Coastal winds drive a two-stage recruitment mechanism for estuarine fisheries

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Abstract

Coastal winds transport larval fish towards the coast and estuaries where they ultimately recruit, yet our understanding of the mechanism of how different coastal winds interact to influence estuarine recruitment is incomplete. Here, we first demonstrate a two-stage recruitment mechanism showing that larvae of coastally spawned species increased in abundance with moderately strong upwelling favourable winds 14 days prior to sampling, reflecting increased nutrient and plankton availability for larval fish. The larvae of coastally spawned species increased in abundance with onshore (downwelling favourable) winds three days prior to sampling, which retain larvae near the coast, facilitating estuarine recruitment through onshore transport. Secondly, we show that effects of wind during the spawning period can be detected 2–8 years later (depending on the species) in estuarine commercial fisheries catch rates. Finally, we show in the southeast Australian region, upwelling favourable winds have increased while downwelling favourable winds have decreased since 1850, potentially reducing larval recruitment to estuaries. The two-stage wind mechanism identified in this study is likely applicable to other regions where wind driven upwelling occurs and influences onshore and offshore transport. Future research should incorporate coastal winds into predictions of estuarine catch rates.

Keywords: larval fish, retention, wind driven upwelling, fisheries production, *Mugil*, *Acanthopagrus*, *Platycephalus*, Harald Dannevig

Introduction

For many 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 (Houde, 2008; Schilling *et al.*, 2018). Some environmental conditions are more 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 these environmental factors benefit survival of the cohort (Garvine *et al.*, 1997; Helbig and Pepin, 1998; Pepin, 2016), producing a strong year class when this cohort is eventually harvested.

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 catch 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, therefore increasing recruitment to estuarine fisheries, and found a positive correlation between estuarine commercial catch rates and onshore winds lagged by three or four years (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) have been demonstrated for larval 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, some research has shown an opposite effect for larval fish in a persistent upwelling region (Morgan *et al.*, 2012).

The importance of wind during the juvenile phase for coastally spawned species in relation to commercial fisheries has been demonstrated with increased productivity and enrichment due to wind induced upwelling (Lloret *et al.*, 2004; Rykaczewski and Checkley, 2008) and wind induced

transport of larvae (Jenkins, 2005), both proposed as drivers of inter-annual variation in commercial harvest. Despite these findings, demonstrating both wind dynamics increasing recruitment and a detectable effect on commercial fisheries remains problematic.

The winds in many of the world's coastal upwelling systems are being altered due to climate change, resulting in both increases and decreases 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, alternations 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 five species, 10-year catch-per-unit-effort (CPUE) time-series dataset from eight east Australian estuaries (Gillson *et al.*, 2009), we evaluate interacting offshore/onshore winds (upwelling favourable and downwelling favourable) as a driver of estuarine fisheries production.

The present study investigates a coastal wind recruitment mechanism influencing advection and retention of fish larvae in three ways. Firstly, we examine whether or not coastal winds influence larval fish abundance near the coast. Secondly, we evaluate whether or not the same winds during the spawning period influence 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 following a period of upwelling. 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, Larval Fish, Commercial Catch and Wind Data

The present study uses data from the southeast Australian region (Figure 1), where the East Australian Current (EAC) is the dominant oceanographic feature. The EAC flows poleward, generally transporting 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 (McClean-Padman and Padman, 1991; 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). Using R v3.6.1 (R Core Team, 2019), we subset the larval fish abundance data to include samples only between 30–36° S; these were taken on the continental shelf (≤ 1000 m bathymetry; Figure 1). 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 over 1,000 larval fish samples in the database for this region. Within each larval fish sample, we excluded oceanic and estuarine spawning species, and only included commercially important families of fish known to spawn coastally; Sparidae, Girellidae, Labridae, Terapontidae, Monacanthidae and Mugilidae (Ford *et al.*, 2010). To avoid any one family dominating the abundance of coastal larvae, the abundance of each family 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 family had equal weighting during subsequent analysis. Following normalisation, the normalised relative coastal abundance across all samples had a mean of 0.004 (SD = 0.009), with a maximum of 0.138.

To assess if 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 of five different species; yellowfin bream (*Acanthopagrus australis*; Sparidae), sea mullet (*Mugil cephalus*; Mugilidae), luderick (*Girella tricuspidata*; Girellidae), dusky flathead (*Platycephalus fuscus*; Platycephalidae) and sand whiting (*Sillago ciliata*; Sillaginidae). It is important to note that in the calculation of CPUE, gillnet catch data for all five species were summed and then divided by total gillnet effort data (monthly timescale).

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 R v3.6.1 (R Core Team, 2019) with the '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 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) as well as 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 abundances, 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 and previous three days. These two time periods were selected to describe upwelling and retention against the coast and can have both immediate and lagged effects on larval abundance through physical transport and enrichment of nutrients (Dalley *et al.*, 2002; Ings *et al.*, 2008). A three-day time period has been previously used to model the physical effects of upwelling and downwelling on transport of larvae (Roughan *et al.*, 2005), while 14 days is the approximate period of time 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).

