelling favourable winds that promote increased productivity and food for larvae (Borja *et al.*, 2008; Coffin and Mueter, 2016; Teixeira *et al.*, 2016), followed by a relaxation event or onshore winds that induces increased shoreward transport or retention of larvae near the coast, increasing juvenile recruitment (Botsford *et al.*, 2006; Queiroga *et al.*, 2007; Yokomizo *et al.*, 2010). Alternatively, an opposite effect for larval fish in a persistent upwelling region has been demonstrated where during relaxation events larvae are pushed offshore due to coastal boundary currents (Morgan *et al.*, 2012).

The importance of wind during the juvenile phase for coastally spawned species in relation to commercial fisheries has also been demonstrated. Wind induced upwelling increases productivity and enrichment (Lloret *et al.*, 2004; Rykaczewski and Checkley, 2008) while wind driven transport (often via downwelling) of larvae can increase retention near suitable juvenile habitat (Jenkins, 2005). Both wind driven upwelling and downwelling have been proposed as drivers of inter-annual variation in commercial fisheries harvest. Despite this, demonstrating both wind dynamics on recruitment and a detectable effect on commercial fisheries remains uncertain.

The winds in many of the world's coastal upwelling systems are being altered due to climate change, resulting in both increases (California, Benguela and Humboldt systems) and decreases (e.g. Iberian system) in upwelling favourable winds (Sydeman *et al.*, 2014). Changing winds are likely to have a range of effects including enrichment of waters, regional changes in stratification and basin-scale changes in thermocline structure, all of which may influence the productivity of local fisheries (Bakun *et al.*, 2010). Concerns have been expressed with regards to changing coastal winds altering upwelling regimes which provide important nutrients to ecosystems (Bakun and Weeks, 2008; Bakun *et al.*, 2010). In addition to changes in nutrient supply, variation in upwelling patterns may also affect the recruitment of larval fish.

In the present study, we test the original hypothesis of Dannevig (1907) using both larval fish abundance and commercial fisheries data. By combining three datasets, the Australian Integrated Marine Observing System (IMOS) Larval Fish database (Smith *et al.*, 2018), the Australian Bureau of Meteorology Atmospheric high-resolution Regional Reanalysis for Australia (BARRA; Chun-Hsu *et al.*, 2019) and a 10-year catch-per-unit-effort (CPUE) time-series dataset for four fish species from eight east Australian estuaries (Gillson *et al.*, 2009), we evaluate offshore and onshore winds (upwelling favourable and downwelling favourable respectively) as a driver of estuarine fisheries production.

The aim of this study was to investigate a coastal wind recruitment mechanism influencing the advection and retention of fish larvae in three ways. Firstly, we examine whether coastal winds influence larval fish abundance near the coast. Secondly, we evaluate whether the same winds during the spawning period influence commercial fisheries harvest when lagged by an appropriate growth period. Finally, we explore changes in the upwelling and downwelling (onshore) favourable winds since 1850. We expect that coastally spawned larval abundance will be greatest during onshore winds. If the onshore transport of coastal fish larvae does occur during downwelling favourable winds, then the effects of this retention should result in increased larval supply to estuarine habitats, and assuming juvenile fish are resident in estuaries until size of capture, lead to a detectable effect on commercial fisheries catch rates.

Method

East Australian Current Oceanography and Larval Fish Data

The present study uses data from the southeast Australian region (Figure 1), dominated by the East Australian Current (EAC). The EAC generally transports larvae poleward and adjacent to coastal and estuarine areas, which are juvenile nursery and rearing habitats (Roughan *et al.*, 2011; Schilling *et al.*, 2020). Together with the EAC, onshore winds are an important driver of upwelling and downwelling through Ekman transport mechanisms (Schaeffer *et al.*, 2013, 2014). Winds from the northeast (NE) blow along the coastline, promoting offshore Ekman transport and upwelling of cold nutrient-rich water along the coast, while winds from the southeast (SE) blow onto the coast, promoting onshore transport and downwelling (Griffin and Middleton, 1992; Middleton *et al.*, 1996).

To investigate the effects of both unfavourable advection due to upwelling favourable (NE) winds and onshore transport from downwelling favourable (SE) winds on larval fish abundance, we compiled sampling data from the Australian IMOS Larval Fish Database (Smith *et al.*, 2018). Fish larvae were collected with horizontal and oblique tows using variety of plankton nets with 300 – 500 µm mesh, see Smith *et al.* (2018) for full dataset description. Using R v4.0.2 (R Core Team, 2020), we subset the larval fish abundance data to include samples taken on the continental shelf (≤ 1000 m bathymetry; Figure 1) between 30–36° S for the period 1990 to 2016 (to match wind data described later). These criteria were selected because in this latitude region the coastline is relatively straight (an approximate angle of 24°), wind is an important driver of cross-shelf flows in the area (McClean-Padman and Padman, 1991; Middleton *et al.*, 1996) and there are 1,489 larval fish samples in the database for this region. In order to investigate recruitment mechanisms affecting all coastally spawned fish, within each larval fish sample we focused only on taxa known to spawn coastally in this region (Table S1; Neira *et al.*, 1998, Miskiewicz Unpublished Data). To avoid any one taxa dominating the abundance of coastal larvae, the abundance of each taxa was normalised (i.e. the abundance of each family summed to 1) by transposing the dataset and using the '*normalize.rows()*' function from the 'vegetarian' R package (Charney and Record, 2012). This created a relative abundance measure and ensured that each taxa had equal weighting during subsequent analysis. Following normalisation, the normalised relative coastal abundance across all samples had a mean of 0.07 (SD = 0.11), with a maximum of 1.48 and the mean abundance was stable between sampling projects (Figure S1). By using the relative abundance of a suite of species, the possibility exists that some individual species-level effects may be missed, but during the larval stage (and without size information) we are assuming that swimming ability is poor and that all species will respond similarly to coastal winds. To test the inverse of this mechanism, we used only 'oceanic' spawning taxa and

conducted the same analysis under the assumption that in this case, we should observe an opposite result with downwelling and retention potentially being unfavourable to oceanic larvae.

Commercial Catch

To assess whether the effects of onshore winds during the spawning period could be detected at the commercial fisheries scale, we used an estuarine catch-per-unit-effort (CPUE) dataset from the same region. This dataset consisted of ten years of monthly CPUE data (combined to annual values; July 1997 – June 2007) from gillnet fisheries in eight different estuaries and was extensively described in Gillson *et al.* (2009). Briefly, these CPUE data comprised monthly catch (kg of harvest) and effort (fishing days) for four fish species; yellowfin bream (*Acanthopagrus australis*; Sparidae), sea mullet (*Mugil cephalus*; Mugilidae), dusky flathead (*Platycephalus fuscus*; Platycephalidae) and sand whiting (*Sillago ciliata*; Sillaginidae). These fish species represent the dominant contribution to both commercial and recreational estuarine fisheries harvest. Luderick (*Girella tricuspidata*; Girellidae) was in the original data but was not included in this study due to the variable spawning periods between populations in this region (Gray *et al.*, 2012). Due to reporting requirements at the time, effort represents total gillnet effort on monthly timescale, not differentiated between species. For our investigation, we aggregated all monthly data to an annual scale (July – June). Over the ten-year period, there were no major regulation changes within this fishery and both total catch and CPUE fluctuated despite relatively stable fishing effort within each estuary (Figures S2 – S4). We therefore proceeded under the assumption that fluctuations in CPUE may be a reliable proxy for fish abundance.

Wind Data

To provide a consistent estimate of winds, we used the wind speed and direction data from the Australian Bureau of Meteorology Atmospheric high-resolution Regional Reanalysis for Australia (BARRA; Chun-Hsu *et al.*, 2019). This re-analysis product provides hourly wind speeds at a 12 km resolution over the Australian domain with downscaled 1.5 km resolution within several sub-domains between 1990 and 2019. For all analyses in the present study, we used 1.5 km resolution data from within the Eastern New South Wales subdomain. Using the R packages 'tidyverse' (Wickham, 2017), 'raster' (Hijmans, 2019), 'ncdf4' (Pierce, 2019) and 'RedaS' (Hatzinger *et al.*, 2015) packages, we extracted wind speed and direction data based upon the specific dates and locations of samples. For each sample/location the wind direction and speed were taken as the mean of 100

pixels (15 km x 15 km) centred over the sample latitude/longitude. To provide a long-term context we also used wind speed and directions from the 20th Century Reanalysis V2c data collated by the NOAA/OAR/ESRL PSD (www.esrl.noaa.gov/psd/), which provides three-hourly wind speed and direction data from 1850 to 2014 at a resolution of ≈200 km (Compo *et al.*, 2015). As both wind products are reanalysis datasets, the models are constrained by observed values.

