

Predicting spawning locations and modelling the spatial extent of post hatch areas for fishes in a shallow coastal habitat in South Africa

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ABSTRACT: Early studies within Algoa Bay, temperate South Africa, have predicted that coastal fish species with pelagic eggs spawn offshore. More recent studies on larval fish assemblages in the nearshore have shown that spawning may take place closer to shore based on the prevalence of preflexion larvae. The aim of the present study was to investigate whether species that are important from a fishery and ecological perspective are potentially spawning in Algoa Bay. Larval fish abundance data, from a mosaic of coastal habitats in Algoa Bay, were used to model (1) the spatial distribution of larvae and (2) the spawning location of species. A novel approach using a maximum entropy machine-learning algorithm to model larval distribution was coupled with reverse progressive vector plots (RPVPs) to predict potential spawning areas. The results demonstrated that larval fishes in the nearshore habitats of Algoa Bay exhibit species-specific spatial variability. Results from RPVPs indicate that larvae occurring at any location within Algoa Bay could be hatched and transported extensively within the bay before reaching a suitable size to swim independently of nearshore currents. The spawning of several important fishery species, namely *Engraulis encrasicolus* (Engraulidae), *Sardinops sagax* (Clupeidae) and *Argyrosomus inodorus* (Sciaenidae), was modelled in Algoa Bay. Our results indicate that spawning occurs closer to shore than what was previously thought. Eggs and larvae typically remained in close proximity to their spawning origin. Larval fish distributions, although variable amongst all study species, correspond to known adult distributions and potential reef habitats in the study region.

KEY WORDS: MaxEnt · Spawning origin · Species distribution modelling · Fish larvae · Reverse progressive vector plot · RPVP

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INTRODUCTION

The pelagic larval stage plays a critical role in structuring marine fish populations (Werner et al. 2007) because dispersal at this stage is the primary determinant of the geographic size of populations and the connectivity amongst local populations (Roberts 1997, Cowen 2002, Kinlan & Gaines 2003, Sale

2004). Dispersal of eggs and preflexion larvae is largely passive because newly hatched larvae have limited behavioural and swimming capabilities (Mora & Sale 2002). Once larvae have undergone flexion, dispersal is no longer a passive process because larvae have sensory and swimming abilities that strongly influence their net dispersal trajectories (Leis 1991a, Stobutzki & Bellwood 1997, Stobutzki

2000, Leis 2006, Patrick & Strydom 2009). Ocean currents therefore play a pivotal role in the distribution of eggs and newly hatched larvae (Leis & Goldman 1983).

The small size of eggs and preflexion larvae in such a vast and dynamic ocean environment renders the quantification of dispersal notoriously difficult; nevertheless, predicting dispersion is a major goal of population ecology (Roughgarden et al. 1988). Ultimately, this information is important by providing data pertaining to important habitats for spawning and early life-history stages. Elucidation of such areas using mapping techniques could yield information on habitat bottlenecks at the early life-history stages that may limit the abundance of later adult stages (Sundblad et al. 2014).

Mapping species distributions, by relating the occurrence of species to environmental descriptors, allows for a better understanding of population dynamics, including distribution, and the mechanisms regulating the dynamics (Guisan & Wilfried 2005, Kozak et al. 2008). Species distribution modelling (SDM) is based on the concept that certain environmental characteristics of a particular habitat are needed to host specific species. MaxEnt is a high performing SDM method that uses species occurrence and environmental data to predict potential species distributions (Elith et al. 2006, Phillips et al. 2006). The relationship between the species and the environment provides information on habitat preferences and predictions of distributions of species. Within the terrestrial environment, presence-only modelling of species distributions has been extensively used, with only a recent increase in the interest of predicting fish species distribution in the marine environment (Ready et al. 2010). Particularly for marine fish, machine-learning algorithms such as MaxEnt have proven to consistently outperform more conventional modelling techniques including generalised additive models and linear regression (Knudby et al. 2010). Within the past decade, MaxEnt has been used to model distributions of marine fishes and invertebrates (Close et al. 2006, Bigg et al. 2008, Cheung et al. 2009, Ready et al. 2010, Pittman & Brown 2011).