To test the effects of upwelling favourable (NE) and downwelling favourable (SE) winds on larval fish abundance, two generalised linear mixed models with a tweedie error distribution and a log link function were used. A Tweedie error distribution was used because the abundance data had a continuous, positively skewed, distribution. Both 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). Separate models were run for the 3-day lagged winds and the 14-day lagged winds using the 'glmmTMB' R package (Brooks *et al.*, 2017) with model assumptions checked using the 'DHARMa' R package (Hartig, 2019; Figures S1 and S2). The models 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 methodologies (Smith *et al.*, 2018), the model also included a random intercept effect for Project. The fitted model thus had the form:

$$Abund_{it} \sim Tweedie(\mu_{it})$$

$$E(Abund_{it}) = \mu_{it}$$

$$\log(\mu_{it}) = UpWind_{it} + DownWind_{it} + DistanceCoast_{it} + UpWind_{it} \times DownWind_{it} + UpWind_{it} \times DistanceCoast_{it} + DownWind_{it} \times DistanceCoast_{it} + UpWind_{it} \times DownWind_{it} \times DistanceCoast_{it} + UpWind_{it}^2 + DownWind_{it}^2 + UpWind_{it}^2 \times DistanceCoast_{it} + DownWind_{it}^2 \times DistanceCoast_{it} + Project_t$$

$$Project_t \sim N(0, \sigma^2)$$

Where $Abund_{it}$ is the relative abundance of coastally spawned larvae in the *i*th sample in Project *t*, and *t* = 1,…7, and $Project_t$ is the random intercept. $UpWind$ is the standardised upwelling favourable winds, $DownWind$ is the standardised downwelling favourable winds and $DistanceCoast$ is the distance from the coastline (km). To visualise the effects of the model predictors, marginal effects were calculated using the 'ggeffects' (Lüdecke, 2018), and 'effects' (Fox and Weisberg, 2018) R packages. The marginal and conditional R^2 values for the GLMMs were calculated using the method of Nakagawa *et al.* (2017).

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 NSW Department of Primary Industries drought situation maps. A linear mixed model 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. To normalise the variances, CPUE values were $\log_{10}$ transformed. 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. All linear mixed models were fit and assessed using the 'lme4' (Bates *et al.*, 2015), 'lmerTest' (Kuznetsova *et al.*, 2017), 'bootpredictlme4' (Duursma, 2019),

'LMERConvenienceFunctions' (Tremblay and Ransijn, 2015) and 'merTools' (Jared E. Knowles and Carl Frederick, 2019) R packages. The fitted model thus had the form:

$$\begin{aligned}\log_{10}(CPUE_{jns}) &= UpWind_{jns} + DownWind_{jnsit} + UpWind_{jns} \times DownWind_{jns} \\ &+ UpWind_{jns}^2 + DownWind_{jns}^2 + EstuaryType_{jns} + DroughtMonths_{jns} \\ &+ EstuaryType_{jns} \times DroughtMonths_{jns} + Estuary_n \times Species_s\end{aligned}$$

$$Estuary_n \sim N(0, \sigma_1^2)$$

$$Species_s \sim N(0, \sigma_2^2)$$

Where $CPUE_{jns}$ is the *j*th catch rate 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 and $DroughtMonths$ is the number of months of 'declared drought' during the year. To investigate species-specific responses in more detail, a separate linear mixed model was generated for each species with the same model structure (except without the random slope for species) following an identical procedure.

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 linear models for upwelling favourable (NE) and downwelling favourable (SE) winds with a fixed effect of year. Initial model runs 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, 2019). Therefore, for the final analysis we only used the wind data from every third year to remove the presence of temporal autocorrelation (Figures S3 and S4).

Models were checked for violations of the assumptions of normality and homogeneity of variance using density histograms of residuals, normal quantile-quantile plots, and plots of Pearson's

residuals *vs* fitted residuals generated using the 'plot' function in R (Figures S3–S10). For interpretation of model outputs in this study we used a strength of evidence and the language of statistical clarity approach rather than define a hard p-value threshold to mark significance (Murtaugh, 2014; Dushoff *et al.*, 2019).

Results

Larval Fish and Historical Winds

A total of 11,610 larval fish from six coastal spawning families (Sparidae, Girellidae, Labridae, Terapontidae, Monacanthidae, Mugilidae (Ford *et al.*, 2010)) were present in 1,489 observations on the continental shelf between 30 and 36° S. Examining the winds 14 days prior to sampling, revealed strong evidence of both a positive interaction between upwelling favourable (NE) and downwelling favourable (SE) winds (χ^2_1 = 13.303, $P < 0.001$) and a clear negative effect of distance from the coast on coastally spawned larval fish abundance (χ^2_1 = 11.157, $P < 0.001$; Figures 2 and 3). When the winds three days prior to sampling were investigated, there was strong evidence for a positive effect of downwelling favourable winds (χ^2_2 = 18.393, $P < 0.001$), a nonlinear effect of upwelling favourable winds (χ^2_2 = 14.058, $P < 0.001$), and a negative effect of distance from the coast on coastally spawned larval fish abundance(χ^2_1 = 17, $P < 0.001$; Figures 2 and 4).

The relative abundance of coastally spawned larval fish taxa consistently declined with distance from the coast for both the 3-day and 14-day models. Moving 20 km from the coast results in a decline of almost 50% in relative abundance (Figures 3 and 4). In the 14 days prior to sampling larval fish, upwelling and downwelling favourable winds interact to affect coastal species abundance. The highest abundances are predicted following slightly above average upwelling favourable winds and strong downwelling favourable winds (Figure 3). The influences of upwelling and downwelling favourable winds are similar at the 3-day and 14-day time scales except the negative quadratic influence of upwelling favourable winds peaks at mean speeds, with predicted abundance declining with both increasing and decreasing upwelling favourable winds (Figure 4). The influence of downwelling favourable winds on the relative abundance of coastally spawned larval fish continues to be positive and almost linear (Figure 4).

Commercial Catch Rates and Historical Winds

The multi-species model showed strong evidence for a negative non-linear effect of upwelling favourable winds (t_{137} = 2.662, P = 0.009) and weak evidence of a positive non-linear effect of downwelling favourable winds (t_{351} = 1.702, P = 0.090; Figures 5 and 6) on commercial CPUE when lagged by the modal age of capture for each species. There was no evidence for an interaction between upwelling favourable (NE) and downwelling favourable (SE) winds during the spawning period (t_{203} = -1.305, P = 0.193; Figure 5). In addition to the wind effects, estuary type and number of drought months also showed strong evidence for an interaction (F_2 = 10.988, P < 0.001; Figure S11). Overall, the model predicted the highest CPUE (lagged by an appropriate time) following strong onshore transport (downwelling favourable winds) with weak upwelling favourable (advection causing) winds during the spawning period.