Statistical Analysis

To investigate the interaction between offshore advection/upwelling favourable (NE) and retention/downwelling favourable (SE) winds, we separated the onshore winds in eastern Australia into SE and NE components. To calculate the magnitude of wind in a particular direction (SE or NE winds) from the known direction and speed, we applied a sine function to create an effect size for wind displacement. If the wind was directly from 45° (for NE winds; 135° for SE), then it was a full effect (1); but if it was at a slight angle, then it was adjusted (< 1) and offshore winds would be negative. The effect size was then multiplied by the wind speed to get the displacement in each direction per hour. Displacement values were then summed to generate a total net displacement over the time span of interest. A positive net displacement means that a greater amount of air moved onto the coast than off the coast during the time period. This use of net displacement aligns with the original work of Dannevig (1907) and Suthers *et al.* (2020).

To separate the effects of advection from upwelling favourable (NE) winds and onshore transport from downwelling favourable (SE) winds on larval fish abundance, winds were calculated as the net air displacement in the southeast to northwest and northeast to southwest directions as described above. The net air displacement for NE and SE winds was calculated by summing the hourly displacement measurements of the previous 14 days. This time period was selected to quantify both potential upwelling and retention against the coast as there is often lagged effects on larval abundance through physical transport and enrichment of nutrients (Dalley *et al.*, 2002; Ings *et al.*, 2008). While larval transport can happen over short periods of time 14 days is the approximate period it takes for upwelling to generate secondary production (increased phytoplankton and zooplankton) in this region and therefore provide a potentially favourable environment for fish larvae to develop (Baird *et al.*, 2006).

Of the 1,489 larval fish samples, 60 (4%) contained no (zero) coastally spawned larvae, therefore we used a two stage gamma hurdle model to test the effects of upwelling favourable (NE) and downwelling favourable (SE) winds on larval fish abundance. This gamma hurdle first analyses all the

data in a presence absence method using a Bayesian binomial model with a logit link. This is followed by a Bayesian generalised linear mixed model with a gamma error distribution using a log link for the presence only data because the abundance data had a continuous, positively skewed, distribution. Distance to coast, upwelling favourable (NE) and downwelling favourable (SE) winds were centred and standardised to assist the model fitting process and increase interpretability of the model coefficients (Schielzeth, 2010). This means a wind of 0 is interpreted as moderate (mean) while positive values are stronger winds and negative values are weaker than the mean.

The model included the fixed effects of downwelling favourable winds, upwelling favourable winds and distance from the coast (km) as well as interaction terms and separate quadratic terms for both downwelling and upwelling favourable winds with interactions with distance to coast. Both linear and quadratic terms for the downwelling and upwelling favourable winds were included in the models because it was hypothesised that the winds would have a disproportionate effect on larval fish abundance at low or high speeds, hence a non-linear fit may be appropriate. Since the Australian IMOS Larval Fish database includes data from a variety of projects which used slightly different sampling methodologies (Smith *et al.*, 2018), the model also included a random intercept effect for Project. As each Project occurred in a discrete time period, this random effect also controls for any temporal inconsistencies such as a traditional year effect. The use of normalised larval abundances also creates a more consistent dataset despite the differences in sampling over time. The fitted model thus had the form:

$$Abund_{it} = \begin{cases} 0 & \text{with probability } p \text{ and} \\ Gamma(\mu_{i,t}, \varphi) & \text{with probability } 1-p \end{cases}$$

$$\eta_{i,t} = \alpha + \theta X_{i,t} + \nu_t$$

$$\nu_t \sim Normal(0, \sigma_t)$$

Where the probability that the relative abundance of coastally spawned larvae ($Abund$) is 0 was modelled as logit(p); α is a constant intercept; θ = β1, β2, …, βk is a vector of K parameters relating X = x1, x2, …, xk wind and distance to coast variables to the abundance of coastally spawned larvae in sample *i* from project t. $Abund$ was modelled as Gamma distributed with mean $\mu_{i,t}$ fitted via a log link with linear predictor $\eta_{i,t}$, and shape parameter φ. ν_t is a random intercept by project with mean 0 and variance σ_t^2. Model parameters were estimated by MCMC using Stan (Carpenter *et al.*, 2017) run using the function brm() of R package 'brms' (Bürkner, 2018). Four parallel MCMC chains were run for 10,000 iterations (5,000 warm up and 5,000 samples each chain) and all parameter estimates were presented with their 95% Bayesian credible intervals. Convergence was assessed by visually examining MCMC trace plots and assessment of the Gelman–Rubin statistic (Brooks and Gelman,

1998), and The overall model fit was assessed by extracting residuals from the model and generating standard Pearson's residual vs fitted plots and normal quantile plots, following the model checking procedure of Gillson *et al*. (2020). The model was considered stable as the chains were well mixed (Figure S5) and the Gelman–Rubin test statistic < 1.01 for all parameters. The shape and hurdle parameter estimates did not overlap zero (shape 95% CI: 0.54 – 0.62, hu 95% CI: 0.13 – 0.17), thereby justifying the added model complexity in this case. There was some deviance from model fit (Figure S6), particularly in the tails of the dataset but due to the large number of samples and appropriateness of the gamma hurdle structure we proceeded with the analysis.

Default weakly informative priors were used for all parameters: improper flat priors over the reals for covariate effects, Student-t(μ = -3.1, σ = 2.5, ν = 3) for the intercept, Student-t(μ = 0, σ = 2.5, ν = 3) for the standard deviation terms, Gamma(0.01, 0.01) for φ and logistic(0, 1) for the zero $Abund$ probability parameter. To visualise the effects of the model predictors, marginal effects were calculated using the '*ggeffects()*' function in the 'ggeffects' R package (Lüdecke, 2018).

To investigate the effects of upwelling and downwelling favourable winds during the spawning periods of the commercially important fish species and the effects on lagged annual CPUE, onshore winds were calculated for each estuary (located 0.15°E of the estuary mouth; Figure 1), centred, and scaled according to the above method with upwelling (NE) and downwelling (SE) favourable components. The net air displacement during the spawning period was determined by identifying the spawning periods of each species from published literature (Table 1). Rather than exploring multiple lags, we identified lags *a priori* by using the modal age of these species caught by gillnets in these estuaries (Gray *et al.*, 2015). This age was then used to lag the spawning period winds to correspond to the most abundant age class, which are therefore most likely to show an effect of the onshore winds if they were influencing larval recruitment. As drought has previously been shown to be an important driver for this CPUE dataset (Gillson *et al.*, 2009), we included drought as the number of months an estuary was 'drought declared' during each 12-month CPUE period based on the New South Wales Department of Primary Industries drought situation maps. A Bayesian linear mixed model with gaussian error distribution was used to assess the effects of coastal winds by including fixed effects of downwelling favourable winds, upwelling favourable winds (NE), drought months and estuary type (barrier river, drowned river valley, barrier lagoon), interactions between drought months and estuary type, upwelling and downwelling favourable winds as well as quadratic terms for both upwelling and downwelling favourable winds. Lagged upwelling and downwelling favourable winds were found to have peaks and troughs over the same time period as the CPUE dataset (Figures S7 & S8).

To investigate the overall effect of onshore winds on annual CPUE and incorporate the dependency structure among observations from the same estuary or species, we used estuary as a random intercept and species as a random slope effect as part of a Bayesian linear mixed model. Using the annual CPUE as the response variable, the linear mixed model was fit and assessed using the same method described above for the larval fish analysis. The fitted model thus had the form:

$$CPUE_{jns} = UpWind_{jns} + DownWind_{jnsit} + UpWind_{jns} \times DownWind_{jns} + UpWind_{jns}^2 + DownWind_{jns}^2 + EstuaryType_{jns} + DroughtMonths_{jns} + EstuaryType_{jns} \times DroughtMonths_{jns} + Estuary_n \times Species_s$$

$$Estuary_n \sim N(0, \sigma_n)$$

$$Species_s \sim N(0, \sigma_s)$$

Where $CPUE_{jns}$ is the *j*th CPUE observation of $Species\ s$ in $Estuary\ n$. $Estuary_n$ is the random intercept and $Species_s$ is the random slope effect. $UpWind$ is the standardised upwelling favourable winds, $DownWind$ is the standardised downwelling favourable winds, $EstuaryType$ is the type of estuary an observation was from, $DroughtMonths$ is the number of months of 'declared drought' during the year. Uninformative flat priors were used for all variables except the overall intercept and random intercepts for $Estuary$ and $Species$. The overall intercept used a Student-t(μ = 30.8, σ = 40.3, ν = 3) and the random intercepts for $Estuary$ and $Species$ both used Student-t(μ = 0, σ = 40.3, ν = 3). The CPUE model showed good convergence of chains with Gelman–Rubin test statistic < 1.01 for all parameters but there was some divergence in model fit towards the tails (Figures S9 & S10)

To investigate whether or not upwelling or downwelling favourable winds have changed over time in southeast Australia, we used the 20th Century Reanalysis V2c dataset (1850–2014; Compo *et al.*, 2015) and calculated upwelling favourable (NE) and downwelling favourable (SE) winds as described above, except net annual displacement was derived by summing all winds during a Gregorian calendar year (centred on Sydney 33.839° S 151.309° E; Figure 1). To ensure consistency with the high-resolution BARRA model used for the prior analyses, we initially tested the correlation between the BARRA model and 20th Century Reanalysis V2c model using both annual displacement for upwelling favourable (NE) and downwelling favourable (SE) winds for the overlapping years (1990–2014) centred over Sydney. There was a moderate to high correlation for both upwelling favourable (r = 0.599, t_{23} = 3.589, P = 0.002) and downwelling favourable (r = 0.697, t_{23} = 4.658, P < 0.001) winds. We then applied two separate Bayesian linear models with gaussian error distributions for upwelling favourable (NE) and downwelling favourable (SE) winds with year as a fixed effect (flat uninformative prior). Initial exploration revealed temporal autocorrelation in the first and second

year of the wind time-series data as measured with the '*acf*' function from the 'stats' R package (R Core Team, 2020). Therefore, for the final analysis we only used the wind data from every third year to remove the presence of temporal autocorrelation. Bayesian linear models were fit and assessed using the same method described above for the larval fish analysis with good mixing of chains and model fit (Figures S11 – S14).