SDM is a rapidly advancing field and its applicability for fish reproduction habitats is relatively unknown (Sundblad et al. 2009). Many fish species display ontogenetic habitat shifts, with juvenile habitats in shallow coastal areas and adult assemblages more widely distributed. Habitats important for spawning and for fish larvae remain poorly understood worldwide (Seitz et al. 2014, Nagelkerken et al. 2015). In eastern South Australia, populations of *Argyrosomus*

japonicus (Sciaenidae) have been depleted by habitat loss and overfishing. Management recommendations suggest that the identification and preservation of spawning areas will rebuild these populations (Ferguson et al. 2014). SDM would therefore serve as a valuable approach to conservation in such cases. In addition, recruitment has been shown to be substantially dependent on the availability of essential fish habitats, such as nursery areas (Sundblad et al. 2014).

Early studies on larval fishes in South Africa proposed that fishes may undertake spawning migrations farther offshore (Beckley 1986), but more recent studies of fish larvae showed that spawning occurs closer to shore based on the prevalence of preflexion larvae belonging to various coastal fish species close to shore (Patrick & Strydom 2008). Consequently, it was hypothesized that spawning may be linked to the coast (Patrick & Strydom 2008). The main aim of our study was thus to test the hypothesis that fish species spawn closer to shore than previously thought, and to predict the likely occurrence of larvae based on modelling of the spatial interaction of the fish larvae with their physico-chemical environment. In so doing, priority areas involved in coastal fish reproduction can be identified.

MATERIALS AND METHODS

Study area

Algoa Bay is a large, logarithmic-spiral-shaped bay on the temperate south-east coast of South Africa (Goschen & Schumann 2011) and is characterised by a variety of habitat and ocean conditions. These range from sheltered to very exposed intertidal habitats along the shore, and shallow to deep neritic habitats that include both unconsolidated sediments, subtidal reefs and small rocky islands. Accordingly, we established 23 sampling stations across the study region (Fig. 1): 10 in the surf zone (Stns A–J), 6 on island-associated reefs (K–P); 1 on a sand habitat at 20 m depth (Q); and 6 in the nearshore at 30 m depth (R–W).

Data collection of larval fishes

Given the variety of habitats in the study design, sampling required multiple gear types of 500 µm mesh size. Surf zones (Stns A–J) were sampled using a modified beach seine net (Strydom 2003a) This net was pulled parallel to shore by 2 people in depths

