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Evaluation of hydrodynamic ocean models as a first step in larval dispersal modelling

Roxana Vasile[a,b,*], Klaas Hartmann[a], Alistair J. Hobday[b], Eric Oliver[a,c], Sean Tracey[a]

[a] Institute for Marine and Antarctic Studies, University of Tasmania, 20 Castray Esplanade, Battery Point, TAS 7001, Australia
[b] CSIRO Oceans and Atmosphere, Castray Esplanade, Battery Point, TAS 7001, Australia
[c] Australian Research Council Centre of Excellence for Climate System Science, Hobart, TAS 7000, Australia

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ABSTRACT

Larval dispersal modelling, a powerful tool in studying population connectivity and species distribution, requires accurate estimates of the ocean state, on a high-resolution grid in both space (e.g. 0.5–1 km horizontal grid) and time (e.g. hourly outputs), particularly of current velocities and water temperature. These estimates are usually provided by hydrodynamic models based on which larval trajectories and survival are computed. In this study we assessed the accuracy of two hydrodynamic models around Australia – Bluelink ReANalysis (BRAN) and Hybrid Coordinate Ocean Model (HYCOM) – through comparison with empirical data from the Australian National Moorings Network (ANMN). We evaluated the models' predictions of seawater parameters most relevant to larval dispersal – temperature, u and v velocities and current speed and direction - on the continental shelf where spawning and nursery areas for major fishery species are located. The performance of each model in estimating ocean parameters was found to depend on the parameter investigated and to vary from one geographical region to another. Both BRAN and HYCOM models systematically overestimated the mean water temperature, particularly in the top 140 m of water column, with over 2 °C bias at some of the mooring stations. HYCOM model was more accurate than BRAN for water temperature predictions in the Great Australian Bight and along the east coast of Australia. Skill scores between each model and the in situ observations showed lower accuracy in the models' predictions of u and v ocean current velocities compared to water temperature predictions. For both models, the lowest accuracy in predicting ocean current velocities, speed and direction was observed at 200 m depth. Low accuracy of both model predictions was also observed in the top 10 m of the water column. BRAN had more accurate predictions of both u and v velocities in the upper 50 m of water column at all mooring station locations. While HYCOM predictions of ocean current speed were generally more accurate than BRAN, BRAN predictions of both ocean current speed and direction were more accurate than HYCOM along the southeast coast of Australia and Tasmania. This study identified important inaccuracies in the hydrodynamic models' estimations of the real ocean parameters and on time scales relevant to larval dispersal studies. These findings highlight the importance of the choice and validation of hydrodynamic models, and calls for estimates of such bias to be incorporated in dispersal studies.

1. Introduction

Hydrodynamic ocean models have improved significantly over the last two decades, leading to their use in an ever-increasing range of studies and disciplines. Applications of hydrodynamic ocean models to marine biology studies include modelling of primary production, food webs and population dynamics (Nisbet et al., 1997; Wright, 2001), investigation of fish behaviour (Lukeman et al., 2010), design and evaluation of networks of Marine Protected Areas (Botsford et al., 2003), bioclimatic modelling with applications to the ecology of invasive species (Jeschke and Strayer, 2008), ecophysiology (Neill et al., 2004) and environmental impacts of changes in sea-level on ecosystems, hydrodynamics and sediment transport (Storlazzi et al., 2011). Larval dispersal studies, population genetics and demographic connectivity have also greatly benefited from the development and optimization of hydrodynamic models (Cowen et al., 2006; Miller, 2007; Tracey et al., 2012; Werner et al., 2007). Hydrodynamic models have been used in combination with Lagrangian dispersal kernels (Siegel et al., 2003), drift probability density functions (Brickman et al., 2007), biological behaviour (Fiksen et al., 2007), growth parameters

* Corresponding author at: Institute for Marine and Antarctic Studies, University of Tasmania, 20 Castray Esplanade, Battery Point, TAS 7001, Australia.
E-mail addresses: Roxana.Vasile@utas.edu.au (R. Vasile), Klaas.Hartmann@utas.edu.au (K. Hartmann), Alistair.Hobday@csiro.au (A.J. Hobday), Eric.Oliver@utas.edu.au (E. Oliver), Sean.Tracey@utas.edu.au (S. Tracey).

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(Punt et al., 2006), variations in reproductive timing (Carson et al., 2010) and temperature-based survival (Tracey et al., 2012).

The importance of high-performance ocean models to larval dispersal studies has become more obvious in the recent literature as knowledge and understanding of the ocean's complex and interacting hydrodynamics has evolved (Adams and Flierl, 2010). Modelling simulations of dispersal of larvae or any other planktonic forms use hydrodynamic models as the underlying engine driving the transport of the virtual particles. Successful modelling of larval dispersal relies on accurate three-dimensional estimates of ocean currents and water physical parameters throughout the domain of interest. A high-resolution representation of current velocities is crucial for the computation of realistic advection trajectories (Putman and He, 2013). This is particularly important in coastal regions where, on one hand, hydrodynamic processes have a higher spatial and temporal variability (Greenberg et al., 2007) and on the other, propagule release and larval recruitment of many important species take place. The coastal hydrodynamics can determine the degree of dispersal or retention of propagules, the survival rates (e.g. onshore wash of the propagules) or successful recruitment to suitable habitats. Accurate representation of ocean current velocities is also critical to broader applications of hydrodynamic models such as tracking missing boats and plane wrecks (Chen et al., 2012), locating flotsam sinks, modelling oil spills (Galt, 1997), dispersal of debris (Prasetya et al., 2012) and pollutants (Heldal et al., 2013; Wilcox et al., 2015).

Hydrodynamic models are often designed for a particular purpose or tuned to perform well on a particular spatial or temporal scale, either on the continental shelf or in the adjacent deep water and they may perform poorly outside this context. For example, Oliver and Holbrook (2014) demonstrated that the Bluelink ReANalysis has lower accuracy in estimating sea surface temperatures over the Australian continental shelf than in the offshore domain. These biases can have significant impacts on the outcomes of the hydrodynamic-model based dispersal studies. A second important limitation of many hydrodynamic ocean models for larval dispersal studies is the poor reproduction of features on the mesoscale (10–100 km) and sub-mesoscale (< 10 km) (North et al., 2009). This is particularly relevant to coastal areas, which are highly dynamic regions where ocean processes vary on scales of meters to a few kilometres (e.g., bores, tides, upwelling, filaments, fronts) (Pineda, 1991). Ideally, a hydrodynamic model for use in a study on the continental shelf should capture all the small-scale coastal features on a high-resolution grid (e.g., 0.5–1 km horizontally), with accurate near-shore tidal and meteorological forcing and the implementation of data assimilation (Werner et al., 2007). Global and basin-scale oceanographic models are usually not designed to resolve the processes on the continental shelf, hence they often compromise on at least one of the requirements listed above, failing to accurately reproduce the coastal ocean dynamics in this domain. While regional high-resolution models can meet all these requirements (McKiver et al., 2015; Moum et al., 2008), their restricted domain (e.g. < 100 km^2) is a major limitation for studies over broader areas. Ocean modelling studies that work with downscaled coarse-grid models suggest that an accurate representation of coastlines and bathymetry is more important than data assimilation in resolving processes in the coastal domain (e.g. Oliver et al., 2016).

While advection is critical for all dispersal studies, additional seawater properties including temperature, salinity, and nutrients play an important role in the survival, growth and development of biological propagules. Water temperature, for example, has major biological implications such as the survival of eggs and larvae, which makes it an indispensable parameter for larval dispersal modelling (Tracey et al., 2012).

When modelling the fitness and survival of a marine organism, time scales of hours or days are most relevant because they capture short events such as extreme temperatures that the marine organism would experience in the real ocean, events that may be outside the organism's physiological tolerance. However, some hydrodynamic models capture only the seasonal and inter-annual cycles reasonably well, not being able to reproduce the high frequency of biologically-relevant processes in the real ocean.