The species-specific models showed mixed results, with models for some species capturing more variation in CPUE than others (Table 2). The model for bream explained the most variance in CPUE (marginal R^2 = 0.266, Table 2) and was the only species to show evidence of an interaction between downwelling favourable and upwelling favourable winds ($F_{64,1}$ = 5.570, P = 0.021) with the highest CPUE being predicted after strong downwelling favourable winds and weak upwelling favourable winds during spawning (Figure S12), similar to the multi-species model. There was some evidence of a non-linear negative effect of upwelling favourable winds on dusky flathead CPUE (t_{64} = -1.977, P = 0.052) and weak evidence for a positive non-linear effect of upwelling favourable wind on sand whiting CPUE (t_{64} = 1.816, P = 0.074; Figure S12). Evidence for a large effect of downwelling favourable winds on sea mullet CPUE was very weak (Estimate$_{64}$ = 1.469, P = 0.190). In contrast to the other species, there was no evidence of an effect from either upwelling favourable ($F_{64,2}$ = 0.375, P = 0.689) or downwelling favourable winds ($F_{64,2}$ = 0.229, P = 0.796; Figure S12) on luderick CPUE.

Aside from the wind effects, evidence of a positive effect of drought on CPUE was found in the models for bream ($F_{64,1}$ = 14.975, P < 0.001) and whiting ($F_{64,1}$ = 8.710, P = 0.004; Figure S12). In addition to this, evidence of an interactive effect between number of drought months and estuary type was detected for mullet ($F_{64,2}$ = 5.4364, P = 0.007), luderick ($F_{64,2}$ = 4.172, P = 0.020) and flathead ($F_{64,2}$ = 9.612, P < 0.001; Figure S12).

There was clear evidence of an increase in upwelling favourable winds ($F_{53,1}$ = 10.39, P = 0.002) and moderate evidence for a decline in onshore transport causing downwelling favourable winds ($F_{53,1}$ = 4.754, P = 0.034) between 1850 and 2014. 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 7).

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 a two-stage mechanism by which coastal winds influenced the recruitment of coastally spawned taxa to estuaries (Figures 2–4), resulting in detectable effects on commercial fisheries catch rates (Figures 5 and 6). Both upwelling and downwelling favourable winds are important for fish larvae, with moderate amounts of upwelling favourable winds driving increased chlorophyll production (Armbrecht *et al.*, 2014), and strong downwelling favourable winds driving onshore transport, facilitating estuarine recruitment (Agostini and Bakun, 2002). Despite the coarser temporal resolution of commercial fisheries catch data, using lagged winds from the species-specific spawning season showed a negative effect of strong upwelling favourable winds on CPUE possibly due to the advection of larvae away from favourable habitat, with weak evidence of the positive influence of onshore transport from downwelling favourable winds on CPUE. The interplay of upwelling (enrichment and advection) and downwelling (onshore transport and retention) favourable winds is highly important for estuarine recruitment and future studies should consider interactive effects of wind during the larval phase for coastally spawned fish species. While the overall variance explained by the fixed effects of upwelling and downwelling favourable winds, drought months and estuary type in the CPUE models in this study was low (marginal $R^2 \leq 0.27$), 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 around the globe (Bakun *et al.*, 2010; Sydeman *et al.*, 2014).

A two-stage recruitment mechanism

The differing effects of upwelling favourable (NE) and downwelling favourable (SE) winds with different lead up periods (three or 14 days) highlight a two-stage recruitment mechanism for coastally spawned larval fish. Upwelling was more important over the 14-day period, with increased upwelling favourable winds resulting in higher coastally spawned larvae abundances. This is likely due to the time it takes for upwelling to generate increased nutrients at the surface and for this energy to flow into the lower trophic levels (Gasol *et al.*, 1997; Buesa, 2019). The resultant increase in prey (e.g. nauplii) availability for larval fish may increase growth and survival rates (Zenitani *et al.*, 2007). In combination with this, onshore transport from downwelling favourable winds is also

important as it retains larvae near the coast. The positive effects of this retention are most visible after upwelling preconditions the ecosystem with nutrients (Rykaczewski and Checkley, 2008).

In contrast, the shorter 3-day period had a physical influence on the community. This is shown by the reduced effect of unfavourable advection (upwelling driven) as larval abundance peaked around intermediate speeds for upwelling favourable winds and declined as wind velocities became either too strong or weak. Strong upwelling favourable winds at this short time scale likely result in unfavourable advection away from the coast. Increasing downwelling favourable winds in the three days prior to sampling showed a positive effect on coastal larval fish abundance due to onshore transport. Combined with the observed negative distance to coast relationship, this strongly supports the hypothesis that onshore downwelling favourable winds were facilitating retention of coastally-spawned larval fishes against the coastline, closer to estuarine nursery habitats. This short-term transport by downwelling winds has previously been demonstrated for larvae of multiple taxa in various locations (Natunewicz *et al.*, 2001; Ings *et al.*, 2008). Increased recruitment into estuaries by these 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

The present study shows that 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. We believe this is indicative the same wind-driven mechanism demonstrated with the abundance of coastally spawned larval fish. However, owing to the coarse temporal resolution, we are unable to show the two distinct stages of upwelling followed by onshore transport. Using the CPUE multi-species model, we showed a strong increase in CPUE when there were weaker than average upwelling favourable winds during the spawning period and a weak positive effect of onshore transport (downwelling favourable winds), towards suitable juvenile habitat. 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 generate larval prey), followed by periods of onshore transport (downwelling). Coastal winds could influence recruitment for any estuarine fishery located in a region where coastal winds influence upwelling, given that this recruitment mechanism is likely to occur in other dynamic boundary systems such as the Californian

Current and Peruvian systems (Bakun and Weeks, 2008; Bakun *et al.*, 2010; Raimonet and Cloern, 2017).