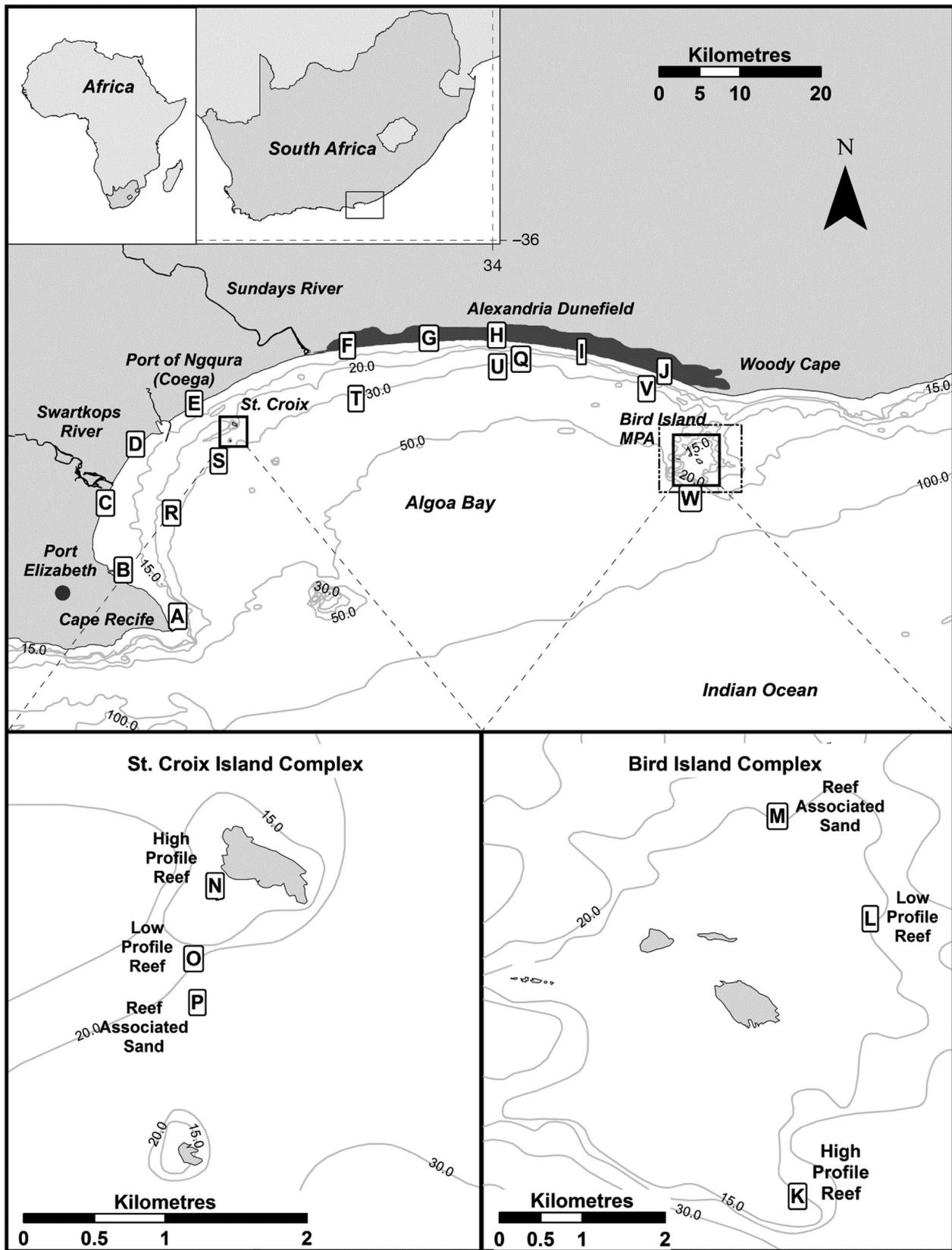


Fig. 1. Study area, showing sampling stations in the coastal nearshore of Algoa Bay, South Africa

<1.5 m for a distance of 25 m. Samples were taken in triplicate (3 independent hauls) at each of the 10 sites, on spring low tides, for 2 consecutive months in each of the 4 austral seasons, for 2 years (December 2010 to October 2012). This gave 16 sampling sessions and 480 samples (Patrick & Strydom 2014a). Catch is expressed as catch per unit effort: the number of larval fishes caught in a single 25 m seine haul. Subtidal habitats (Stns K–W) were sampled using plankton ring nets: a 12 mm thick stainless steel ring fitted with a 500 μm plankton net, 4.0 m \times 0.75 m, and a PVC cod-end. Water flow was measured with a Kahlsico flowmeter suspended from the frame at the opening of the net. This ring net was pulled using a stepped oblique tow at a speed of 2 knots. Three water levels (surface, mid-water, bottom) were each sampled for 2 min (8 min including hauling). Catch is expressed as larvae 100 m^{-3} . Nearshore stations (R–W) were sampled monthly during the day, although sea conditions limited this to 20 sampling trips (120 samples) between August 2010 and July 2013 (Patrick & Strydom 2014b). Sampling at Stns K–Q targeted known spawning times and seasons of coastal and pelagic fishes, i.e. night sampling in summer and winter, and were taken in triplicate (3 independent nights) per season for 2 yr (June 2010 to February 2012), giving 84 samples. In addition, 1 light trap, based on a modification of the design of Stobutzki & Bellwood (1997), was deployed on a fixed mooring in the water column at a depth of 4 m at each of Stns K–Q. All samples were fixed on site with 10% formalin in seawater. In the laboratory, larval fish were extracted from each sample, identified (Beckley 1990, Smith & Heemstra 1995, Neira et al. 1998, Leis & Carson-Ewart 2000), counted, measured and developmental stage identified according to Kendall et al. (1984). Six fish species important from either a recreational or commercial fishery perspective, or with an important ecological status in southern Africa, were selected for predictive spatial modelling: dusky kob *Argyrosomus japonicus* (Scaenidae) is a commercially ecologically and culturally important species, and is among the coastal species most affected by fishing pressure in South African coastal waters. Similarly, silver kob *A. inodorus* is also a highly exploited temperate species. Blacktail *Diplodus capensis* (Sparidae) is a common coastal inshore species and is important in the recreational fishing industry in South Africa. Both European anchovy *Engraulis encrasicolus* (Engraulidae) and South American pilchard *Sardinops sagax* (Clupeidae) are small pelagic fish species harvested by the large purse-seine fishery in South Africa. These