When considering the specifics of larval dispersal modelling, it is necessary to mention additional factors, independent from the ocean state, that may influence the dispersal trajectories of larvae in the real ocean and their successful recruitment. Larval behaviour, such as swimming ability or dial vertical migration, is governed by a complex interaction of factors (e.g. physiological, ontogenetic, phylogenetic, biogeographic), making it hard to decipher and even more difficult to model (e.g. Bradbury and Snelgrove, 2001; Cowen and Paris, 2003; Leis, 2007). No matter how much the implementation of larval behaviour in a dispersal model may alter the results of an otherwise passive-advection model, understanding the accuracy of the hydrodynamic ocean model is of primary importance and the validation of the hydrodynamic model of choice should be the first step in any dispersal modelling study.

This study tests the performance of hydrodynamic ocean models through comparison with empirical ocean data in order to assess their applicability in larval dispersal modelling. We use in situ mooring observations to evaluate the accuracy of model predictions of water temperature and ocean current velocity on the Australian continental shelf. This is a crucial and generally overlooked step in larval dispersal studies, which inherently rely on the accuracy of hydrodynamic models to capture the variability of coastal processes on timescales of days to months. The hydrodynamic models considered in this study are Bluelink ReANalysis (BRAN) and Hybrid Coordinate Ocean Model (HYCOM). We compared the models' daily outputs of water temperature and ocean current velocities and speed against in situ measurements from locations in the Australian National Moorings Network (ANMN). Our results show the relative ability of the two hydrodynamic models at capturing the observed mean state and variability of these parameters in the study region. Unlike previous studies on the performance of these two models (e.g. Kara et al., 2008; Oke et al., 2013) our work focused on validating the predictions of these ocean models as a first step in larval dispersal studies. We looked at oceanographic parameters that are most relevant to larval dispersal and the accuracy of these two ocean models in predicting them in the near-shore domain, on small spatial and time resolutions ecologically important to larval dispersal.

2. Data and methods

Two hydrodynamic models were examined by comparing their ocean state predictions against in situ observations of water temperature and u and v components of current velocity at 27 mooring stations around the Australian coastline.

2.1. Ocean models

The hydrodynamic models used include BRAN, provided by the Commonwealth Scientific and Industrial Research Organisation (CSIRO), and HYCOM, provided by the Centre for Ocean-Atmospheric Prediction Studies (COAPS). Details of each model are summarized in Table 1.

BRAN (Bluelink ReANalysis) is a multi-year integration of the Ocean Forecasting Australia Model (OFAM) version 2.0 – a global model based on version 4.1d of the Modular Ocean Model (Oke et al., 2013). The current version of the model – BRAN 3p5 – uses version 8.2 of the Bluelink Ocean Data Assimilation System (BODAS) (Oke et al., 2013, 2008) for incorporating the observed ocean state, such as in situ temperature and salinity observations, satellite sea-surface temperatures (SSTs) and along-track sea level anomalies from altimeters and tide gauges, into the model. The model was defined on a horizontal grid of 1191 × 968 cells with a horizontal resolution of 0.1° latitude and longitude around Australia (90-180°E, south of 17°S) which decreases

Table 1
Hydrodynamic models and their properties in the region of interest. Resolution is specified in degrees latitude and longitude. Minimum depth (Min. depth) refers to the shallowest level provided in the model output.

Model	Start date	End date	Horizontal grid		Vertical grid		Frequency of outputs
			Resolution	Grid size	Levels	Min. depth	
BRAN 3p5	1 Jan 1993	31 Jul 2012	0.1°	1191 × 997	51	2.5 m	Daily
HYCOM GLBa0.08	18 Sep 2008	10 Dec 2014	0.08°	4500 × 3298	32	3 m/1 m[a]	Daily

[a] 3 m for model runs before 2011 (experiment 90.8); 1 m for model runs since 2011 (experiment 90.9 and above).

gradually to 0.9° across the rest of the Indian Ocean and the Pacific (to 10°E, 60°W and 40°N) and 2° in the Atlantic and far north Pacific Ocean. The model has 47 z-levels (vertical grid), with 10 m resolution down to 200 m depth. The bathymetry is a composite of different sources including the Naval Research Laboratory Digital Bathymetry Data Base (DBDB2) and the General Bathymetric Chart of the Oceans (GEBCO). The model successfully reproduces much of the observed mesoscale variability around Australia (Oke et al., 2013) and spans circa 20 years of data (Table 1), with daily three-dimensional gridded water temperature, salinity and ocean current velocities.

HYCOM (Hybrid Coordinate Ocean Model) uses a hybrid grid that was developed to address the shortcomings of the Miami Isopycnic-Coordinate Ocean Model, on which it is based. HYCOM uses isopycnic vertical coordinates in the open, stratified ocean, which smoothly transition to z-level coordinates in the mixed upper-ocean layer or other unstratified regions and to sigma coordinates in shallow water regions and then back to z-level coordinates in very shallow water (Wallcraft et al., 2003). Therefore, HYCOM combines the advantages of different types of coordinate systems to optimally simulate both coastal and open-ocean oceanographic features, extending the geographic range of applicability of traditional isopycnic coordinate circulation models.

In this study we use version GLBa0.08 of the HYCOM model, which has been run in near real time since September 2008 to the present day (Table 1). This integration uses a native Mercator-curvilinear horizontal grid of 0.08° cell size and 33 vertical levels, generating daily outputs of surface water flux, mixed layer depth, mixed layer thickness, surface heat flux, sea surface height, surface salinity trend, surface temperature trend, salinity, water temperature and ocean current velocities. In this study we examined the water temperature and ocean current velocity. Data assimilation is performed using the Navy Coupled Ocean Data Assimilation (NCODA) system (Chassignet et al., 2007) which integrates available satellite altimeter observations via the Naval Oceanographic Office (NAVOCEANO) Altimeter Data Fusion Centre, satellite and in-situ SST, as well as available in-situ vertical temperature and salinity profiles from XBTs, Argo floats and moored buoys. MODAS synthetics are used for downward projection of surface information.

2.2. In situ coastal observation stations

The empirical data used to compare the models against consisted of time series of in situ observations from the Australian National Moorings Network (ANMN) available through the Integrated Marine Observing System (IMOS) portal. The ANMN is a collection of national reference stations and regional moorings that monitor oceanographic parameters in coastal ocean waters (Lynch et al., 2014). We used the data series from the ANMN ADCP platforms, which are a network of 48 moorings deployed in the coastal waters all around Australia (Fig. 1; Supplementary material Table 1). The ocean current speeds were measured at different depths in the water column using a range of Acoustic Doppler Current Profiler (ADCP) and Acoustic Doppler Current Meter (single point measurement) instruments. The exact instrument configuration, including measurement depths and frequency of measurements varied from one station to another and from one deployment to another for the same station. Water temperature, salinity and other chemical properties are also recorded at the instrument depth. In this model evaluation study for the purpose of larval dispersal, we used the time-series observations of zonal and meridional components of the current velocity – u and v respectively – and the water temperature.

2.3. Data processing

All data processing and analysis was performed in Matlab v8.3 (Mathworks). Data from the 48 mooring stations (Supplementary material Table 1) were assessed for completeness and reliability. Stations that had missing dimensions (e.g. depth), or where the quality control flags in the dataset indicated some issues were excluded. A final set of 27 stations providing good coverage along the Australian coastline (Fig. 1) was used in this study. At each mooring, the variables investigated were water temperature at the instrument depth and u and v ocean current velocities at the various depths recorded by ADCP. The data pooled together from all deployments per station formed almost complete time series ranging from one to up to six years (Supplementary material Table 1).

All data were filtered prior to analysis using the IMOS quality control flags. The quality flags were 1 (Good data), 2 (Probably good), 3 (Bad data that are potentially correctable) and 4 (Bad data). In our analysis we retained data with quality control flags 1 and 2. More details on the quality check toolboxes used for setting the data quality flags are available on the IMOS portal and the project's website (https://github.com/aodn/imos-toolbox/wiki/QCProcedures).
Whenever this was not included in the original data files, we applied a magnetic declination correction to u and v vectors in order to compute the components of current velocity along the geodetic East and North directions, respectively.