The influence of wind on the recruitment of individual species is less clear, with species responding differently to upwelling and downwelling favourable winds during the spawning period. While the CPUE values of sea mullet and bream (the largest contributors to annual CPUE) were positively influenced by downwelling favourable winds (Figure S12), CPUE values for the other species considered (dusky flathead, luderick and sand whiting) did not show strong responses to the downwelling favourable winds and were likely influenced by other factors not considered here, such as changes in fisher behaviour. Previous research in this region has revealed sand whiting spawning movements coincide with high water temperatures linked to downwelling favourable coastal winds and downwelling oceanographic conditions (Van der Meulen, 2018). So, it is surprising that sand whiting CPUE showed weak positive responses to lagged upwelling favourable winds, which is a contrasting result to Van der Meulen (2018). It is possible that this mismatch is due to the downwelling favourable winds and subsequent increased water temperature, which stimulated spawning (as identified in Van der Meulen, 2018), whereas the overall upwelling favourable winds during the whole spawning season were influencing larval growth and survival. Previous research on other whiting populations has also shown recruitment is strongly determined by wind-driven transport in southern Australia due to their extended larval durations of over three months (Jenkins, 2005). We suggest that the coarse temporal resolution of the CPUE data and long larval duration are increasing variability and obscuring the detection of wind driven retention effects in this study as we did not extend our analysis of winds beyond the initial spawning period.

The generally weak positive effect of drought on CPUE for all species (with different effects in some types of estuaries) agrees with previous research using this data set that found monthly bream CPUE increased during periods of drought (Gillson *et al.*, 2009). Despite this, previous research also showed that the other species generally had a decline in monthly CPUE during periods of drought suggesting that the effect of drought on CPUE needs to be further investigated (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 in the analysis. These different scales likely reflect different processes within the estuaries with shorter timescales likely more representative of changes in both fish and fisher behaviour.

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 as changes in 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 would 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 individual fish species spawn (and therefore recruit) 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 and Conclusions

While our study successfully combined datasets to assess the effects of wind on larval fish retention and recruitment, it does have limitations. 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, 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 could be better understood.

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. However, ours is the first study to demonstrate that both enrichment and offshore transport from upwelling, followed by onshore transport, play an important role in influencing fish recruitment in estuaries. We suggest a two-stage recruitment mechanism of wind driven coastal enrichment and larval retention during the spawning season, which is detectable 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 can be detected in commercial estuarine fisheries data when appropriate lags are applied, and incorporating spawning period winds into recruitment models may improve predictions of commercial fisheries catch rates. As climate change drives changes in wind patterns, it is likely that wind driven ocean dynamics will continue to change as demonstrated in this study and it is important that future fisheries consider potential changes in recruitment.

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Author contributions

HTS & JPG collected the data, HTS & IMS conceived the ideas, HTS, CH, JPG 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.

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708 **Table 1** Details of the spawning season and modal age of capture in gillnet fisheries for five coastally
709 spawning fish species, used to define the choice of lags for winds during the spawning season with
710 an example of the wind intervals used for the annual catch-per-unit-effort (CPUE) between July 1997
711 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
luderick (*Girella elevata*)	December – February (Stocks *et al.*, 2015)	5	December 1992 – February 1993
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

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Table 2 Marginal and conditional R^2 values for the generalised linear mixed models including larval fish abundance data and the linear mixed models using catch-per-unit-effort (CPUE) data and lagged winds during the spawning period.

Model	**Marginal R^2**	**Conditional R^2**
3-day lagged winds larval fish	0.097	0.378
14-day lagged winds larval fish	0.101	0.440
multi-species CPUE	0.193	0.975
bream CPUE	0.266	0.913
flathead CPUE	0.249	0.989
luderick CPUE	0.152	0.969
mullet CPUE	0.148	0.964
whiting CPUE	0.127	0.874