species are ecologically important and are both significant predators of plankton and important prey for several marine species. Cape sole *Heteromycteris capensis* (Soleidae) is a numerically abundant marine-estuarine dependent species common within the study area.

Environmental predictor variables

Six environmental variables were considered important potential drivers or predictors of larval distributions and movement. Four of these variables were measured during each sampling event at the surface, middle and the bottom of the water column using a YSI 6600 multi-parameter meter: temperature ($^{\circ}\text{C}$), salinity, turbidity (NTU) and pH. These data were supplemented with wind and current speed recordings from 2 long-term monitoring programmes in the area. Wind speed (m s^{-1}) was calculated as a daily average of hourly readings from the 3 closest South African Weather Service stations: Bird Island, Port Elizabeth Airport and the Port of Coega. Current speed (in both north–south and east–west directions) was measured by three 1200 kHz Acoustic Doppler Current Profilers (ADCPs; RD Instruments) spread across the study site (see Fig. 1). ADCPs 1 and 3 were moored in approximately 30 m of water configured to sample the water column in 0.5 m bins at 10 min intervals with continuous data collection since December 2008, and only intermittent gaps when the instruments were removed for servicing. ADCP 2 was deployed at 20 m depth configured to sample the water column in 1 m depth intervals every 30 min using an ensemble size of 120 pings, with 1 ping used per second.

Predicting spawning grounds and dispersal paths of eggs and preflexion larval fishes

RPVPs were constructed to determine the original spawning grounds and subsequent potential transport (total progressive displacement) of fish eggs and preflexion larvae. The 10 and 30 min raw current data were filtered by low-pass cosine-Lanczos filters to 1-hourly values, in order to obtain a common sampling period, from which RPVPs were generated. Reverse progressive vectors are simply progressive vectors (Emery & Thomson 2004) plotted backwards in time. Since the end position of the larvae was known (the geographic coordinates where they were sampled) and the currents that transported them

there were known, their position of origin could be calculated by progressively adding the negative of the velocity vectors. This gave the upstream displacement of a parcel of water from its end point, assuming the hourly values of currents represented the average currents between the start and end coordinates of each vector. It was also assumed that the larvae travelled at the same velocity as the water. The RPVPs were generated backwards between 5 and 15 d. RPVPs require 4 data inputs: egg dispersal start time, i.e. spawning periods; time spent dispersing, i.e. pelagic larval duration (PLD); depths occupied by eggs/larvae; and local current speeds with depth. To acquire these inputs, first likely spawning periods for each species were estimated by quantifying larval fish abundances across the study region per month. Second, species-specific PLDs (Shanks et al. 2003) were determined by estimating the age (in days) of preflexion larvae from their notochord length (NL) (Brownell 1979, Connell 2007). Calculating the total time spent by each cohort within the pelagic water column, per species, was done by totaling PLD with egg incubation time. Third, a previous study on the vertical behaviour and distribution of Sparidae and Sciaenidae larvae showed that the smallest (5–7 mm) larvae spend the majority of their time in the 2.6–5.0 m depth bin (Leis et al. 2006). The final input, current speeds, was obtained from the ACDP data described above. RPVPs were then constructed from these inputs.

Predicting aggregation areas of larvae

Due to the season-driven reproductive biology of these fish species, it would have been ideal to model aggregation areas of larval fish in both space and time. However, there were insufficient data for such fine-scale analyses; thus, only spatial patterns were modelled. Selection of a modelling algorithm was constrained by 2 features of the data. First, sample sizes of the 6 fish species' distributions were relatively small. Second, because fish larvae are dynamic in space and time, and because not observing a species in a particular session would not necessarily mean they are absent from a site, the data were of presences only and did not include absences. There-

fore, SDM was performed using MaxEnt 3.3.3k (Phillips et al. 2004) because it is robust to small sample sizes ($n = 10\text{--}30$; Hernandez et al. 2006, Wisz et al. 2008) and is based explicitly on presence-only data (Phillips et al. 2004, 2006, Phillips & Dudík 2008, Elith et al. 2011).