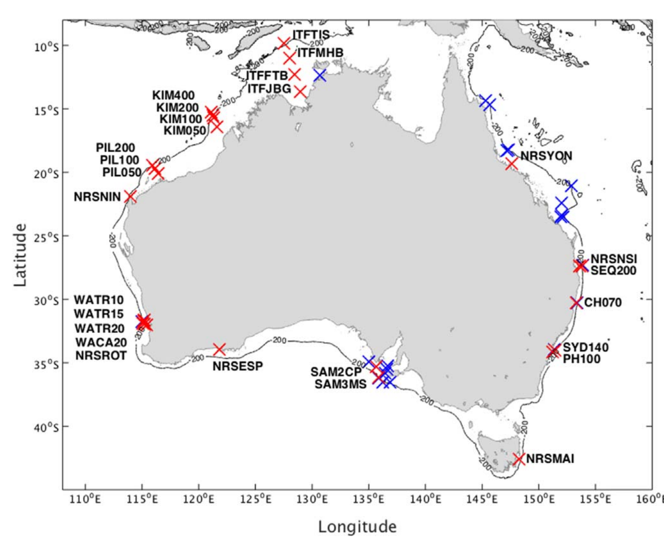

Fig. 1. The Australian National Moorings Network (ANMN). The (27) stations used in this study are indicated by red crosses; blue crosses indicate the (21) stations rejected from the analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The depth of the upward-pointing ADCP sensor at each ANMN station was derived from the mooring's pressure gauge and as such it incorporates variations due to tides. This variability was not reflected in the models' output, which use fixed depth levels relative to mean sea level. Consequently, we have assumed a constant depth computed as the average depth of all measurements across all deployments. The extreme depth deviations recorded during deployment or retrieval of the equipment, identified as 5 standard deviations from the mean, have been discarded from our analysis. Mooring coordinates of successive deployments varied by up to 200 m horizontally from the nominal location stored in the file metadata. Therefore, we used an average latitude and longitude across all deployments at each station.

At each mooring, the ADCP instrument measured u and v current velocities at a fixed number of regularly spaced levels above the instrument depth. The type of ADCP sensor and the number of levels differed among moorings and in the case of some moorings they differed between deployments. To create a comprehensive time series of current velocity for as many depth levels as possible, the data from each mooring was pooled into depth classes of 0.5 m and from here on we report the mean depth of each class as the depth of ADCP measurements.

The ocean model data were extracted at the model's grid cell closest to the mooring location and depth of measurements and over a time period common to the mooring deployments. This time series is hereafter referred to as the nearest neighbour. Linear interpolation of model predictions to the mooring location was also considered; however, our analysis showed that there was no systematic difference between the two methods, consequently only the nearest neighbour method is presented here. The ANMN moorings measure all environmental parameters up to 4 times an hour. In contrast, model outputs are provided as daily averages. To match these two timescales, we computed daily averages of all variables of interest recorded by the mooring sensors.

2.4. Analysis methods

We assessed the accuracy of BRAN and HYCOM ocean models in reproducing the real ocean state by comparing the summary univariate statistics of model outputs to in situ mooring observations and computing an index of agreement between each corresponding time series. The raw variables analyzed were water temperature and the u and v components of ocean current velocity. Because in hydrodynamic models a suboptimal (i.e. coarse) representation of the coastline and bathymetry can result in poor predictions of ocean current direction independently of ocean current speed, we also included in our analysis the speed and direction derived from u and v. This allowed us to investigate whether the models were better at capturing the magnitude of the ocean current or its direction. For calculations involving directions, we used the Circular Statistics Toolbox for directional statistics available in Matlab (Berens, 2009).

We denote the time series of in situ observations as O, the BRAN predicted time series as P^B and the HYCOM predicted time series as P^H. For each variable we investigated, each predicted value in P^B and P^H corresponds to an observation in O, in regards to location, depth of measurement and time. To ensure stable estimates of the distribution statistics we discarded any time series of less than 100 data records at any each station and depth. For each time series of O, P^B and P^H we report the mean values and the standard deviations.

To assess each model's accuracy in matching the in situ observations, we computed two skill measures for each P^B and P^H: the mean absolute error (MAE_B and MAE_H) and Willmott's index of agreement (d; Willmott et al., 2012). MAE is the most natural measure of average error (Willmott and Matsuura, 2005) and it is expressed as:

$$MAE = \frac{1}{n}\sum_{i=1}^{n}|P_i - O_i|$$

where P_i refers to either P_i^B or P_i^H, O_i refers to the observed variables, and $i = 1,2,\ldots n$ are the time indices. Just like the means and the standard deviations, MAE takes the same units as the time series variables. Willmott's index of agreement (d), hereafter referred to as the "skill score", is the most appropriate skill metric for evaluation of hydrodynamic models because it takes into account both the type and the magnitude of possible correlations (Allen and Greenslade, 2013; Willmott, 1982). Being a standardized measure, the skill score also allows the cross-comparison of the performance of different models in matching observational data. We used Willmott's refined version of the skill score (Willmott et al., 2012), expressed as:

$$d = \begin{cases} 1-\frac{\sum_{i=1}^{n}|P_i - O_i|}{c\sum_{i=1}^{n}|O_i - \bar{O}|}, & when \; \sum_{i=1}^{n}|P_i - O_i| \le c\sum_{i=1}^{n}|O_i - \bar{O}| \\ \frac{c\sum_{i=1}^{n}|O_i - \bar{O}|}{\sum_{i=1}^{n}|P_i - O_i|}-1, & when \; \sum_{i=1}^{n}|P_i - O_i| > c\sum_{i=1}^{n}|O_i - \bar{O}| \end{cases}$$

where P_i refers to either P_i^B or P_i^H, O_i refers to the observed variables, $i = 1,2,\ldots n$ are the indices of the time series, $\bar{O}$ is the observed mean, and $c = 2$. In its refined form, the skill score is scaled from − 1 to 1. While d values of or near 1 indicate that the deviations about the observed mean $\bar{O}$ are well captured by the model, values of or near − 1 identifies that the model poorly captures the deviations about $\bar{O}$ or that there is little observed variability (Willmott et al., 2012).

For water temperature we report the means, standard deviations, MAE, and the skill metric at the sensor depth at each mooring station. For current u and v components of velocity and current speed, which have several time series at each mooring station according to the levels of ADCP measurements, we pooled these values from all mooring stations and we present them in the form of averages over every 10 m water column. For ocean current velocities and speed we also present an average of the skill score over the top 50 m of water column, at each mooring station.

3. Results

3.1. Distribution statistics

In comparison with the observed data, both BRAN and HYCOM models overestimated the water temperature at almost all mooring stations (Fig. 2a). The most notable exceptions from this were a few mooring stations with depths between 150 and 200 m, where both models showed an underestimation of water temperature. The bias in predicted mean temperatures ranged from − 1.4 °C to 2.7 °C for BRAN and from − 0.6 °C to 2.3 °C for HYCOM. BRAN had larger errors in mean temperature than HYCOM, in particular between 60 and 200 m depth. Both BRAN and HYCOM models showed comparable differences between their predicted standard deviation and the observed standard deviation, with no consistent positive or negative bias (Fig. 2f). The bias in predicted standard deviations of temperature ranged from − 0.4 °C to 0.5 °C for BRAN and from − 0.3 °C to 0.5 °C for HYCOM.