Interpretation and Sensitivity Analysis

For interpretation of all model outputs in this study we used the median posterior estimate for parameters and the 95 % Bayesian credible interval (CI). If the 95% CI did not overlap zero, we deemed a parameter important (van der Linden and Chryst, 2017). Conditional and marginal *R*2 values were calculated using the method of Gelman *et al.* (2019) and implemented in the function '*r2_bayes()*' of R package "performance" (Lüdecke *et al.*, 2020).

For both the larval and CPUE models we performed a sensitivity analysis on the lag times used to assess the robustness of our findings. This involved running the models multiple times while altering the lag period. For the larval models, we varied the lead up time for winds by 9 – 20 days previous to sampling and for the CPUE models we simulated altering the lag by ± 2 years from the identified modal age. This is important for the CPUE models as there are potential influences in the data due to the harvesting of multiple age classes. As we choose the modal age from gill net sampling our original lag should have the strongest effect, and if multiple age classes are present in a sample, then the effects of wind should be similar but potentially weaker if an age class is less abundant.

Results

Coastally Spawned Larval Fish

A total of 175,112 larval fish from 132 coastal spawning taxa were present in 1,489 observations on the continental shelf between 30 and 36° S. Examining the winds 14 days prior to sampling revealed evidence of an interaction between distance to the coast, upwelling favourable (NE) wind and downwelling favourable winds (Estimate = -0.48, 95% CI: --0.85 – -0.13; Figure 2). An overall decline in abundance was observed with increasing distance from the coast (Figure 3). Upwelling favourable winds had a nonlinear effect where when upwelling favourable winds increased from below average to moderate amounts (0 on standardised axis), larval abundance increased but then as the winds strengthened further, coastal larval abundance declined (Figure 3). This resulted in an optimum where coastally spawned larvae were most abundant following moderate amounts of upwelling favourable wind. Downwelling favourable winds showed a linear positive effect on the abundance of coastally spawned larvae (Figure 3). Both the up and downwelling favourable wind relationships were strongest near the coast and the relationships weakened with increasing distance from the coast.

Our 14 day wind model had a low amount of variance explained (conditional R^2 = 0.059, marginal R^2 = 0.044) and the sensitivity analysis of the wind lead up times in the larval fish model showed that while estimates of the effect size for each parameter did change slightly with different wind lead up periods (9 – 20 days; Figure S15), there were no changes in the direction of the effects or abrupt changes in the magnitude of the effect. Upwelling favourable winds showed a stronger negative effect size on larval abundance with shorter lead up periods and weaker effect size with longer lead up times, although the estimate ± SE overlapped for all lag periods. Downwelling favourable winds showed an increase in effect size on larval abundance with shorter lead up times and decrease in effect size with longer lead up times and again the estimate ± SE overlapped for all lags. When the models were run using oceanic rather than coastally spawned species the effects of downwelling (onshore) favourable winds were consistently negative, opposite to the coastally spawned larvae results.

Commercial Catch Rates and Historical Winds

The multi-species model performed well (conditional R^2 = 0.822, marginal R^2 = 0.506), and showed strong evidence for a negative effect of upwelling favourable winds during the spawning period on CPUE (Estimate: -230.48, 95% CI: -374.58 - -85.05; Figures 4 & 5). There was no evidence of any

effect from downwelling favourable winds on CPUE (Estimate: -88.62, 95% CI: -227.90 – 50.63; Figure 4).

Aside from the wind effects, there was evidence of a positive effect of drought on CPUE (Estimate = 8.16, 95% CI: 4.56 – 11.70) although this effect was variable depending on estuary type. Barrier Lagoon estuaries had a more positive response to drought compared with Barrier Rivers and Drowned River Valleys (Figure S16).

The sensitivity analysis of the wind lag times in the CPUE model showed that altering the lag times had minimal changes to wind effects with the standard error of almost all estimates overlapping (Figure S17). The lag times used in our models were consistently one of the strongest effects.

Between 1850 and 2014, there was clear evidence of an increase in upwelling favourable winds (Estimate of annual change: 52.86, 95 % CI: 19.00 – 85.59; Figure 6) and a decline in onshore transport causing downwelling favourable winds (Estimate of annual change: -40.93, 95 % CI: -78.18 – -3.71; Figure 6). The upwelling favourable winds shifted from a negative net displacement to a positive net displacement, while the downwelling favourable winds remained net positive but declined to approximately half of their initial levels (Figure 6).

Discussion

By combining three datasets from a larval fish database, a high resolution wind re-analysis model and commercial CPUE time-series data, we have demonstrated that coastal winds may influence the recruitment of coastally spawned taxa to estuaries (Figures 2–4), resulting in detectable effects on commercial fisheries catch rates (Figures 5 and 6). While we initially expected samples following strong onshore winds to have the highest abundance of coastal larvae, we found both upwelling and downwelling favourable winds are important for fish larvae, with moderate amounts of upwelling favourable winds potentially driving increased planktonic production (Armbrecht *et al.*, 2014), although above average upwelling favourable winds negatively affected coastal larvae abundance. Strong downwelling favourable winds had a positive influence on the abundance of coastally spawned larvae, likely driving onshore transport which may facilitate estuarine recruitment (Agostini and Bakun, 2002). Using lagged winds from each species' spawning season, we showed a detectable negative effect of strong upwelling favourable winds on CPUE, possibly due to the advection of larvae away from favourable habitat. This was a similar effect to that observed in the larval fish with strong upwelling favourable wind being correlated with low relative abundance of coastal larvae. The moderate variance explained in the CPUE models (conditional R^2 = 0.82) in this study shows that incorporating wind from the spawning period into future recruitment models might improve forecasts of estuarine fisheries CPUE. This is important as we have demonstrated that coastal winds have changed since 1850 and are expected to continue changing in the future (Bakun *et al.*, 2010; Sydeman *et al.*, 2014).

A proposed recruitment mechanism

Over an approximate 14 day cycle, upwelling can generate increased nutrients and chlorophyll at the surface which may in turn flow into the lower trophic levels (Gasol *et al.*, 1997; Buesa, 2019). The resultant increased prey availability for larval fish may increase growth and survival rates (Zenitani *et al.*, 2007). Despite this increased productivity, we showed a negative effect of upwelling favourable wind when it was above average strength. This is likely caused by offshore transport as strong upwelling drives advection away from the coast and juvenile estuarine and nearshore habitat. Subsequently, onshore transport from downwelling favourable winds is important as it retains larvae near the coast. Based upon previous research, the positive effects of this retention are most visible after upwelling preconditions the ecosystem with nutrients, thereby creating a favourable environment near juvenile habitat (Rykaczewski and Checkley, 2008).

Our sensitivity analysis showed that the negative effects of upwelling favourable wind increase when the lag period is shortened. This may be due to the more immediate effects of offshore transport compared with production of nutrients (Figure S15). This aligns with previous research demonstrating rapid changes in larval fish transport and retention due to upwelling and downwelling for larvae of multiple taxa in various locations (Natunewicz *et al.*, 2001; Ings *et al.*, 2008). The consistently positive effect of downwelling favourable winds regardless of lag time supports our hypothesis that onshore transport may increase recruitment into estuaries by larval fishes is likely as they are geographically closer and stochastic dispersal will be reduced (Bruno *et al.*, 2018; Schilling *et al.*, 2020).