MaxEnt is a machine-learning method based on presence-only information, that approximates an unknown probability distribution using maximum entropy, given the constraints that the expected value of each environmental variable equals its empirical average from the presence data (Phillips et al. 2006, Phillips & Dudík 2008). The analysis thus requires 2 data inputs: background data of candidate environmental predictors, and presence locations of each species. Both data inputs were prepared in ArcGIS 10.3 (Environmental Systems Research Institute). First, the study area was delineated, extending along the coast from Cape Recife to Woody Cape, with the seaward boundary approximately following an 8 km buffer around the sampling stations farthest offshore (Fig. 2). This area was then divided into a $10' \times 10'$ grid for modelling purposes. Second, data for each of the environmental predictor variables (sea temperature, salinity, turbidity, pH and wind speed) were pooled across sampling sessions and represented as the mean, minimum, maximum and range across the 2 yr sampling period, per station. Raster surfaces of each variable in each metric were interpolated across the study area using the 'spline with barriers' function (Spatial Analyst), from which val-

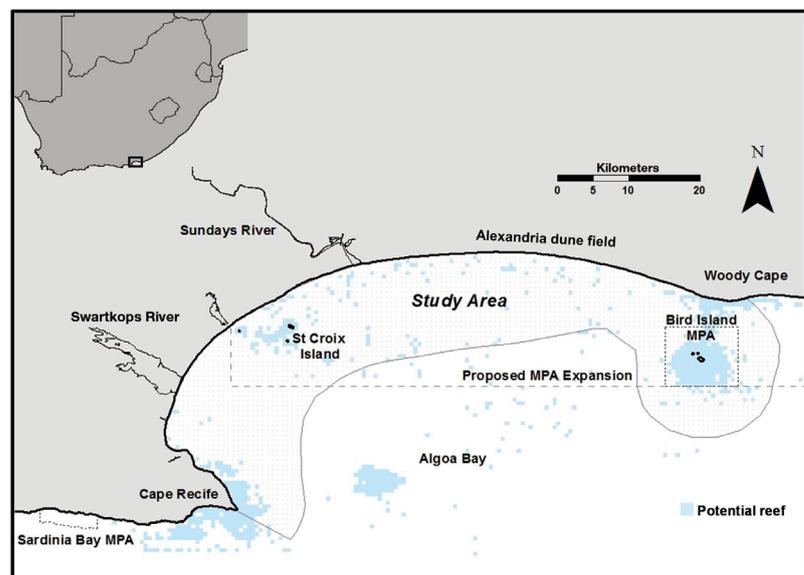


Fig. 2. Study area defined for species distribution modelling in the coastal nearshore of Algoa Bay and the presence of potential reef areas in the bay. Reef areas courtesy of Chalmers (2011)

ues were extracted to centroids of the 10' grid using the Spatial Analyst function 'extract multi values to points'. These data served as the background data ($n = 1801$ points) in the model. Third, species presence was delineated as a buffer of 400 m around each station where larvae of the species were recorded ($n = 26$ –64 points, depending on the species; see Table 2). This distance was chosen because it is the total area sampled around each station (8 min tow at 2 knots). Based on these areas of species presence, environmental data were subset out of the background dataset to give the 'species' data in the model (see Appendix 1 for environmental ranges for all presence and background records).

Initially, data were randomly partitioned into a 70% training set and a 30% testing set to respectively train a model and test its performance, and MaxEnt was run using all other default settings. Model accuracy was validated based on receiver operating characteristic (ROC) plots which provide an area under the curve (AUC) value ranging between 0.5 and 1. Following the classification of Maggini et al. (2006), values below 0.7 are regarded as poor, 0.7–0.9 as reasonable, and above 0.9 as very

good. ROC plots are widely used to evaluate SDM performance (Manel et al. 2001, Francis et al. 2005, Maggini et al. 2006, Sundblad et al. 2009), and the AUC statistic is broadly considered as a robust measure of model performance (Fielding & Bell 1997, Manel et al. 2001, McPherson et al. 2004). Once model performance was evaluated for acceptable accuracy, models were rerun using all of the data, to obtain the most robust output. The output probabilities of occurrence for each species were plotted and interpolated as continuous raster surfaces across the study region using the 'spline with barriers' function in Spatial Analyst (ArcGIS 10.3).