For u and v current velocities, neither of the models performed better than the other throughout the water column (Fig. 2b, c). For u velocity, the bias in predicted means ranged from − 0.02 to 0.04 m s^{-1} for BRAN and from − 0.05 to 0.01 m s^{-1} for HYCOM (Fig. 2b). The largest deviations were observed in both models in the top 10 m of the water column, where BRAN overestimated the mean u velocity and HYCOM underestimated it. For v velocity, the bias in predicted means ranged from − 0.10 to 0.04 m s^{-1} for BRAN and from − 0.19 to 0.04 m s^{-1} for HYCOM (Fig. 2c). The largest deviations were observed in the top 10 m of the water column, where both models underestimated the mean v velocity.

HYCOM and BRAN both underestimated u and v standard deviation throughout the water column although the average bias was lower for HYCOM (Fig. 2g, h). For u velocity, the bias in predicted standard deviations ranged from − 0.19 to − 0.02 m s^{-1} for BRAN and from − 0.25 to 0.00 m s^{-1} for HYCOM (Fig. 2g). The largest deviations were

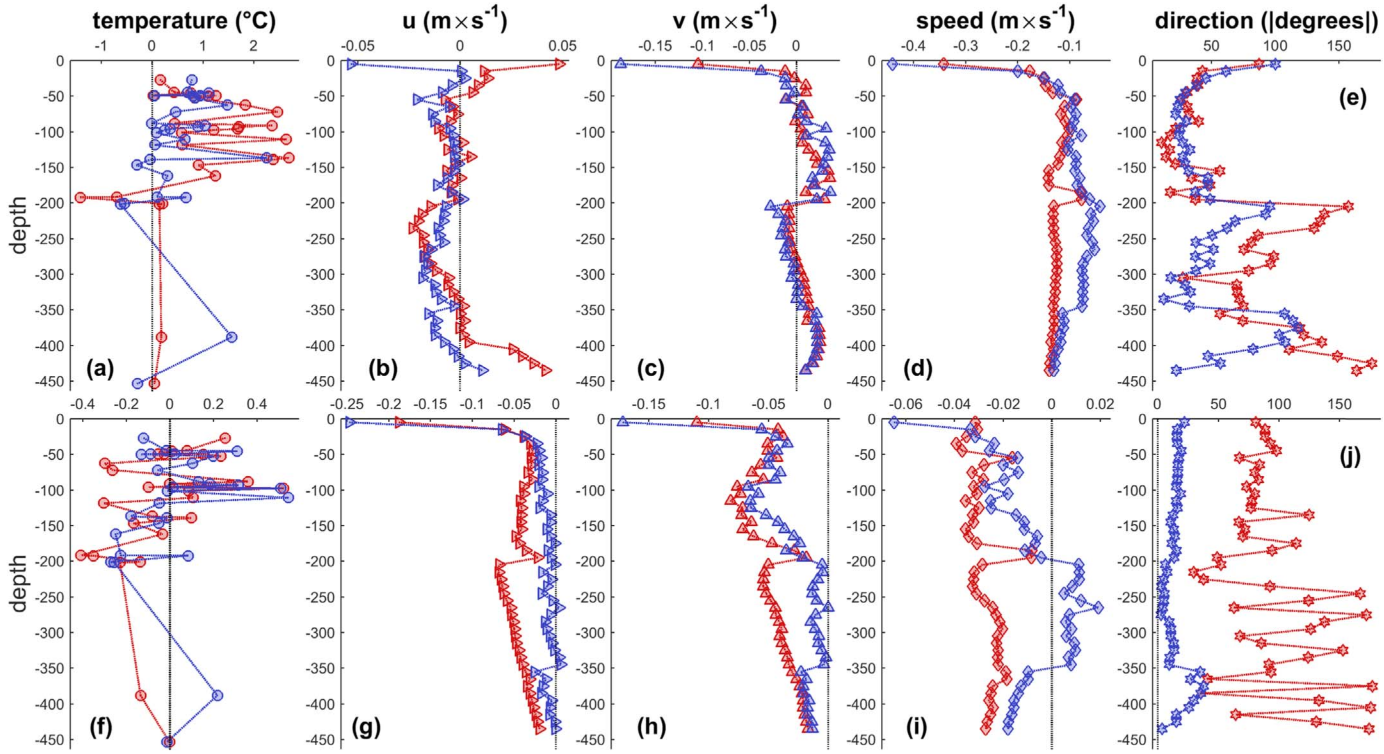

Fig. 2. Difference in means (top row) and standard deviations (bottom row) between BRAN and in situ observations (in red) and HYCOM and in situ observations (in blue) at 27 ANMN mooring stations. For u and v velocity vectors, current speed and direction the values were averaged across all stations in 10 m water column bins. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

observed in the top 10 m of water column, where both models underestimated the variability in u velocity. For v velocity, the bias in predicted standard deviations ranged from − 0.11 to − 0.02 m s^{-1} for BRAN and from − 0.17 to 0.00 m s^{-1} for HYCOM (Fig. 2h). The largest deviations were observed in the top 10 m of water column, where both models underestimated the magnitude of variability in v velocity.

Both models underestimated the mean current speed throughout the water column. The bias in predicted mean speed ranged from − 0.34 to − 0.08 m s^{-1} for BRAN and from − 0.44 to − 0.04 m s^{-1} for HYCOM (Fig. 2d). The largest deviations were observed in the top 10 m of water column, where both models underestimated the mean current speed. With the exception of the top 20 m, HYCOM predicted means of current speed were more accurate than BRAN predictions throughout the water column. Both models also underestimated the variability in the current speed, with the exception of HYCOM time series of predictions between 200 and 350 m depth, which showed a minor positive bias. The bias in predicted standard deviations of current speed ranged from − 0.04 to 0.00 m s^{-1} for BRAN and from − 0.06 to 0.02 m s^{-1} for HYCOM (Fig. 2i).

Both HYCOM and BRAN estimations of mean current direction were less accurate in the top 10 m of water column. The absolute bias in predicted mean current direction ranged from 11.05 degrees to 175.98 degrees for BRAN and from 12.77 degrees to 117.74 degrees for HYCOM (Fig. 2e). Below 200 m depth, HYCOM predicted means of current direction were consistently more accurate than BRAN predictions except between 350 and 370 m depth. The largest deviations were observed in BRAN predictions between 200 and 300 m depth and below 400 m depth. HYCOM estimations of variability in the current direction were more accurate than BRAN estimations throughout the water column. The bias in predicted standard deviations of current direction ranged from 29.59 degrees to 177.16 degrees for BRAN and from 2.84 degrees to 37.99 degrees for HYCOM (Fig. 2j).

3.2. Skill measures

The mean absolute errors of the predicted water temperatures showed a consistent positive bias for both models, throughout the water column (Fig. 4a). The MAE ranged from 0.2 to 2.7 °C for BRAN and from 0.4 to 2.3 °C for HYCOM. Overall, the MAE for BRAN predictions of water temperature was 21% larger than for HYCOM.

The mean absolute errors for u and v velocities indicate that BRAN predictions were more accurate than HYCOM predictions, throughout the water column (Fig. 4b, c). The MAE for u velocity ranged from 0.04 to 0.27 m s^{-1} for BRAN and from 0.03 to 0.99 m s^{-1} for HYCOM. Overall, the MAE for HYCOM predictions of u velocity was 31% larger than for BRAN predictions. The MAE for v velocity ranged from 0.02 to 0.24 m s^{-1} for BRAN and from 0.02 to 0.85 m s^{-1} for HYCOM. Overall, the MAE for HYCOM predictions of v velocity was 21% larger than for BRAN predictions.

The mean absolute errors for current speed indicate that HYCOM predictions were more accurate than BRAN predictions, throughout the water column with the exception of top 25 m of water column (Fig. 4d). The MAE for current speed ranged from 0.10 to 0.39 m s^{-1} for BRAN and from 0.07 to 0.47 m s^{-1} for HYCOM. Overall, the MAE for BRAN predictions of current speed was 18% larger than for HYCOM predictions.