Commercial Estuarine Fisheries

Consistent with Dannevig's (1907) observation, we found coastal winds during the spawning period can influence commercial fisheries catch rates in subsequent years, despite the coarse annual temporal resolution of the CPUE data used in our analysis. This is consistent with the relationships we found between coastal winds and the abundance of coastally spawned larval fish. However, owing to the coarse temporal resolution, the positive effect of downwelling favourable winds which increase during shorter time periods are not observed. At the coarser scale of annual spawning seasons, alternating upwelling and downwelling favourable winds were not detected using our method. However, based on the demonstrated effects of these winds on coastal larval fish abundance, the events most likely to contribute to successful recruitment would be short periods of upwelling (to precondition the area and generate larval prey), followed by periods of onshore transport (downwelling). We propose our results are showing a negative effect of upwelling favourable winds on CPUE because offshore transport is increased during strong upwelling, which negatively affects recruitment. As our analysis is correlative rather than a manipulative experiment, the exact mechanisms underlying the relationship between upwelling favourable winds and CPUE cannot be pinpointed. Temperature mediated changes in growth and survival are likely to be a key driver of this relationship. Upwelling favourable winds cause upwelling which draws colder water up from depth. If larvae are not advected offshore with the displaced surface water they would remain in a much cooler habitat which would likely result in slower growth (Pepin, 1991; Buckley *et al.*, 2008). To understand possible temperature dynamics, future work should potentially consider incorporating water temperature into studies of both larval abundance and growth as well as commercial catch data.

The generally weak positive effect of drought on CPUE (with different effects in some types of estuaries) agrees with previous research using this data set that found monthly bream (*Acanthopagrus australis*) CPUE increased during periods of drought (Gillson *et al.*, 2009). Despite this, previous research also showed that the monthly CPUE of other species generally declined during periods of drought suggesting that the effect of drought on CPUE needs further investigation (Gillson *et al.*, 2009). We believe the different results in our study compared to Gillson *et al.* (2009) are the result of using different temporal scales with shorter timescales likely more representative of changes in both fish and fisher behaviour.

The sensitivity analysis conducted on the lag times between the winds and year of capture identified that the modal ages show the strongest effects of coastal winds, as would be expected with ages (represented by lags) which are less common in the harvest having smaller effect sizes. In the future, it may be possible to conduct more detailed analyses of single species by identifying particular bottlenecks in the lifecycle including recruitment, which may be affected by coastal winds.

Historical changes in onshore winds

Since 1850, upwelling favourable winds have increased while downwelling favourable winds have decreased in the southeast Australian region. While the direct cause of these changes is uncertain, it is possible this has been a response to global climate change. For example, intensification of surface winds have been attributed to a decline in ozone around Antarctica, which resulted in large scale changes in southern hemisphere winds including over Australia (Cai, 2006). The demonstrated changes in wind in southeast Australia would likely have reduced the onshore transport of larval fish, impacting recruitment to estuaries because increased upwelling and decreased downwelling would increase prey availability but reduce retention near the coast, potentially transporting larvae further away from estuaries.

Despite this, very few fish species spawn all year round, and it is possible that seasonal changes in wind may be more important than annual changes. The temporal analysis presented here does not test alternating upwelling and downwelling favourable winds, and it would be useful to calculate a metric that encompasses the alternating nature of upwelling and downwelling favouring winds. A possible approach could be to document the number and duration of upwelling and downwelling events.

Previous research has indicated that the intensity of wind driven upwelling is likely to increase in most regions, with the exception of southwestern Africa (Bakun *et al.*, 2010). This agrees with our

finding that upwelling favourable winds have historically increased in southeast Australia. While this may result in increased fisheries production by increasing nutrient availability, it is a complex system in which changing winds could have a multitude of effects including increasing productivity and nutrient concentrations of source waters, regional changes in stratification and basin-scale changes in thermocline structure (Bakun *et al.*, 2010).

Caveats

While our study successfully combined datasets to assess the effects of wind on larval fish retention and recruitment, it does have limitations. Our study used correlative analyses and several potential explanatory variables were not included in our models, which may have captured additional variance in either larval fish abundance or commercial fisheries catch rates. These include water temperature, oceanographic currents, larval swimming ability, varying population spawning biomasses or the effects of density dependence, all of which influence spawning and/or recruitment (Ottersen and Sundby, 1995; Schilling *et al.*, 2020). The present study also did not investigate the abundance of larval fish entering estuaries, which would be an important metric to confirm increased recruitment following favourable wind conditions. By expanding investigations beyond the larval period, fish recruitment mechanisms in this region might be better understood.

Conclusions

Various studies have demonstrated positive effects (Nelson *et al.*, 1977) and negative effects (Parrish *et al.*, 1981; Takeshige *et al.*, 2013) of wind-driven Ekman transport of larval fish for estuarine recruitment. Despite the low variance explained in the larval fish analysis, potentially caused by the use of a large database containing samples taken over large temporal and spatial scales, ours is the first study to show a correlation between coastal winds and fish larvae and show a similar corresponding effect on the commercial fishery. We suggest a recruitment mechanism involving wind driven coastal enrichment and larval retention during the spawning season, which is evident in commercial fisheries catch rates. This mechanism involves increased productivity from wind-driven upwelling and increased retention near the coastline, which work in tandem to increase overall recruitment of larvae into estuaries. These recruitment dynamics were detected in commercial estuarine fisheries data when appropriate lags are applied and by incorporating spawning period winds into recruitment models, predictions of commercial fisheries catch rates may improve. As

climate change is altering wind patterns, it is likely that wind driven ocean dynamics will continue to vary and it is important that scientists and management consider potential changes in recruitment.

Acknowledgements

This study was prompted by Dennis Reid (Australian Museum) who brought to our attention Harald Dannevig's original insight on the effect of coastal winds on estuarine fisheries. Support for the 20th Century Reanalysis Project version 2c dataset is provided by the U.S. Department of Energy, Office of Science Biological and Environmental Research (BER), and by the National Oceanic and Atmospheric Administration Climate Program Office. HTS was supported by the UNSW Network Laboratory for Ocean Collaboration and NSW Research, Acceleration and Attraction Program. CH is supported by an Australian Government Research Training Program Scholarship. Larval fish data were sourced from the Integrated Marine Observing System (IMOS), an initiative of the Australian Government being conducted as part of the National Collaborative Research Infrastructure Strategy and the Super Science Initiative. This research includes computations using the computational cluster Katana supported by Research Technology Services at UNSW Sydney.

Author contributions

HTS, AM & JPG collected the data, HTS & IMS conceived the ideas, HTS, CH, JPG & AM designed the analysis, HTS performed the analysis and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

The larval fish data is freely available from the Australian Ocean Data Network https://portal.aodn.org.au/ (Smith *et al.*, 2018). The BARRA wind model is freely available upon request to the Australian Bureau of Meteorology (Chun-Hsu *et al.*, 2019). 20th Century Reanalysis V2c data provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado, USA, from their Web site at https://psl.noaa.gov/ (Compo *et al.*, 2015). NSW Commercial Fisheries Catch Data is available upon request to the NSW Department of Primary Industries Fisheries. Extracted data and code used in this analysis is available at https://github.com/HaydenSchilling/Wind-and-Fisheries.

References

Agostini, V. N., and Bakun, A. 2002. `Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fisheries Oceanography, 11: 129–142.

Armbrecht, L. H., Roughan, M., Rossi, V., Schaeffer, A., Davies, P. L., Waite, A. M., and Armand, L. K. 2014. Phytoplankton composition under contrasting oceanographic conditions: Upwelling and downwelling (Eastern Australia). Continental Shelf Research, 75: 54–67.

Baird, M. E., Timko, P. G., Suthers, I. M., and Middleton, J. H. 2006. Coupled physical–biological modelling study of the East Australian Current with idealised wind forcing: Part II. Biological dynamical analysis. Journal of Marine Systems, 59: 271–291.

Bakun, A., and Weeks, S. J. 2008. The marine ecosystem off Peru: What are the secrets of its fishery productivity and what might its future hold? Progress in Oceanography, 79: 290–299.

Bakun, A., Field, D. B., Redondo-Rodriguez, A., and Weeks, S. J. 2010. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. Global Change Biology, 16: 1213–1228.

Borja, A., Fontan, A., Saenz, J., and Valencia, V. 2008. Climate, oceanography, and recruitment: the case of the Bay of Biscay anchovy (*Engraulis encrasicolus*). Fisheries Oceanography, 17: 477–493.

Botsford, L. W., Lawrence, C. A., Dever, E. P., Hastings, A., and Largier, J. 2006. Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. Deep-Sea Research Part II-Topical Studies in Oceanography, 53: 3116–3140.

Brooks, S. P., and Gelman, A. 1998. General Methods for Monitoring Convergence of Iterative Simulations. Journal of Computational and Graphical Statistics, 7: 434–455. Taylor & Francis.

Bruno, D. O., Delpiani, S. M., and Acha, E. M. 2018. Diel variation of ichthyoplankton recruitment in a wind-dominated temperate coastal lagoon (Argentina). Estuarine Coastal and Shelf Science, 205: 91–99.

Buckley, L. J., Caldarone, E. M., and Clemmesen, C. 2008. Multi-species larval fish growth model based on temperature and fluorometrically derived RNA/DNA ratios: results from a meta-analysis. Marine Ecology Progress Series, 371: 221–232.

Buesa, R. J. 2019. Plankton based energy transfer rates in four Cuban coastal lagoons. Estuarine, Coastal and Shelf Science, 216: 118–127.