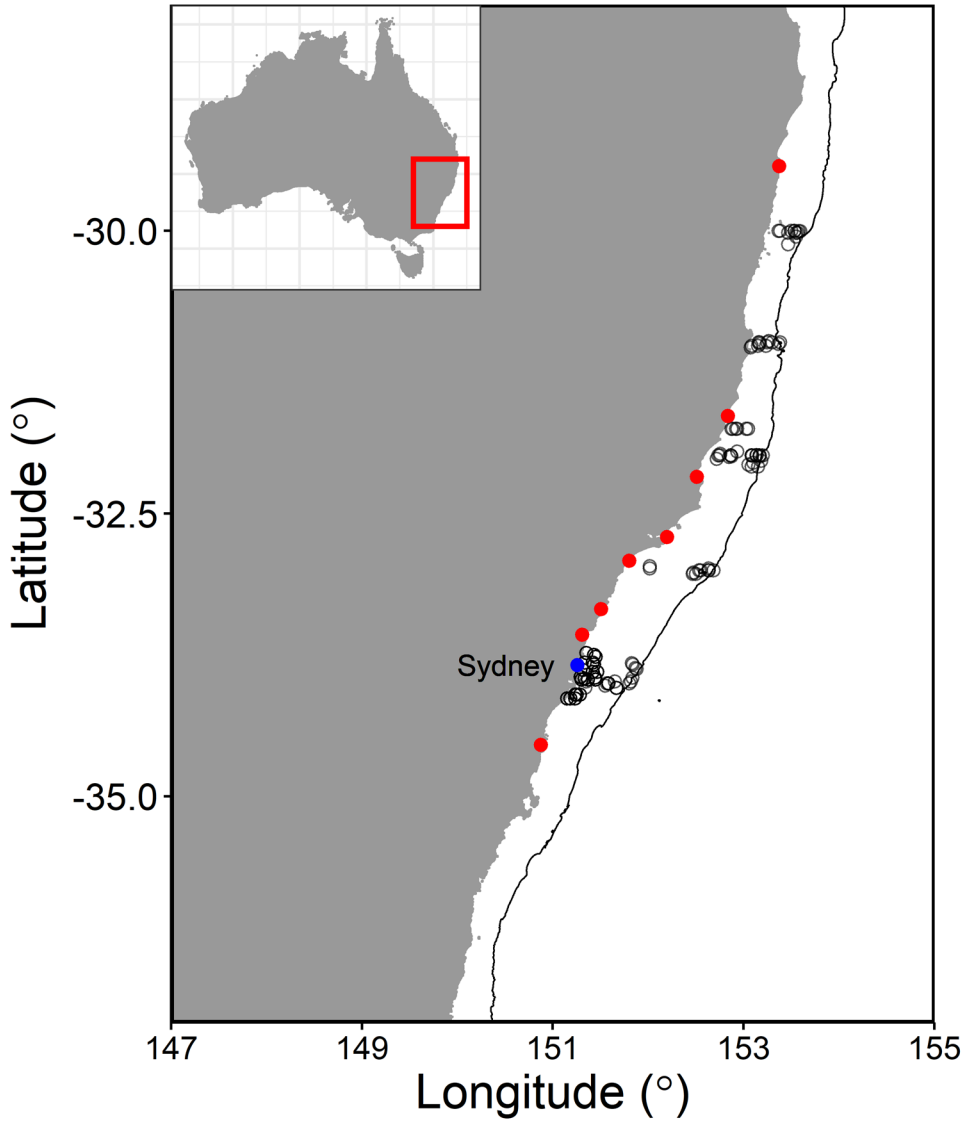

Figure 1 Location of south-eastern Australia showing the position of the larval fish samples included in this study (empty grey circles), the estuaries used in the catch-per-unit-effort analysis (filled red circles) and Sydney (filled blue circle). The black line represents the 1000 m isobath.

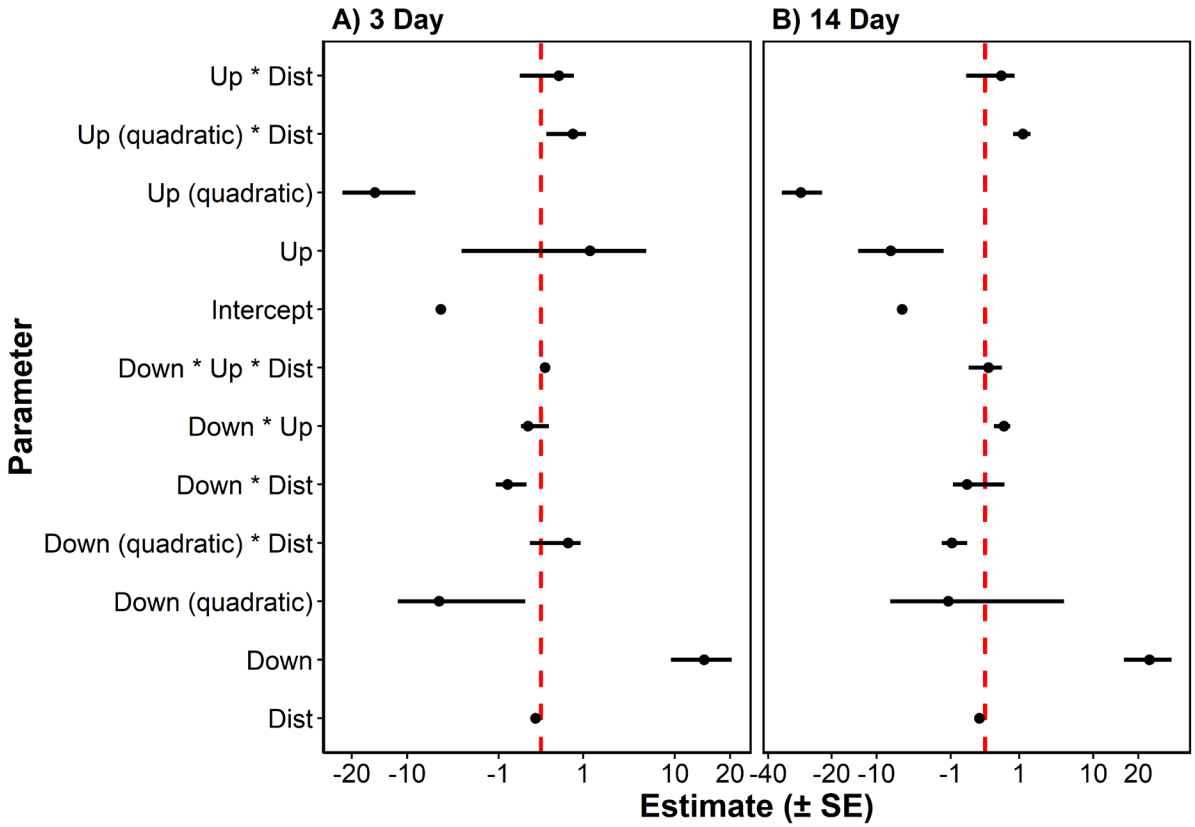

Figure 2 Caterpillar plots showing the coefficients for the 3-day and 14-day coastal larval fish abundance models. Points show the estimate of the parameter with the horizontal bar representing standard error of the estimate. Model terms are abbreviated; distance to coast is abbreviated to Dist, upwelling favourable winds are abbreviated to Up and downwelling favourable winds are abbreviated to Down. The dashed red line marks an estimate of zero. Note the differing x-axis scales for the 3-day and 14-day models, both of which are displayed on a signed square root transformed axis to make small but important effect sizes visible.