The mean absolute errors for current direction indicate that BRAN predictions were more accurate than HYCOM predictions throughout the water column except below 400 m depth (Fig. 4e). The MAE for current direction ranged from 54.12 degrees to 105.42 degrees for BRAN and from 62.00 degrees to 97.08 degrees for HYCOM. In general, above 50 m depth the mean absolute errors in the current direction of both models increased with decreasing depth and below 150 m depth, it increased with increasing depth.

We also compared the models' predictions against the in situ observations using Willmott's skill score (Willmott et al., 2012). For water temperature, neither of the models was consistently better throughout

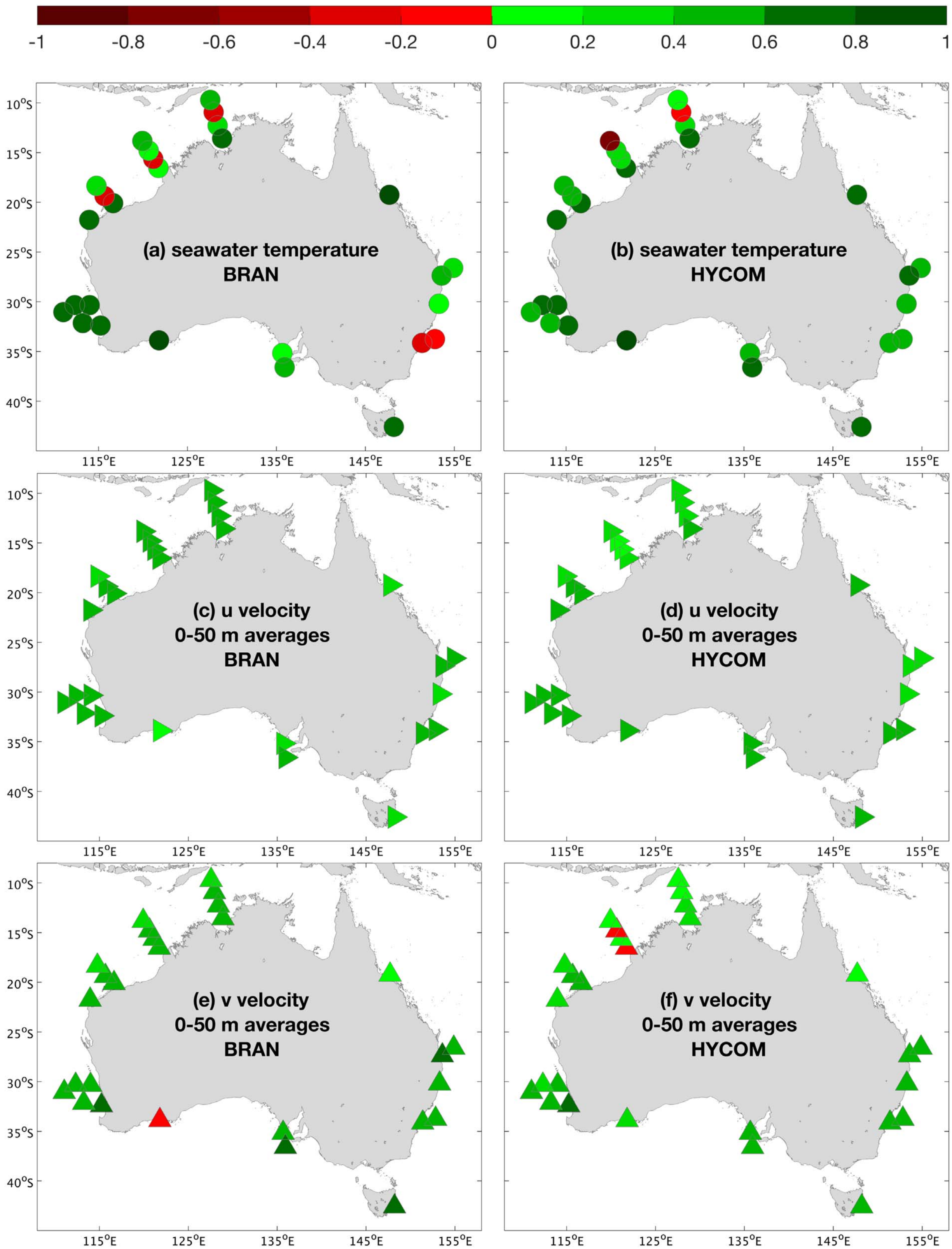

Fig. 3. BRAN and HYCOM Willmott's d-index of agreement with the in situ observations at 27 ANMN mooring stations, for (a, b) seawater temperature, (c, d) u current velocity, (e, f) v current velocity, (g, h) current speed and (i, j) current direction. Water temperature was recorded at each mooring's deployment depth. For u, v, current speed and direction the values were averaged over the top 50 m of water column.

the water column (Fig. 4f). Between 50 and 200 m depth, HYCOM was slightly more accurate than BRAN (average difference +0.29 *d*), while above 50 m and below 200 m BRAN was more accurate than HYCOM (average difference + 0.08 and + 0.43 *d*, respectively). Regionally, HYCOM has a higher accuracy in the Great Australian Bight and along the east coast of Australia while on the south west coast of Australia there is no considerable difference in the performance of the two models (Fig. 5a). Off the northwest coast there are mixed results with

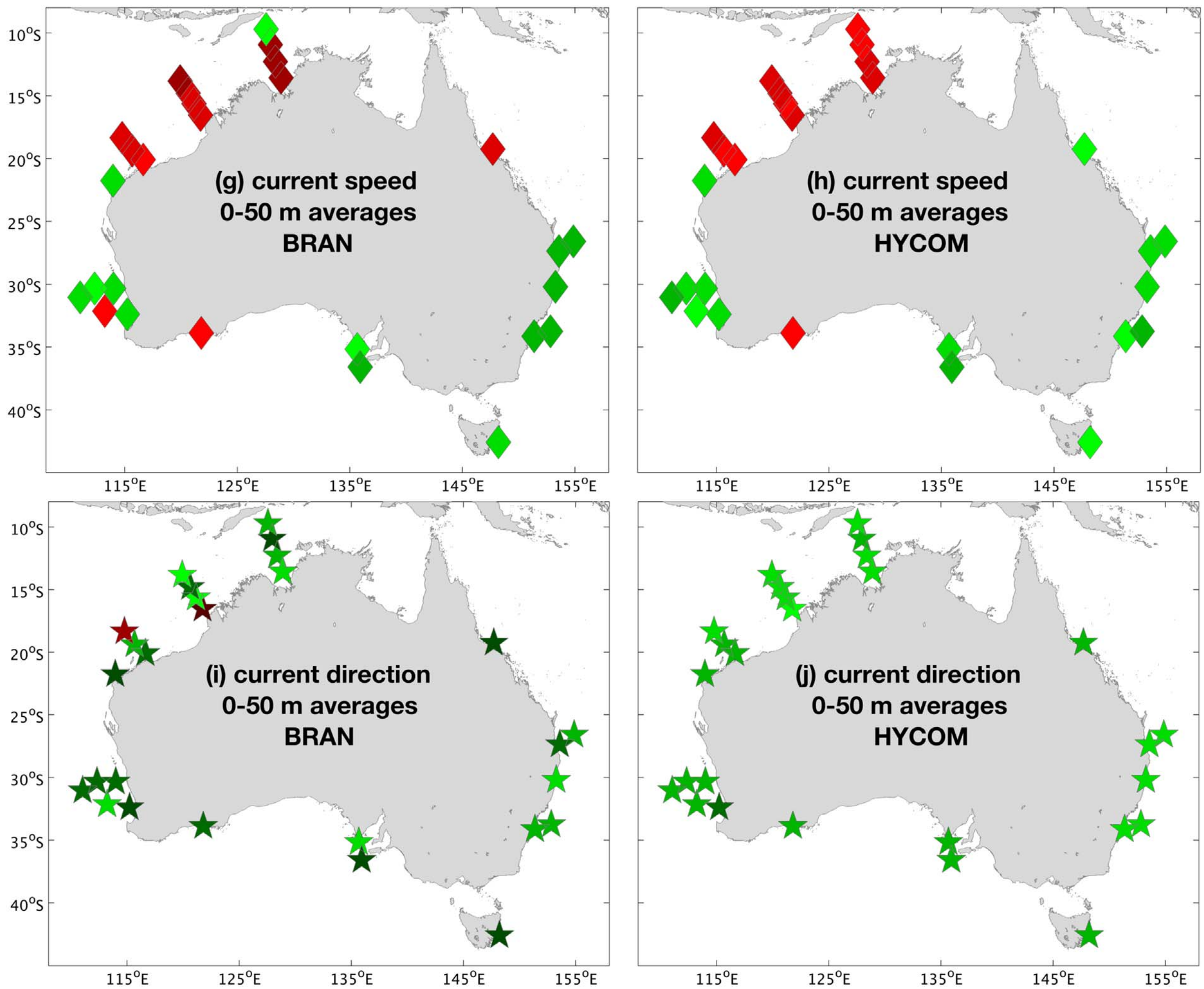

Fig. 3. (*continued*)

some stations showing better performance for BRAN and others for HYCOM.