Burchmore, J. J., Pollard, D. A., Middleton, M. J., Bell, J. D., and Pease, B. C. 1988. Biology of four species of whiting (Pisces: Sillaginidae) in Botany Bay, NSW. Marine and Freshwater Research, 39: 709–727.

Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software, 80: 1–28.

Bürkner, P.-C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. The R Journal, 10: 395–411.

Cai, W. 2006. Antarctic ozone depletion causes an intensification of the Southern Ocean super-gyre circulation. Geophysical Research Letters, 33: L03712.

Caputi, N., Chubb, C., and Pearce, A. 2001. Environmental effects on recruitment of the western rock lobster, *Panulirus cygnus*. Marine and Freshwater Research, 52: 1167–1174.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., *et al.* 2017. Stan: A Probabilistic Programming Language. Journal of Statistical Software, 76: 1–32.

Charney, N., and Record, S. 2012. vegetarian: Jost Diversity Measures for Community Data, R package version 1.3.

Chun-Hsu, S., Eizenberg, N., Steinle, P., Jakob, D., Fox-Hughes, P., White, C. J., Rennie, S., *et al.* 2019. BARRA v1.0: the Bureau of Meteorology Atmospheric high-resolution Regional Reanalysis for Australia. Geoscientific Model Development, 12: 2049–2068.

Coffin, B., and Mueter, F. 2016. Environmental covariates of sablefish (*Anoplopoma fimbria*) and Pacific ocean perch (*Sebastes alutus*) recruitment in the Gulf of Alaska. Deep-Sea Research Part Ii-Topical Studies in Oceanography, 132: 194–209.

Compo, G. P., Whitaker, J. S., Sardeshmukh, P. D., Allan, R. J., McColl, C., Yin, X., Giese, B. S., *et al.* 2015. NOAA/CIRES Twentieth Century Global Reanalysis Version 2c.

Dalley, E. L., Anderson, J. T., and deYoung, B. 2002. Atmospheric forcing, larval drift, and recruitment of capelin (*Mallotus villosus*). ICES Journal of Marine Science, 59: 929–941.

Dannevig, H. C. 1907. On some peculiarities in our coastal winds and their influence upon the abundance of fish in inshore waters. Journal of the Royal Society of NSW, 41: 27–45.

Garvine, R. W., Epifanio, C. E., Epifanio, C. C., and Wong, K. C. 1997. Transport and recruitment of blue crab larvae: a model with advection and mortality. Estuarine Coastal and Shelf Science, 45: 99–111.

Gasol, J. M., del Giorgio, P. A., and Duarte, C. M. 1997. Biomass distribution in marine planktonic communities. Limnology and Oceanography, 42: 1353–1363.

Gelman, A., Goodrich, B., Gabry, J., and Vehtari, A. 2019. R-squared for Bayesian Regression Models. The American Statistician, 73: 307–309. Taylor & Francis.

Gillson, J., Scandol, J., and Suthers, I. 2009. Estuarine gillnet fishery catch rates decline during drought in eastern Australia. Fisheries Research, 99: 26–37.

Gillson, J. P., Maxwell, D. L., Gregory, S. D., Posen, P. E., Riley, W. D., Picken, J. L., and Assunção, M. G. L. 2020. Can aspects of the discharge regime associated with juvenile Atlantic salmon (*Salmo salar* L.) and trout (*S. trutta* L.) densities be identified using historical monitoring data from five UK rivers? Fisheries Management and Ecology, 27: 567–579.

Gray, C. A., Haddy, J. A., Fearman, J., Barnes, L. M., Macbeth, W. G., and Kendall, B. W. 2012. Reproduction, growth and connectivity among populations of *Girella tricuspidata* (Pisces: Girellidae). Aquatic Biology, 16: 53–68.

Gray, C. A., Young, C. L., Johnson, D. D., and Rotherham, D. 2015. Integrating fishery-independent and -dependent data for improved sustainability of fisheries resources and other aspects of biodiversity. Sydney, Australia.

Gray, C. A., and Barnes, L. M. 2015. Spawning, maturity, growth and movement of *Platycephalus fuscus* (Cuvier, 1829) (Platycephalidae): fishery management considerations. Journal of Applied Ichthyology, 31: 442–450.

Griffin, D. A., and Middleton, J. H. 1992. Upwelling and internal tides over the inner New South Wales continental shelf. Journal of Geophysical Research: Oceans, 97: 14389–14405.

Harris, G. P., Davies, P., Nunez, M., and Meyers, G. 1988. Interannual variability in climate and fisheries in Tasmania. Nature, 333: 754–757.

Hatzinger, R., Hornik, K., Nagel, H., and Maier, M. J. 2015. Companion to: *In* R: Einführung durch angewandte Statistik, 2nd Edition. Pearson Studium, München.

Helbig, J. A., and Pepin, P. 1998. Partitioning the influence of physical processes on the estimation of ichthyoplankton mortality rates. I. Theory. Canadian Journal of Fisheries and Aquatic Sciences, 55: 2189–2205.

Hijmans, R. J. 2019. raster: Geographic Data Analysis and Modeling, R package version 3.0.2.

Houde, E. D. 2008. Emerging from Hjort's shadow. Journal of Northwest Atlantic Fishery Science, 41: 53–70.

Ings, D. W., Gregory, R. S., and Schneider, D. C. 2008. Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research, 66: 529–561.

Janzen, C. D., and Wong, K. C. 2002. Wind-forced dynamics at the estuary-shelf interface of a large coastal plain estuary. Journal of Geophysical Research-Oceans, 107: 12.

Jenkins, G. P. 2005. Influence of climate on the fishery recruitment of a temperate, seagrass-associated fish, the King George whiting *Sillaginodes punctata*. Marine Ecology Progress Series, 288: 263–271.

Lloret, J., Palomera, I., Salat, J., and Sole, I. 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). Fisheries Oceanography, 13: 102–110.

Lüdecke, D. 2018. ggeffects: Tidy data frames of marginal effects from regression models. Journal of Open Source Software, 3: 772.

Lüdecke, D., Makowski, D., Waggoner, P., and Patil, I. 2020. performance: Assessment of Regression Models Performance, R package version 0.5.0. https://easystats.github.io/performance/.

McClean-Padman, J., and Padman, L. 1991. Summer upwelling on the Sydney inner continental shelf: The relative roles of local wind forcing and mesoscale eddy encroachment. Continental Shelf Research, 11: 321–345.

McFarlane, G. A., and Beamish, R. J. 1992. Climatic Influence Linking Copepod Production with Strong Year-Classes in Sablefish, *Anoplopoma fimbria*. Canadian Journal of Fisheries and Aquatic Sciences, 49: 743–753.

Middleton, J. H., Cox, D., and Tate, P. 1996. The oceanography of the Sydney region. Marine Pollution Bulletin, 33: 124–131.

Morgan, S. G., Fisher, J. L., McAfee, S. T., Largier, J. L., and Halle, C. M. 2012. Limited recruitment during relaxation events: Larval advection and behavior in an upwelling system. Limnology and Oceanography, 57: 457–470.

Nakata, H., Fujihara, M., Suenaga, Y., Nagasawa, T., and Fujii, T. 2000. Effect of wind blows on the transport and settlement of brown sole (*Pleuronectes herzensteini*) larvae in a shelf region of the Sea of Japan: numerical experiments with an Euler-Lagrangian model. Journal of Sea Research, 44: 91–100.

Natunewicz, C. C., Epifanio, C. E., and Garvine, R. W. 2001. Transport of crab larval patches in the coastal ocean. Marine Ecology Progress Series, 222: 143–154.

Neira, F. J., Miskiewicz, A. G., and Trnski, T. 1998. Larvae of temperate Australian fishes: laboratory guide for larval fish identification. UWA Publishing.

Nelson, W. R., Ingham, M. C., and Schaaf, W. E. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fishery Bulletin, 75: 23–41.

Ochwada-Doyle, F., Roberts, D., Gray, C., Barnes, L., Haddy, J., and Fearman, J. 2012. Characterizing the biological traits and life history of *Acanthopagrus* (Sparidae) hybrid complexes: implications for conservation and management. Journal of Fish Biology, 81: 1540–1558.

Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography, 4: 278–292.

Parrish, R. H., Nelson, C. S., and Bakun, A. 1981. Transport Mechanisms and Reproductive Success of Fishes in the California Current. Biological Oceanography, 1: 175–203.

Pepin, P. 1991. Effect of Temperature and Size on Development, Mortality, and Survival Rates of the Pelagic Early Life History Stages of Marine Fish. Canadian Journal of Fisheries and Aquatic Sciences, 48: 503–518.

Pepin, P. 2016. Reconsidering the impossible — linking environmental drivers to growth, mortality, and recruitment of fish. Canadian Journal of Fisheries and Aquatic Sciences, 73: 205–215.

Perry, H., Johnson, D. R., Larsen, K., Trigg, C., and Vukovich, F. 2003. Blue crab larval dispersion and retention in the Mississippi Bight: Testing the hypothesis. Bulletin of Marine Science, 72: 331–346.