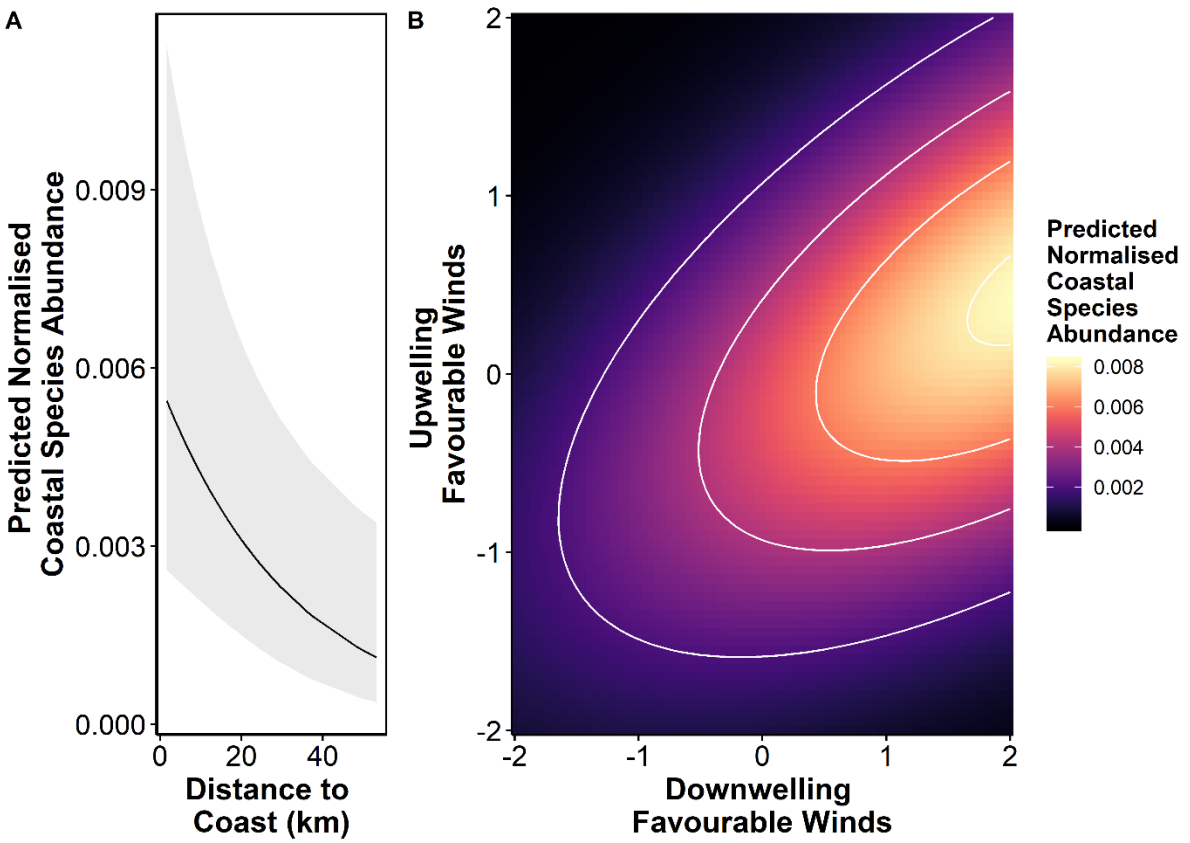

Figure 3 Visualisation of the predicted normalised coastal larval abundance based on the generalised linear mixed model for winds 14 days prior to sampling: A) shows the effect of distance from the coast, based upon mean (0 on the standardised scale) upwelling and downwelling favourable winds with shading showing the 95% confidence interval; and B) shows the interactive effect of upwelling and downwelling favourable winds based upon predictions made for 10 km from the coastline. On both axes, 0 represents mean winds, with 1 and −1 representing 1 and −1 SD from the mean, respectively. White contour lines connect areas of equal value and show intervals of 0.002.