For u and v velocities, BRAN showed a higher accuracy (average difference of + 0.35 *d*) than HYCOM throughout the water column (Fig. 4g, h). This difference in skill scores was most significant for u velocity and for depths below 200 m. Around 200 m depth, the two models showed a significant drop (u: 0.31 *d* for BRAN and 0.21 *d* for HYCOM, v- 0.43 *d* for BRAN and 0.31 *d* for HYCOM) in the accuracy of their predictions of both u and v, and the skill score improved again below 200 m. The average values of the skill score in the upper 50 m of water column showed that BRAN outperformed HYCOM at almost all stations (Fig. 5b, c). The few exceptions where HYCOM outperformed BRAN were stations PIL050 on north west coast, NRSYON on north east coast, and SAM2CP in the Great Australian Bight for u velocity and station NRSESP for both u and v velocities (Fig. 1).

Throughout the water column, both models were less accurate in predicting the current speed than predicting u and v components of velocity (Fig. 3). Willmott's skill score and the average error measure concurred, indicating that HYCOM had a higher accuracy (average difference of +0.12 *d* and average difference of 0.02 m s^{-1} MAE) in predicting current speed than BRAN (Fig. 4i). This was particularly true for depths below 200 m where the skill score for BRAN showed a sudden drop of 0.64. Both models however showed negative values for the skill score at depths below 200 m, which could be explained by low variability in the observed time series rather than poor performance of the models. This is because the skill score is closer to − 1 if either the spread of observations from the observed mean is very small, either the deviations of the model predictions from the observations are much larger compared to the spread of observations from the observed mean. However, in the upper 50 m of water column, BRAN had a higher accuracy on average than HYCOM on the southeast coast of Australian mainland and Tasmania (Fig. 5d).

Throughout the water column, both models were more accurate in predicting the current direction than predicting the current speed (Fig. 3). In both models, the lowest skill scores were observed in the top 10 m of water column, at 200 m depth and at depths below 400 m (Fig. 4j). Overall the average difference between BRAN and HYCOM accuracy in predicting current direction was + 0.06 *d* and 11.50 degrees MAE. The skill scores of the two models were comparable down to 200 m depth; below this depth BRAN had a higher accuracy than HYCOM. Regionally, in the top 50 m of water column, BRAN had a higher accuracy than HYCOM on the north and southeast coast of Australian mainland and Tasmania (Fig. 5e).

4. Discussion

Hydrodynamic models are critical for the investigation of dispersal patterns, yet examination of their performance is often neglected, particularly in biological studies seeking to understand larval dispersal. Ideally, as part of every dispersal modelling study, the different candidate hydrodynamic models should be validated with empirical data in the region of interest (wherever this information is not available in the literature), leading to the choice of the most accurate ocean product for that particular dispersal model. In this study we have illustrated a

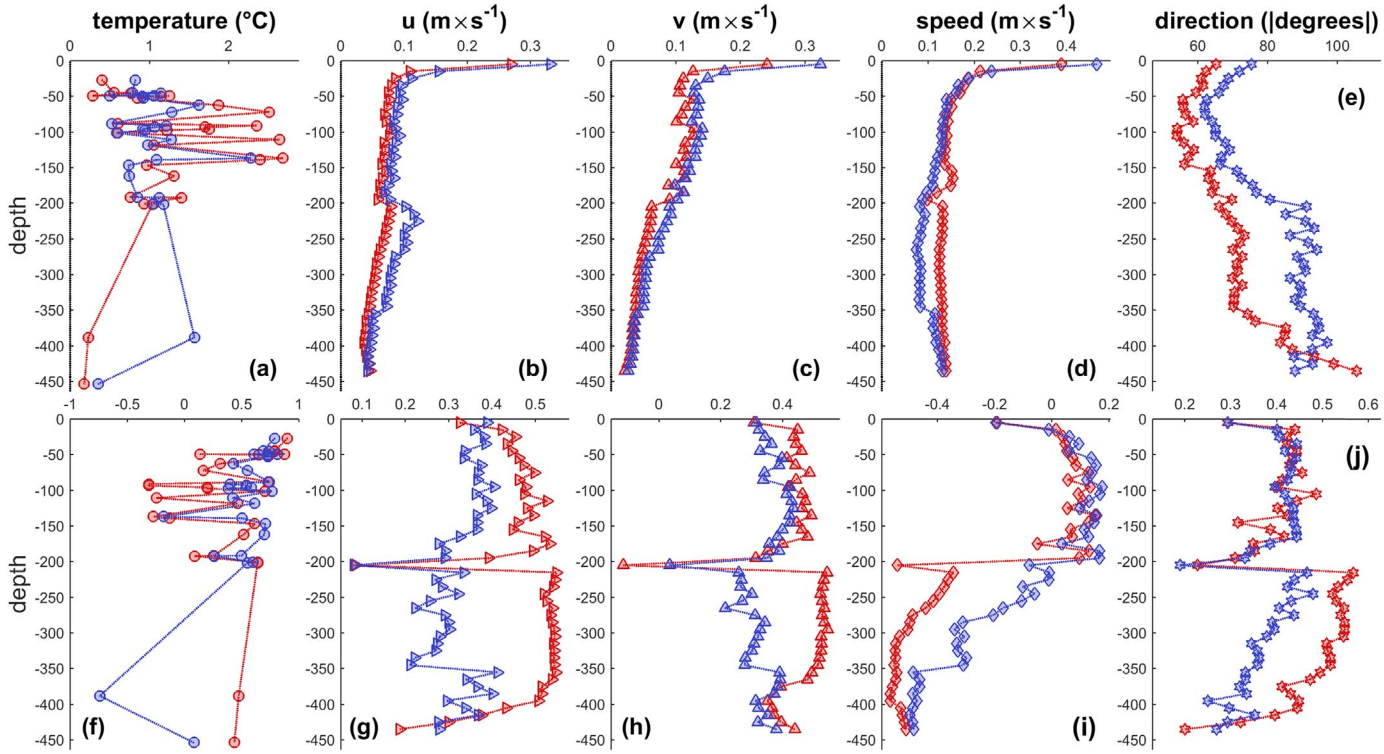

Fig. 4. Mean absolute errors (top row) and Willmott's skill score (bottom row) for BRAN (in red) and HYCOM (in blue) at 27 ANMN mooring stations. For u and v velocity vectors, current speed and direction the values were averaged across all stations in 10 m water column bins. The skill score *d* ranges from − 1 (poor agreement) to 1 (perfect agreement). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

comprehensive validation technique that can be employed to help with such a decision. Additionally, the hydrodynamic model's errors in estimating real ocean parameters should be reported together with the results of the dispersal model, as a measure of reliability of the predictions made.