RESULTS

Spawning grounds and dispersal paths of eggs and preflexion larvae

Spawning appears to be a spring/summer phenomenon for the species evaluated here (Fig. 3). Abundances of preflexion larvae peaked in spring for *Argyrosomus japonicus* and *A. inodorus* (Septem-

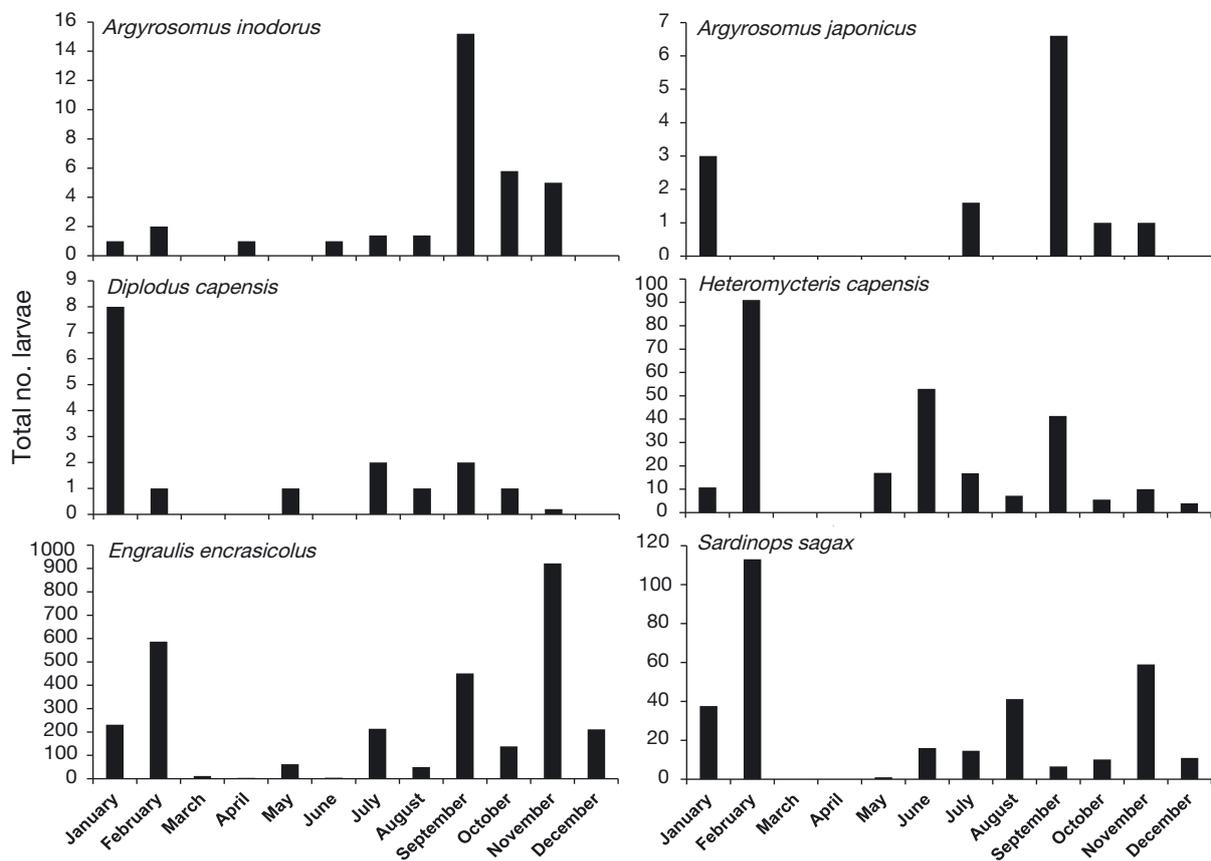


Fig. 3. Abundances of preflexion larvae per month (per 100 m³) (August 2010 to October 2012) of study species selected for modelling within the coastal nearshore of Algoa Bay