Pierce, D. 2019. ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files, R package version 1.17.

Queiroga, H. 2003. Wind forcing of crab megalopae recruitment to an estuary (Ria de Aveiro) in the northern Portuguese upwelling system. Invertebrate Reproduction & Development, 43: 47–54.

Queiroga, H., Cruz, T., dos Santos, A., Dubert, J., Gonzalez-Gordillo, J. I., Paula, J., Peliz, A., *et al.* 2007. Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling ecosystem. Progress in Oceanography, 74: 174–191.

R Core Team. 2020. R: A Language and Environment for Statistical Computing v4.0.2. R Foundation for Statistical Computing, Vienna, Austria.

Reichert, J. M., Fryer, B. J., Pangle, K. L., Johnson, T. B., Tyson, J. T., Drelich, A. B., and Ludsin, S. A. 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. Canadian Journal of Fisheries and Aquatic Sciences, 67: 987–1004.

Roughan, M., Macdonald, H. S., Baird, M. E., and Glasby, T. M. 2011. Modelling coastal connectivity in a Western Boundary Current: Seasonal and inter-annual variability. Deep Sea Research Part II: Topical Studies in Oceanography, 58: 628–644.

Rykaczewski, R. R., and Checkley, D. M. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings of the National Academy of Sciences of the United States of America, 105: 1965–1970.

Schaeffer, A., Roughan, M., and Morris, B. D. 2013. Cross-shelf dynamics in a western boundary current regime: Implications for upwelling. Journal of Physical Oceanography, 44: 2812–2813.

Schaeffer, A., Roughan, M., and Wood, J. E. 2014. Observed bottom boundary layer transport and uplift on the continental shelf adjacent to a western boundary current. Journal of Geophysical Research-Oceans, 119: 4922–4939.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution, 1: 103–113.

Schilling, H. T., Reis-Santos, P., Hughes, J. M., Smith, J. A., Everett, J. D., Stewart, J., Gillanders, B. M., *et al.* 2018. Evaluating estuarine nursery use and life history patterns of *Pomatomus saltatrix* in eastern Australia. Marine Ecology Progress Series, 598: 187–199.

Schilling, H. T., Everett, J. D., Smith, J. A., Stewart, J., Hughes, J. M., Roughan, M., Kerry, C., *et al.* 2020. Multiple spawning events promote increased larval dispersal of a predatory fish in a western boundary current. Fisheries Oceanography, 29: 309–323.

Schroeder, I. D., Santora, J. A., Bograd, S. J., Hazen, E. L., Sakuma, K. M., Moore, A. M., Edwards, C. A., *et al.* 2019. Source water variability as a driver of rockfish recruitment in the California Current Ecosystem: implications for climate change and fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, 76: 950–960.

Smith, J. A., Miskiewicz, A. G., Beckley, L. E., Everett, J. D., Garcia, V., Gray, C. A., Holliday, D., *et al.* 2018. A database of marine larval fish assemblages in Australian temperate and subtropical waters. Scientific Data, 5: 180207.

Stewart, J., Hegarty, A.-M., Young, C., and Fowler, A. M. 2018. Sex-specific differences in growth, mortality and migration support population resilience in the heavily exploited migratory marine teleost *Mugil cephalus* (Linnaeus 1758). Marine and Freshwater Research, 69: 385–394.

Suthers, I. M., Reid, D. D., Moksness, E., and Schilling, H. T. 2020. Novel fisheries investigations by Harald Dannevig: some parallels with Johan Hjort on the other side of the world. ICES Journal of Marine Science.

Sydeman, W. J., García-Reyes, M., Schoeman, D. S., Rykaczewski, R. R., Thompson, S. A., Black, B. A., and Bograd, S. J. 2014. Climate change and wind intensification in coastal upwelling ecosystems. Science, 345: 77–80.

Takeshige, A., Miyake, Y., Nakata, H., Kitagawa, T., and Kimura, S. 2013. Effect of wind stress on the catch of Japanese anchovy *Engraulis japonicus* off northwestern Kyushu, Japan. Fisheries Science, 79: 989–998.

Teixeira, C. M., Gamito, R., Leitao, F., Murta, A. G., Cabral, H. N., Erzini, K., and Costa, M. J. 2016. Environmental influence on commercial fishery landings of small pelagic fish in Portugal. Regional Environmental Change, 16: 709–716.

van der Linden, S., and Chryst, B. 2017. No Need for Bayes Factors: A Fully Bayesian Evidence Synthesis. Frontiers in Applied Mathematics and Statistics, 3. Frontiers. https://www.frontiersin.org/articles/10.3389/fams.2017.00012/full (Accessed 9 November 2020).

Van der Veer, H. W., Geffen, A. J., and Witte, J. I. 2000. Exceptionally strong year classes in plaice *Pleuronectes platessa*: are they generated during the pelagic stage only, or also in the juvenile stage? Marine Ecology Progress Series, 199: 255–262.

Wenner, E., Knott, D., Blanton, J., Barans, C., and Amft, J. 1998. Roles of tidal and wind-generated currents in transporting white shrimp (*Penaeus setiferus*) postlarvae through a South Carolina (USA) inlet. Journal of Plankton Research, 20: 2333–2356.

Wickham, H. 2017. tidyverse: Easily Install and Load the 'Tidyverse'.

Yokomizo, H., Botsford, L. W., Holland, M. D., Lawrence, C. A., and Hastings, A. 2010. Optimal wind patterns for biological production in shelf ecosystems driven by coastal upwelling. Theoretical Ecology, 3: 53–63.

Zenitani, H., Kono, N., and Tsukamoto, Y. 2007. Relationship between daily survival rates of larval Japanese anchovy (*Engraulis japonicus*) and concentrations of copepod nauplii in the Seto Inland Sea, Japan. Fisheries Oceanography, 16: 473–478.

740 **Table 1** Details of the spawning season and modal age of capture in gillnet fisheries for four coastally
741 spawning fish species, used to define the choice of lags for winds during the spawning season with
742 an example of the wind intervals used for the annual catch-per-unit-effort (CPUE) between July 1997
743 and June 1998.

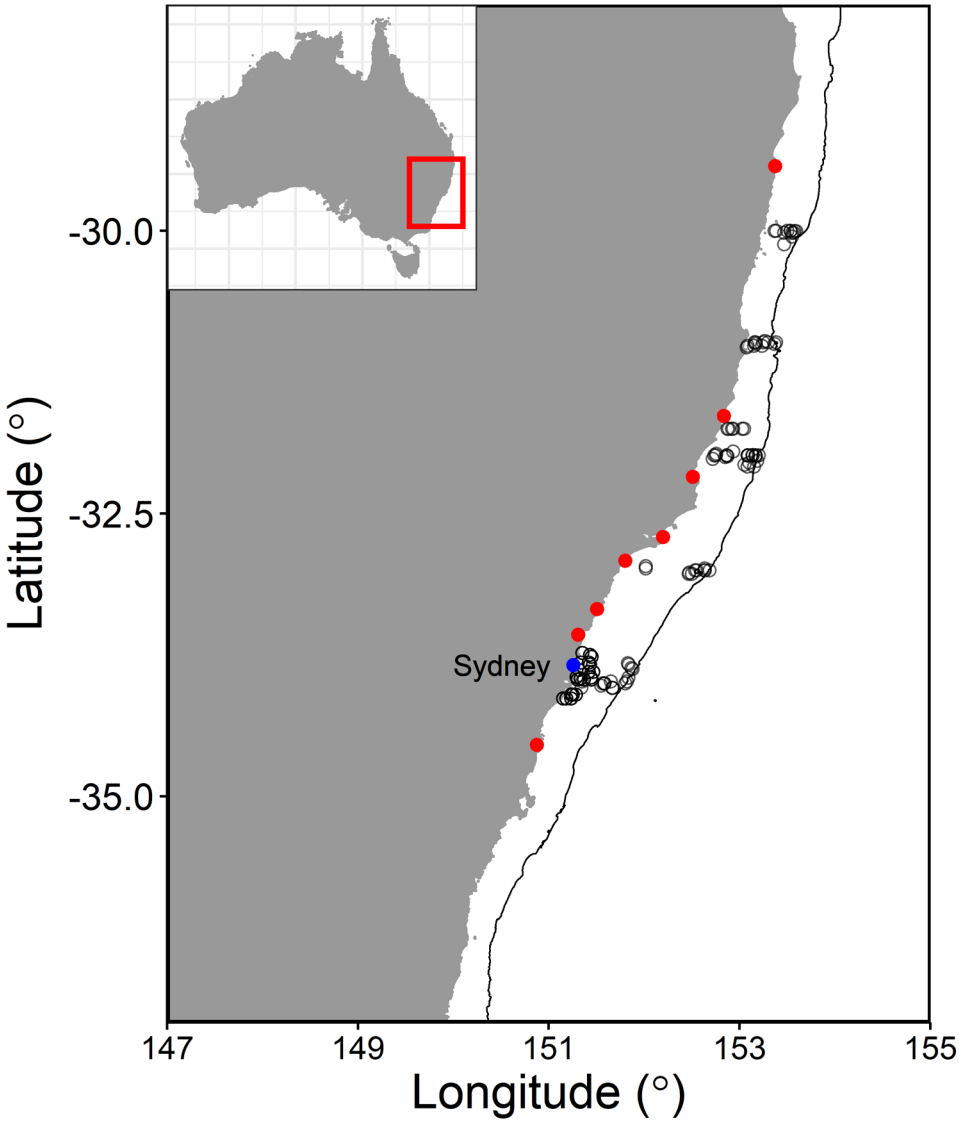
Species	**Spawning season**	**Modal harvested age (Gray *et al.*, 2015)**	**Example wind intervals used for annual CPUE for July 1997 – June 1998**
bream (*Acanthopagrus australis*)	October – February (Ochwada-Doyle *et al.*, 2012)	8	October 1989 – February 1990
dusky flathead (*Platycephalus fuscus*)	December – March (Gray and Barnes, 2015)	4	December 1993 – March 1994
sand whiting (*Sillago ciliata*)	December – February (Burchmore *et al.*, 1988)	6	December 1991 – February 1992
sea mullet (*Mugil cephalus*)	April – July (Stewart *et al.*, 2018)	2	April – July 1995