With the development of new hydrodynamic models, both global and regional, dispersal modellers often have several ocean products to choose from in their work. While ocean modellers seek to implement their models with higher grid resolutions, better coastal coverage or real-time runs, dispersal modelling puts even these models through a rigorous test. Such improvements do not automatically imply that the ocean product will meet the requirements for dispersal modelling. It is therefore important for dispersal modellers to test the accuracy of candidate hydrodynamic products against observed ocean data in the region of their study and for the parameters of interest. Such rigorous tests are necessary to assure the choice of the best candidate, as well as to understand the limitations of the chosen ocean product. Because ocean product evaluation is rarely provided for dispersal models published so far, it is difficult to propose guidelines regarding the minimal accuracy of ocean models needed for the purpose of dispersal studies. If assessing the performance of hydrodynamic models is to become a routine in dispersal modelling, standards for ocean products can be defined, which may feedback developers of the hydrodynamic models.

This work focused on the validation of predictions of two hydrodynamic models - BRAN and HYCOM - on the Australian continental shelf. The continental shelf is the main domain of interest for most larval dispersal studies and for which global ocean models are, by design, rarely well-tuned. We investigated the seawater parameters most relevant to larval dispersal modelling studies: water temperature, u and v current velocities. In addition, we computed the ocean current speed and direction derived from u and v current velocities and included them in our analysis in order to discern whether the models were better at capturing the magnitude of the ocean current or its direction. Our findings showed that the performance of a hydrodynamic model studies depends on the chosen variable(s) and the region of study.

The present study found systematic positive bias in predicted water temperature, the two models consistently overestimating the water temperature by up to 2.7 °C in the top and mid-water layer. BRAN had the largest errors in temperature predictions between 70 and 170 m depth. This warm bias of ocean model predictions of subsurface water temperature has been reported for both BRAN (Oke et al., 2013) and HYCOM (George et al., 2010). Kara et al. (2008) looked at the performance of HYCOM in capturing observed sea surface temperatures in a large area of the Pacific Ocean and found a median warm bias of 0.23 °C over the 1990–2003 period.

Even the use of ocean data obtained through Satellite Remote Sensing - an alternative to numerical hydrodynamic models - cannot circumvent such biases. In a comparative study of satellite-derived ocean data and in situ measurements of subsurface water temperature in the coastal regions of Western Australia, Smale and Wernberg (2009) found that the satellite data overestimated seasonal and annual averages by 1–2 °C. The positive bias was consistent across the study areas for both satellites investigated, with the exceptions of one location for one of the satellites, where winter and spring averages of water temperature were underestimated by 1 °C. A similar study found a smaller positive bias in satellite-derived water temperature reflected in the seasonal averages in Tasmania (0.5 °C) compared to South Australia (1.4 °C), suggesting that at sites where consistent spatial and temporal differences were observed, a correction could be applied (Stobart et al., 2015). Both these studies found that satellite-derived data can capture general patterns in subsurface water temperature variations, such as seasonal trends, but they do not capture the ecologically and biologically relevant small-scale variations (e.g. daily peak temperatures that may exceed the physiological limits of a species), which only in situ measurements can capture accurately.

A warm bias on the order of 2 °C such as the one reported in this study could be considered biologically significant. The influence of temperature on metabolic rates and developmental times governing

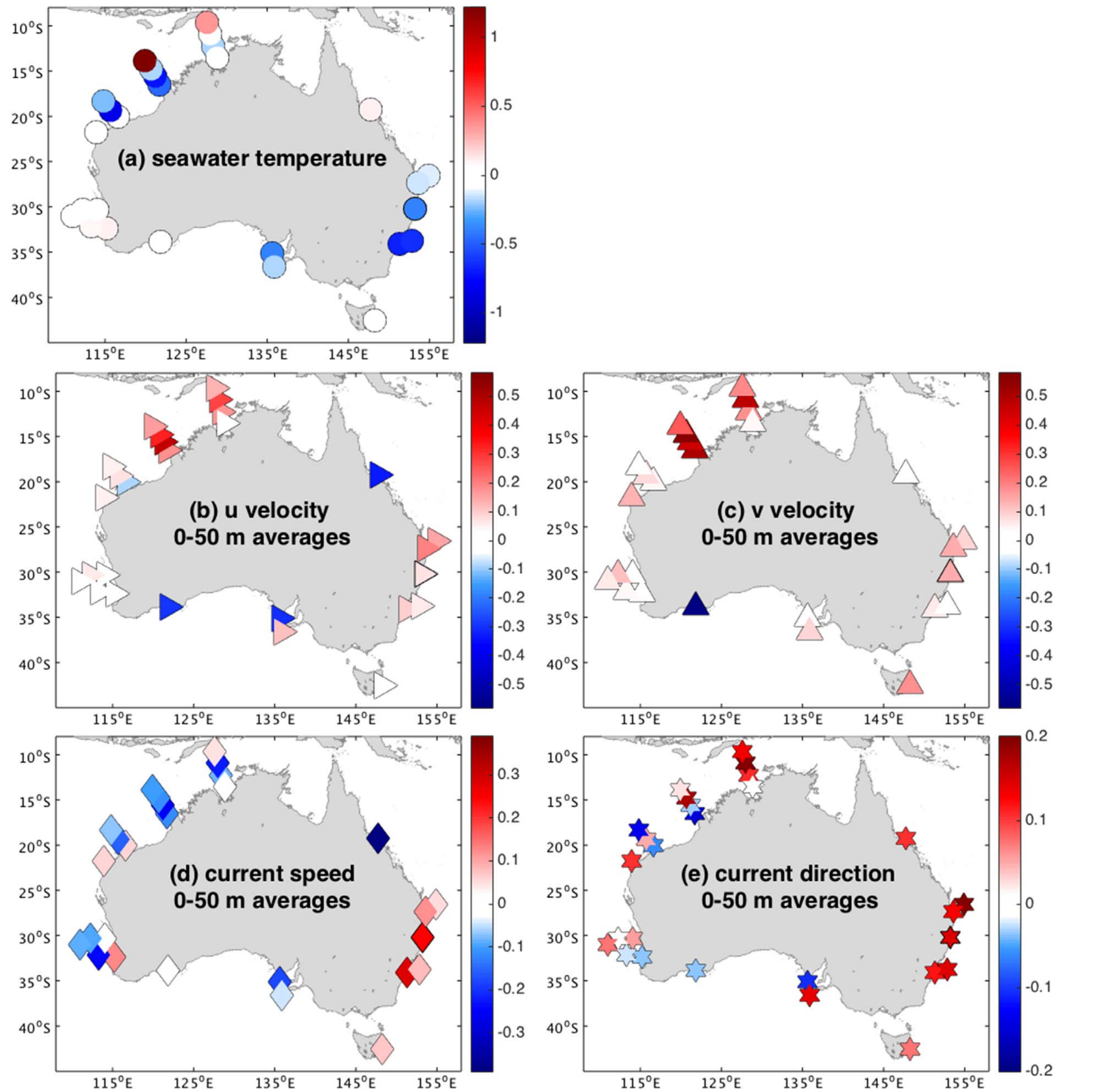

Fig. 5. Difference between BRAN and HYCOM Willmott's *d*-index of agreement with the in situ observations at 27 ANMN mooring stations, for (a) water temperature, (b) u current velocity, (c) v current velocity, (d) current speed and (e) current direction. Water temperature was recorded at each mooring's deployment depth. For u, v and speed the values were averaged over the top 50 m of water column. In red are the stations where BRAN is more accurate; in blue are the stations where HYCOM is more accurate. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

larval fitness and survival and the importance of this parameter in larval dispersal has been reported in literature numerous times (e.g. Gillooly et al., 2001, 2002; O'Connor et al., 2007). Larval dispersal modelling studies often estimate larval survival based on the ambient temperature (e.g. Marta-Almeida et al., 2008; Knickle and Rose, 2010; Tracey et al., 2012). Therefore, an ocean product that accurately reproduces real ocean water temperature is crucial in larval dispersal modelling and it is important to report the level of certainty associated with temperature-based predictions wherever it is known. Dispersal models could account for the bias in a hydrodynamic models temperature predictions by including a margin of error for this water parameter in the dispersal scenario via sensitivity analysis, or by explicit bias correction of the modelled temperature. Sensitivity tests can be used to investigate how different values of ambient temperature influences the model output – with sensitivity values informed by the known error in the model.