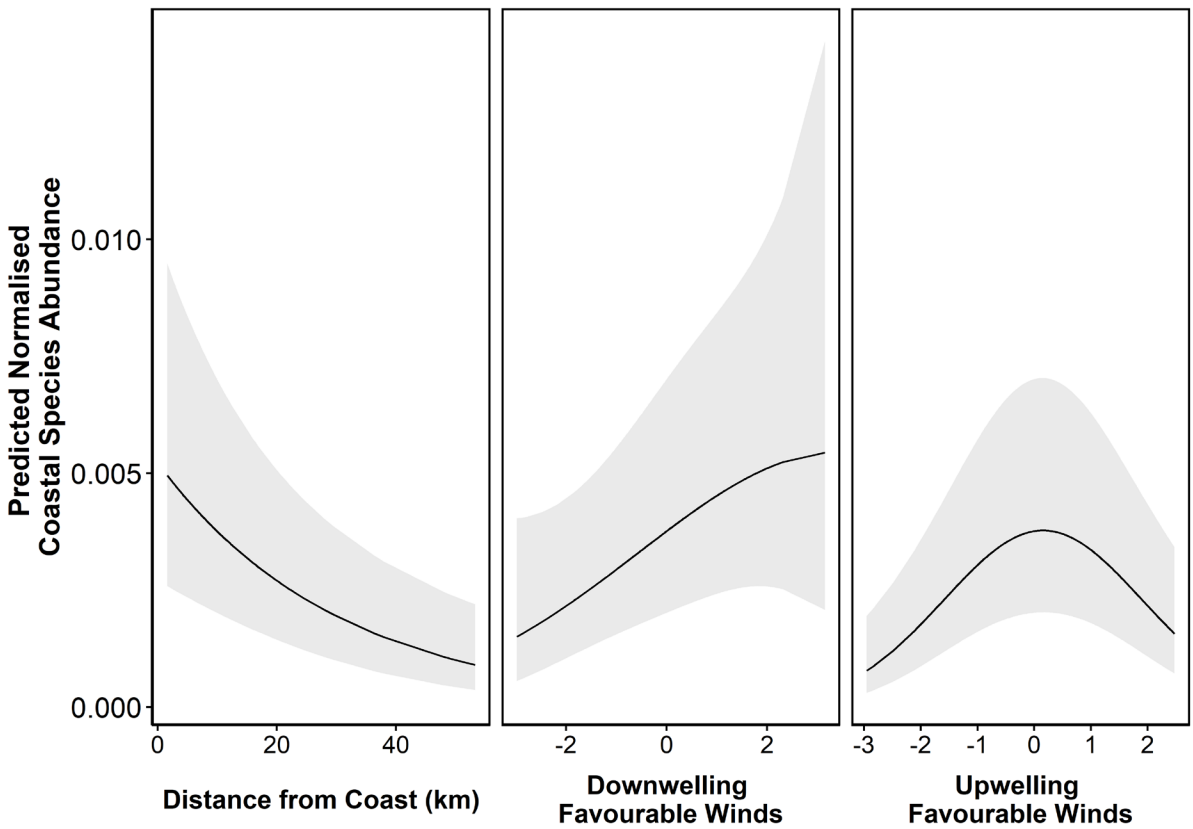

Figure 4 Marginal effects of the generalised linear mixed model for winds three days prior to sampling showing predicted normalised coastal larval fish abundance. The effect of distance from the coast is based upon mean upwelling and downwelling favourable winds (0 on the standardised scale). The effect of downwelling favourable winds was based upon 10 km from the coast and mean upwelling favourable winds. The effect of upwelling favourable winds was based upon 10 km from the coast and mean downwelling favourable winds. Shading shows the 95% confidence interval.

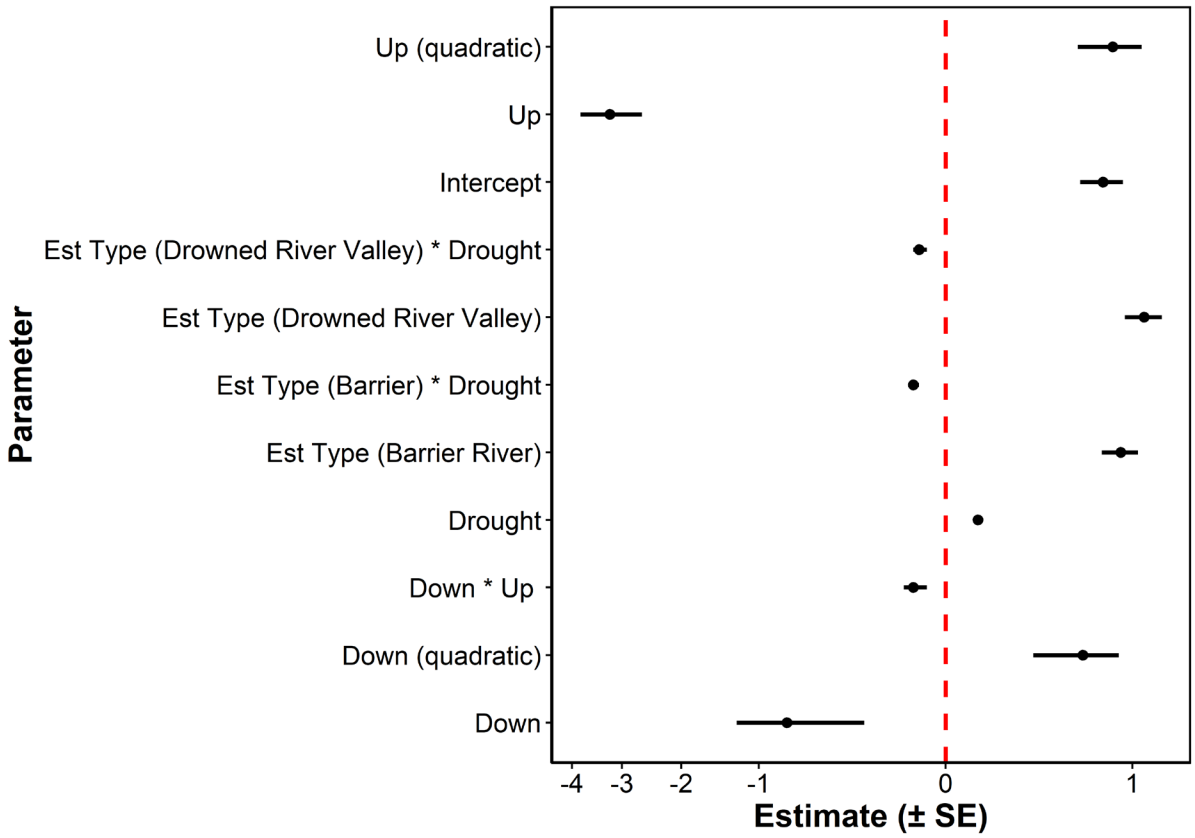

Figure 5 Caterpillar plot showing the coefficients for the multispecies catch-per-unit-effort (CPUE) linear mixed model. Model terms are abbreviated; upwelling favourable winds are abbreviated to Up, downwelling favourable winds are abbreviated to Down and estuary type is abbreviated to Est Type. Points show the estimate of the parameter with the horizontal bar representing standard error of the estimate. The dashed red line marks an estimate of zero. Note the x-axis was signed square root transformed so that small but important effect sizes are visible.