744

745

746

747 **Figures**



748

749 **Figure 1** Location of south-eastern Australia showing the position of the larval fish samples included
750 in this study (empty grey circles), the estuaries used in the catch-per-unit-effort analysis (filled red
751 circles) and Sydney (filled blue circle). The black line represents the 1000 m isobath.

752

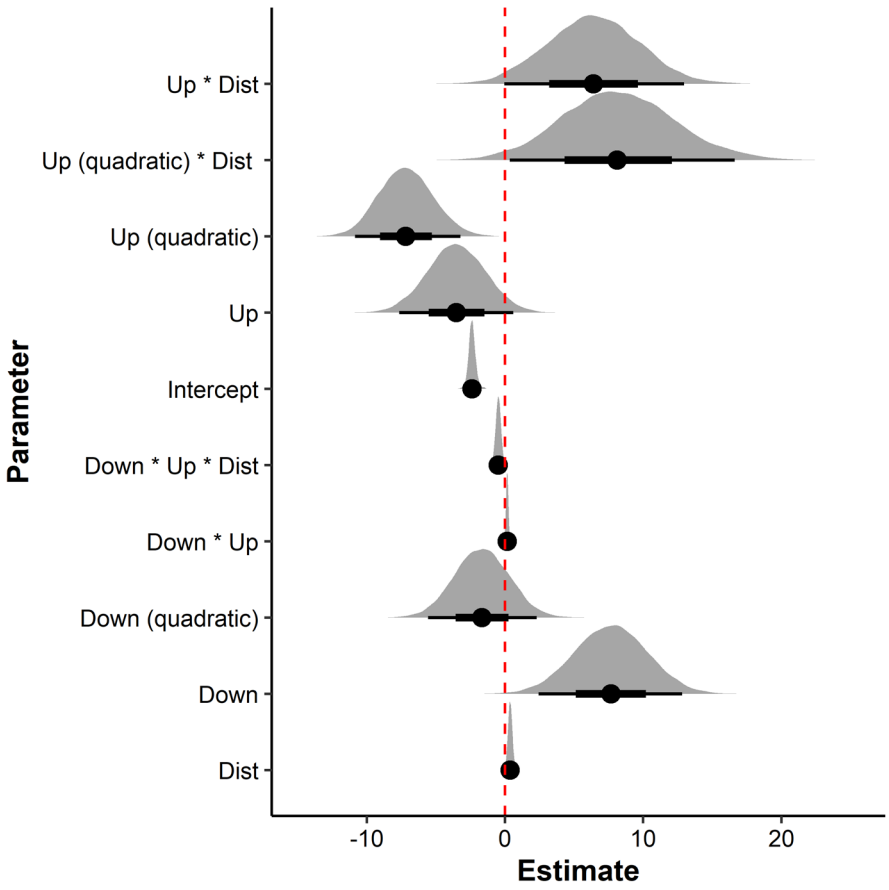


Figure 2 Caterpillar plots showing the Bayesian parameter estimates for the coastally spawned larval fish abundance models based upon winds in the last 14 days. Points show the estimate of the parameter with the horizontal bar representing the 66% (thick bar) and 95% (thin bar) credible interval of the estimate. Model terms include distance to coast (Dist), upwelling favourable winds (Up) and downwelling favourable winds (Down). Parameter estimates are deemed important if the 95% credible interval does not cross the dashed red line which marks an estimate of zero.

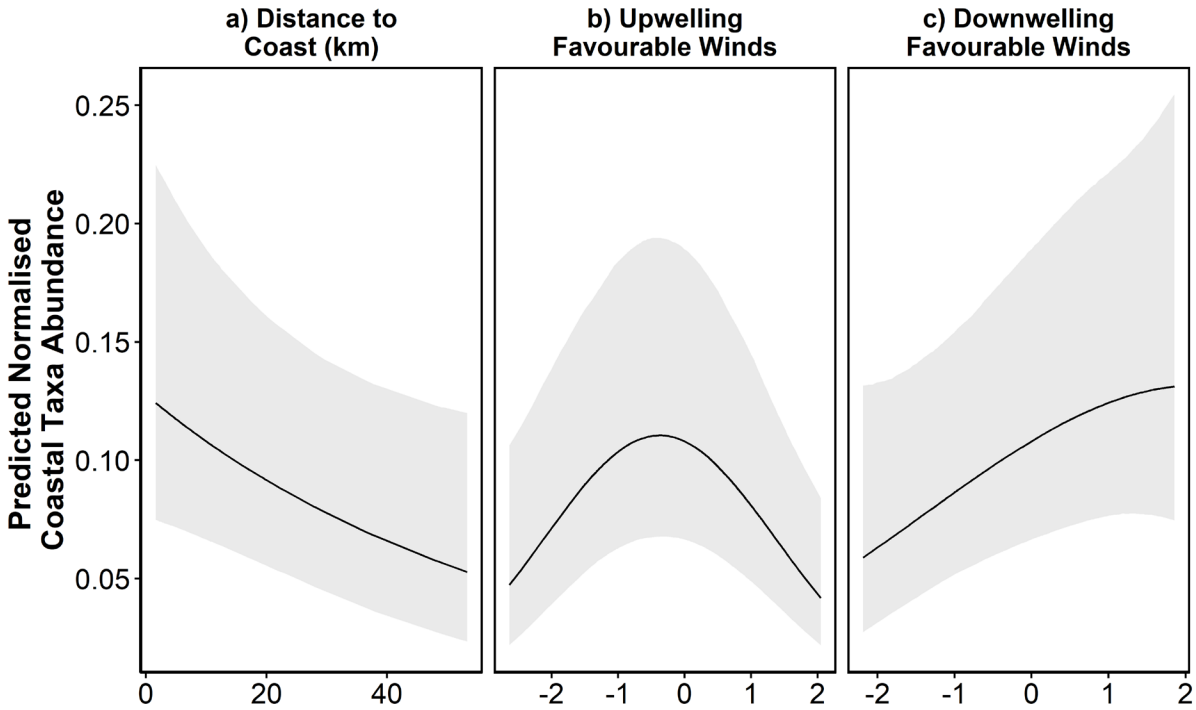


Figure 3 Visualisation of the predicted normalised coastal larval abundance based on the generalised linear mixed model for winds 14 days prior to sampling: a) shows the effect of distance from the coast, based upon mean (0 on the standardised scale) upwelling and downwelling favourable winds with shading showing the 95% credible interval; b) shows the interactive effect of upwelling and downwelling favourable winds. Upwelling and downwelling favourable wind predictions are based upon the mean distance from coastline in our dataset (10km). For the winds, 0 represents mean winds, with 1 and −1 representing 1 and −1 SD from the mean, respectively.