The two models' performance in reproducing water temperature varied from one station to another, which could be explained by the particularities of water column stratification at each station, as noted in other in situ vs. satellite temperature studies (Smale and Wernberg, 2009; Stobart et al., 2015). Ocean models have been shown before to have problems in reproducing a sharp thermocline (Griffies, 2010; Wilson, 2000). It is expected that in situ ocean temperatures are best approximated by the model at least to the depth of the thermocline, which varied from station to station. This is because both models are constrained by SSTs through data assimilation which helps to characterize the well-mixed layer above the thermocline. Below the depth of the thermocline, these hydrodynamic models are less accurate with regard to water temperature, due to difficulty in representing dynamical ocean processes.

Both BRAN and HYCOM ocean models showed considerably higher accuracy in predicting water temperature than in predicting ocean current velocities. This might be expected, since the variability of ocean currents is much higher than subsurface water temperatures, especially in coastal waters, and concomitantly, global ocean models are not particularly designed to resolve this high variability on small spatial and temporal scales (Greenberg et al., 2007). Also, temperature is dominated by the seasonal cycle, largely driven by atmospheric and large-scale ocean variability, which models can capture well while water velocity is relatively more influenced by tidal and non-seasonal variability, such as day-to-day or week-to-week variability that models do not reproduce as accurately as they do the seasonal cycle (Bernie et al., 2005).

Passive larval dispersal is the result of the interplay between both advective and diffusive ocean circulation processes. Between their release from spawning grounds and their settlement to adult habitat, planktonic larvae will experience a range of circulation patterns. The temporal and spatial scales of these patterns relevant to larval dispersal is at the intersection of the scales of variability of the wide range of physical transport mechanisms involved, with the larval biology of which most important is the pelagic larval duration (Pineda et al., 2007). Coastal regions are the main spawning grounds for a majority of fishery species. Flows in these near-shore regions are complex: they are driven by surface and internal tides, large-amplitude internal waves and bores, wind-forcing, surface gravity waves, buoyancy forcing, boundary current flows and they are influenced by topographic features like shoals, headlands, kelp forests or coral reefs (Gawarkiewicz et al., 2007; Pineda et al., 2007). Large-scale ocean models such as those underpinning BRAN and HYCOM have difficulties in reproducing these flows in detail. Near the coastal boundary, flows are weaker, offering opportunities for retention of larvae adjacent to the coast. Features including basins with narrow connections to the ocean (estuaries, enclosed bays) can promote alongshore connectivity, increased self-recruitment and decrease net displacement. Larvae spawned on the open coast can also be entrained into bays, reducing their alongshore transport. In these retention regions, the time scales of retention are determined by the processes that govern bay-ocean exchange (Gawarkiewicz et al., 2007). In contrast, cross-shore transport and shelf break processes (upwelling systems, slope eddies, shelf-break jets) drive the larval exchange between the continental shelf and offshore waters, promoting larval dispersal over larger spatial scales and longer pelagic larval durations (Gawarkiewicz et al., 2007). Ocean models that capture these processes better than circulation through near-shore retention features, would be more appropriate to use in modelling the larval dispersal of species with long PLD.

Tides are an important feature of the real ocean that is not commonly simulated in large-scale hydrodynamic models and which can influence the trajectories of drifting larvae particularly in the near-shore domain. While the two ocean models we investigated do not simulate tides, they do incorporate a parameterization of tidal mixing and they are forced through assimilation of observations including tides (Chassignet et al., 2007; Oke et al., 2013, 2008). This may have limited the discrepancies between the modelled and the in situ measurements of ocean current velocities, through a correct simulation of tidal-influenced stratification, but could still account for some of the differences we identified in our analysis of model performance.

For u and v current velocity, the largest errors in both models were found in the surface layer, where the models significantly underestimated the means and standard deviations. This is possibly due to underestimating the surface and near-surface wind-driven currents due to discretization of the water column in the vertical dimension. As shown by the skill score *d*, BRAN had a higher accuracy than HYCOM in estimating observed u and v velocities, almost consistently throughout the water column. The statistical results suggest that the higher performance of BRAN in reproducing observed u and v velocities is due to lower average errors, in spite of BRAN reproducing the observed variability less accurately than HYCOM. While both models showed larger deviations about the observed means of current speed than about the observed means of u or v velocities, the bias in standard deviation between predicted and observed current speed was much lower than for u and v velocities time series. The errors we observed in BRAN predictions of current speed were similar in magnitude to the ones found in the study of Oke et al. (2013) in the same study region. With regard to the ocean current speed, as opposed to velocities, HYCOM predictions were in closer agreement with the observations than BRAN predictions. This was reflected in the distribution mean and standard deviation as well as in the average error. This suggests that the magnitude of ocean currents is better estimated in HYCOM, while BRAN reproduces the directional component better than HYCOM, confirmed by the analysis of ocean current direction. Although HYCOM captured the variability in the ocean current direction much better than BRAN, it also had larger errors as shown in the distribution means and mean absolute errors of current direction, errors that translated into a lower skill score than BRAN, in particular below 200 m depth.

In dispersal modelling studies, the trajectories of passive drifters are inferred entirely on the hydrodynamic model's predictions of ocean currents, hence the need for accurate estimations of both the current magnitude and direction. Moreover, the ocean products this study investigated showed errors large enough to raise concerns about their reliability, especially when used in larval dispersal studies, which may require highly accurate predictions of ocean state close to the coast where settlement and retention are critical processes (Warner et al., 2000). Subsequently, the longer the dispersal model scenario, the more probable these errors will accumulate and translate into unrealistic results. This aspect is of even more concern for larval dispersal studies, in which the dispersal trajectories can be used not only in connectivity matrices but also to predict larval survival based on the distance travelled (Shima and Swearer, 2010). While sensitivity testing can include these biases for temperature estimates, this would be much more difficult in the case of ocean currents and particle tracking.

Looking at the regional performance of the models (Fig. 3), we note some consistency in capturing the along-shore component of ocean currents better than the across-shore component. In regions where the dominant current flows alongshore in a meridional direction – Leeuwin Current on the coast of West Australia (Cresswell and Golding, 1980), East Australian Current on the coast of East Australia (Godfrey et al., 1980), Zeehan Current on the West coast of Tasmania (Baines et al., 1983), and East Australian Current and Zeehan Current on the East coast of Tasmania, (Oliver et al., 2016) – both BRAN and HYCOM represent the v component of velocity better than the u component. This is not the case in regions such as the North West Shelf, the coastal waters of North Queensland and the east part of the Great Australian Bight where the alongshore flow of major currents – the Indonesian Throughflow, the South Equatorial Current and Leeuwin Current respectively – is a mix of zonal and meridional components of velocity. On the North West Shelf, both models are also less accurate because of a lack of persistent mean flow that would be easier to simulate in the ocean models.

Taking into account the distribution of the mooring stations around the Australian coastline, the performance of one model over the other in estimating each variable differed significantly from one geographic region to another. This regional factor was also shown in Oke and Sakov (2012). For water temperature, HYCOM clearly equalled or outperformed BRAN at all stations. For u and v current velocities in the top 50 m of water column, BRAN outperformed HYCOM with the exception of the Great Australian Bight and north east coast. For current speed in the top 50 m of water column, HYCOM outperformed BRAN at almost all stations except the ones on south east coast and Tasmania. In these two regions, BRAN predictions of u and v velocities, current speed and direction in top 50 m of water column were consistently more accurate than HYCOM predictions. The regional performance differences listed above should be taken into consideration when developing a larval dispersal study in Australian waters using BRAN or HYCOM, while dispersal studies in other regions should be based on validated hydrodynamic models.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.csr.2017.11.001.

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