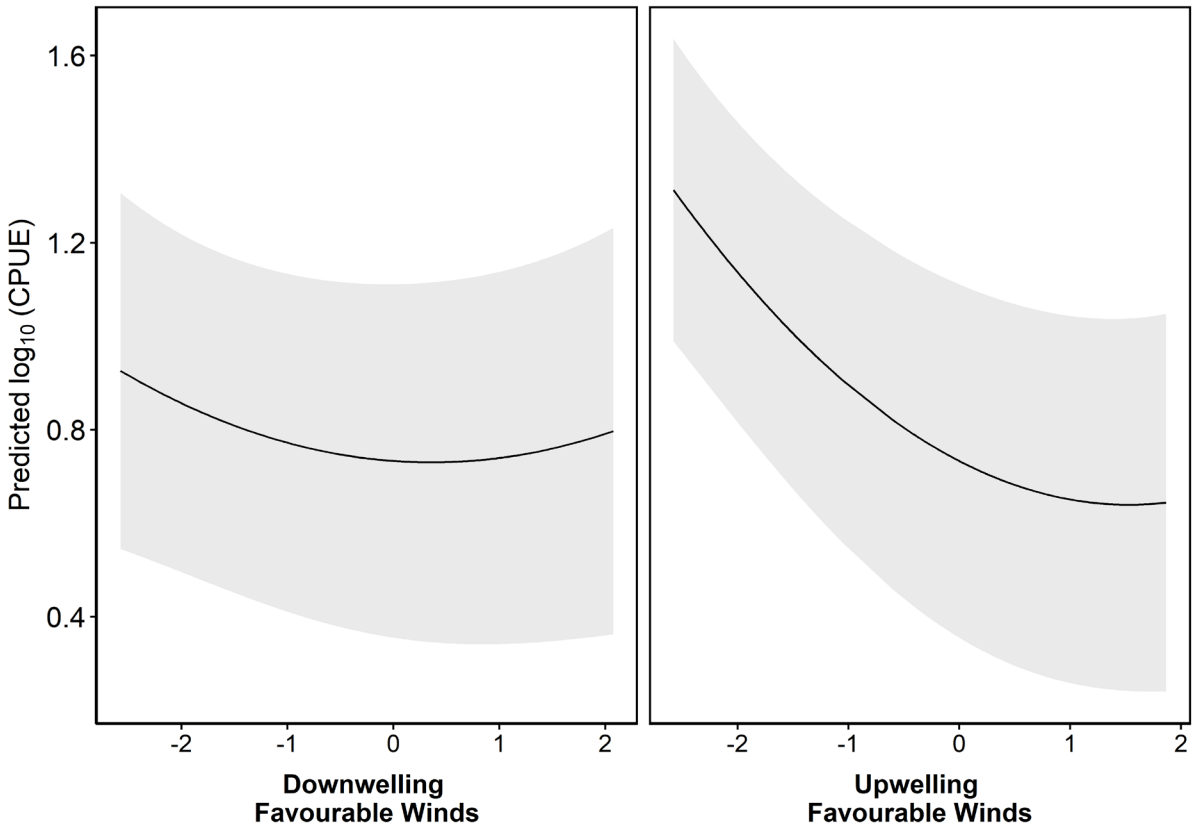

Figure 6 Marginal effects of downwelling and upwelling favourable winds on $\log_{10}$(Catch-Per-Unit-Effort; CPUE) from the multi-species linear mixed model based on lagged winds during the spawning period. Predictions were made using the mean values of the other model terms. Shading shows 95% confidence interval.

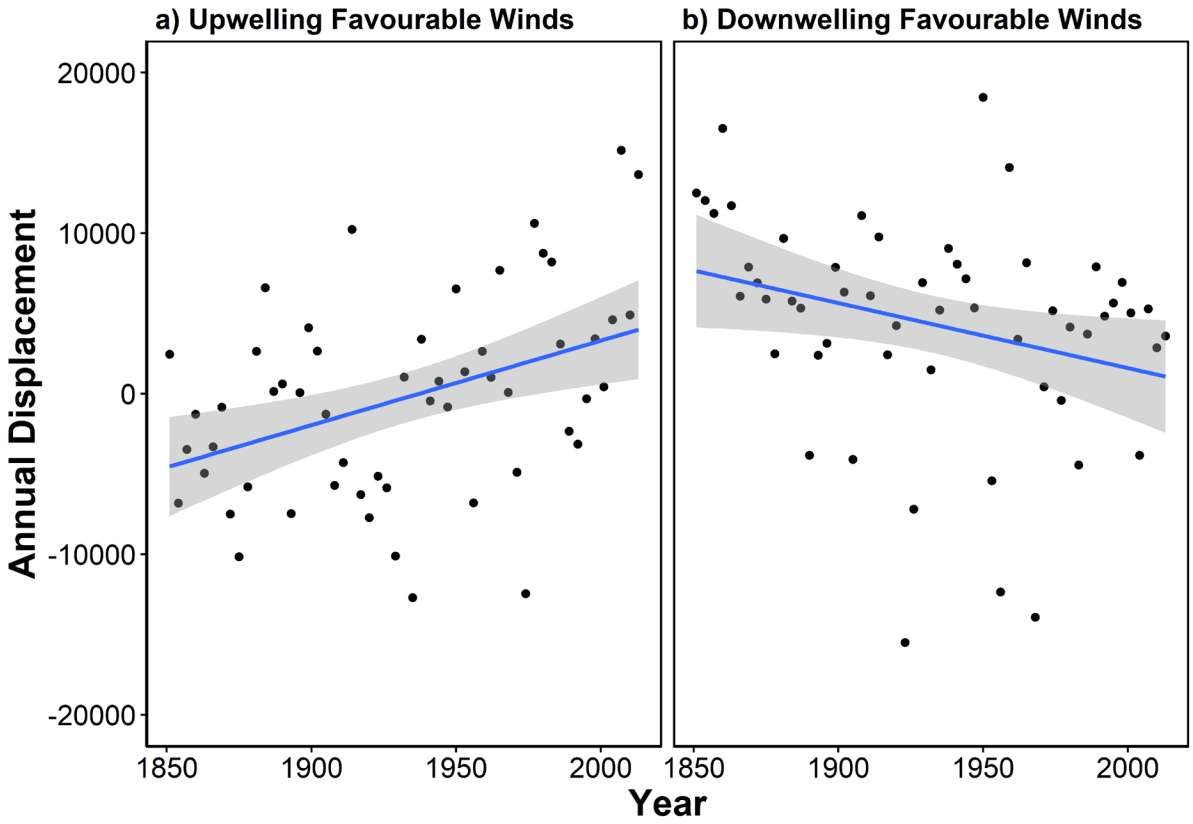

Figure 7 Temporal change in annual net displacement in upwelling (from northeast; P = 0.002) and downwelling favourable (from southeast; P = 0.034) winds between 1850 and 2014. The shaded area shows the 95% confidence intervals around the trend line. Only every third year of annual net displacement data was included in the models to account for temporal autocorrelation in the wind time-series data.