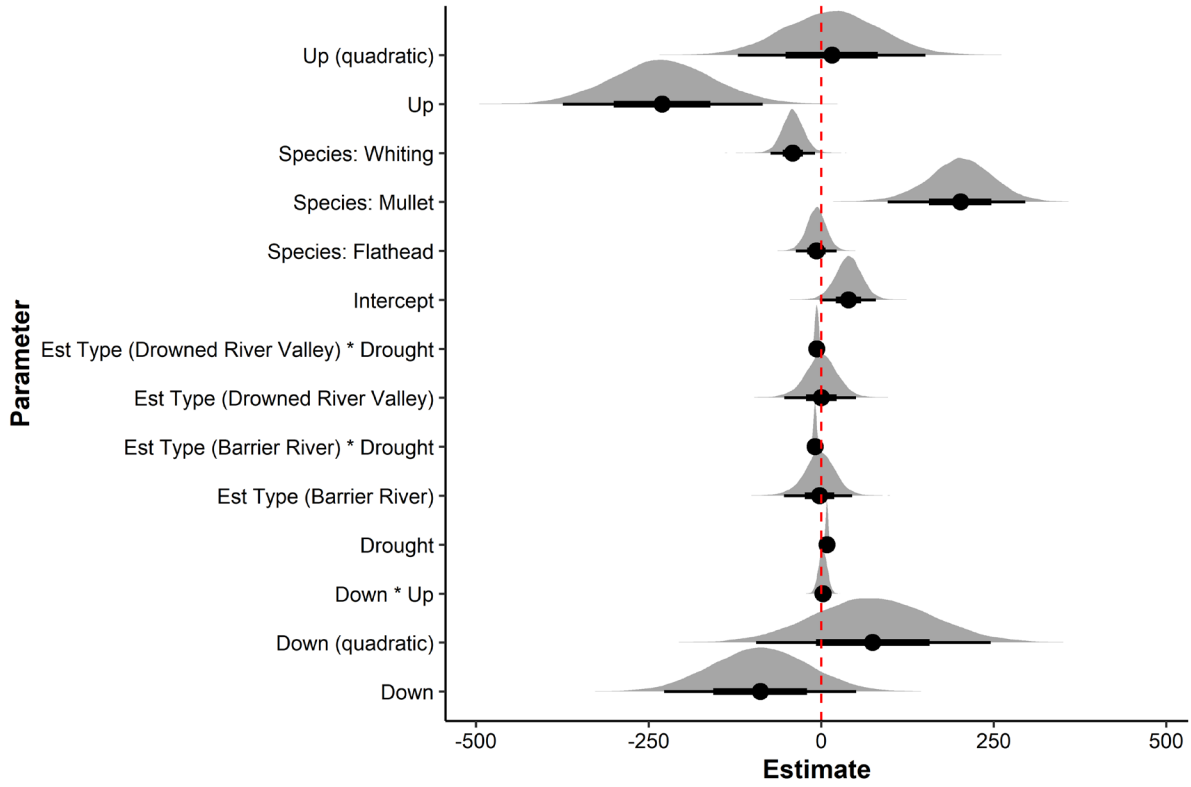


Figure 4 Caterpillar plot showing the Bayesian parameter estimates for the multispecies catch-per-unit-effort (CPUE) generalised linear mixed model. Model terms include upwelling favourable winds (Up), downwelling favourable winds (Down) and estuary type (Est Type). Points show the estimate of the parameter with the horizontal bar representing the 66% (thick bar) and 95% (thin bar) credible intervals (CI) of the estimate. The dashed red line marks an estimate of zero. The 95 % CI does not cross zero for Up Winds, Species: Whiting, Species: Mullet, Drought Months, Estuary Type: Drowned River Valley * Drought Months and Estuary Type: Barrier River * Drought Months.

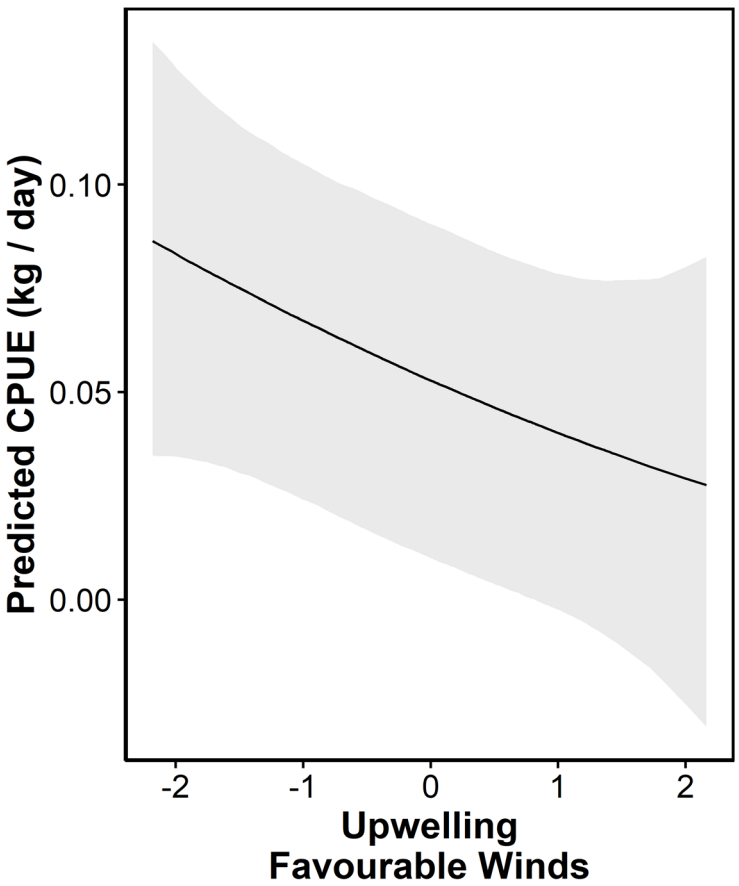


Figure 5 Visualisation of predicted Catch-Per-Unit-Effort (CPUE) based upon upwelling favourable winds during the spawning period as predicted by the results of the CPUE Bayesian linear mixed model. The grey area represents the 95% confidence interval. There were no detectable effects of downwelling favourable winds and the effects of drought are shown in the supplementary material (Figure S16). Predictions were made while holding all other variables within the model to mean values. Note due to the random slope and intercept effects in the model, the actual y scale is relative.

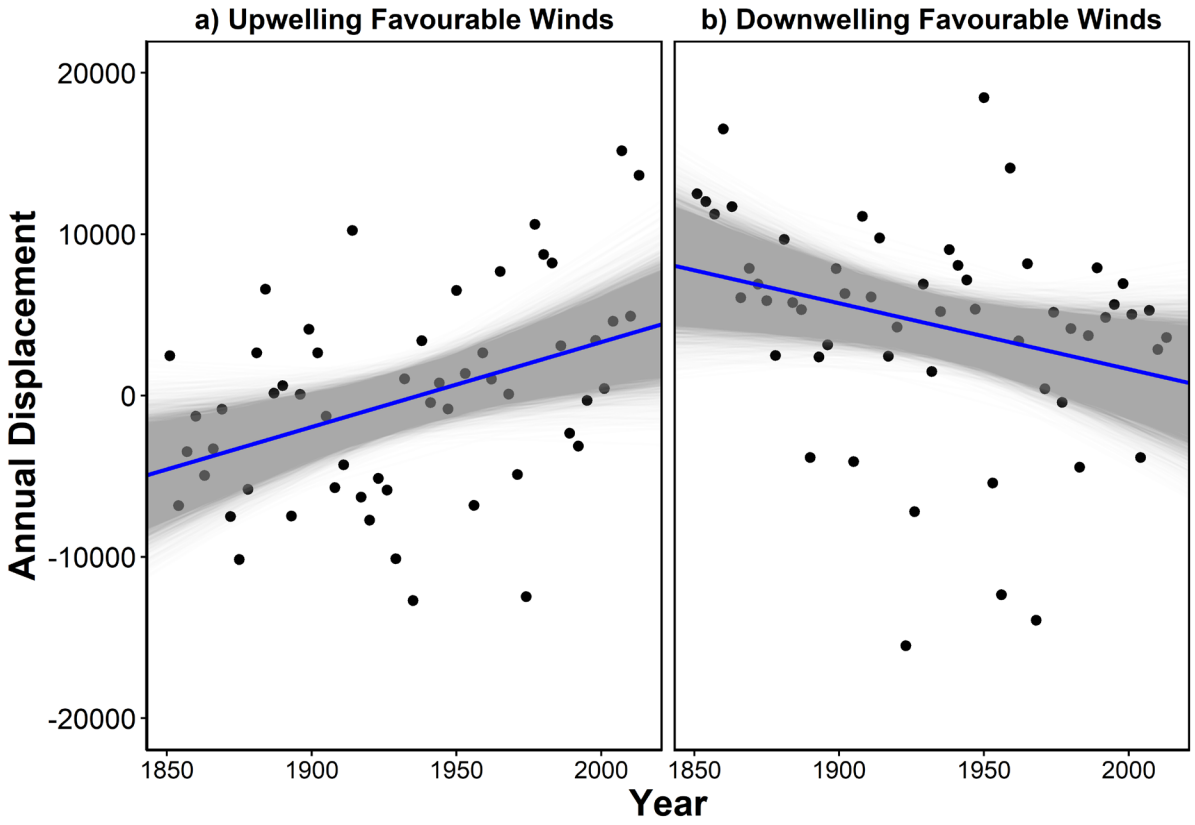


Figure 6 Temporal change in annual net displacement in upwelling (from northeast; Estimate of annual change: 52.86, 95 % credible interval: 19.00 – 85.59) and downwelling favourable winds (from southeast; Estimate of annual change: -40.93, 95 % credible interval: -78.18 – -3.71) between 1850 and 2014. The grey lines show 20,000 posterior sample estimates with the median trend line in blue. Only every third year of annual net displacement data was included in the models to account for temporal autocorrelation in the wind time-series data.