Table 1. Study species for species distribution modelling including month during dominant spawning, egg incubation time and temperature, mean body length, age at mean body length and the total dispersal duration in Algoa Bay, South Africa

Species	Spawning month	Egg incubation (h)	Temperature at incubation (°C)	Mean (range) length (mm)	Age for mean length (d)	Total dispersal duration (d)
<i>Argyrosomus inodorus</i>	September	25	17–22	3.9 (2.0–5.8)	13	14
<i>Argyrosomus japonicus</i>	September	30	17–22	3.2 (1.7–5.5)	5	6
<i>Diplodus capensis</i>	January	40	15–24	3.7 (2.2–4.9)	5	7
<i>Engraulis encrasicolus</i>	November	30	15–19	3.6 (1.5–8.9)	4	5
<i>Heteromycteris capensis</i>	February	24	15–24	2.4 (1.2–6.1)	7	8
<i>Sardinops sagax</i>	February	40	15–21	3.9 (3.0–9.9)	2	5

ber), and in summer for *Diplodus capensis* (January), *Engraulis encrasicolus* (November), and *Sardinops sagax* and *Heteromycteris capensis* (February). During the spawning months of each species, the respective larvae (Table 1) were very small and young, ranging in length from 2.4 to 3.9 mm NL, and in age from 2 to 13 d (Brownell 1979, Connell 2007). With pelagic egg development from fertilization to hatching lasting from 24 to 40 h, the total PLD obtained for the model species ranged from 5 to 14 d. The results from the RPVPs indicate various patterns of dispersal in space among locations (Bird Island, Cape Recife, Alexandria Dune Field), and time among years sampled (2010–2012). Generally, greatest dispersal distances were observed at the deeper depths (~5 m) as opposed to the shallower depths near the surface of the water column (~2 m). The RPVPs predict that the origin of spawning is predominantly within Algoa Bay for *A. inodorus* and *E. encrasicolus* and approximately 40 to 100 km north-east of Algoa Bay for *A. japonicus*. For *D. capensis*, *H. capensis* and *S. sagax*, the origin of spawning is both inside and outside of the bay.

Aggregation areas of larvae

Overall, model performance was very good for all 6 distribution models, with AUC values mostly >0.9 for both the training and testing datasets (Table 2). The strongest environmental predictor with the greatest contribution to the models varied amongst the study species, but in all cases was relatively low (Table 3), suggesting that larval fish responses to environmental drivers are complex. The 2 sciaenid species, *A. inodorus* (Fig. 4a) and *A. japonicus* (Fig. 4b), showed different larval distribution patterns. *A. japonicus* was somewhat confined to the western, leeward sector of the bay in close association with St Croix island, and offshore locations associated with the Alexandria Dune Field in the eastern sector

of the bay. Although *A. inodorus* had a close association with St Croix Island in the western sector of the bay, probability of occurrence of *A. inodorus* was high at Bird Island in the far eastern sector. Furthermore, *A. inodorus* occurred at closer inshore locations associated with the Alexandria Dune Field. Larvae of *D. capensis* (Fig. 4c), *H. capensis* (Fig. 4d) and *E. encrasicolus* (Fig. 4e) were distributed throughout Algoa Bay. Larvae of *S. sagax* (Fig. 4f) had close associations with the islands and the nearshore off the Alexandria Dune Field.

DISCUSSION

Important areas for the larvae of 6 fish species with ecological and fishery value were described and predicted in the coastal nearshore of Algoa Bay, using a combination of SDM and RPVPs. The results from this study confirm that spawning takes place closer to shore than was previously thought (Beckley 1986), with eggs and larvae typically remaining in close proximity to their spawning origin. Strong environmental gradients on multiple spatial scales render the coastal zone of Algoa Bay particularly suitable for modelling the larval fish distribution. The current study presented a widely applicable model of com-

Table 2. Statistics evaluating the performance of the species distribution model, based on N presence records per species. AUC_{TRAIN} and AUC_{TEST} = area under the receiver operating characteristic curve of the model created using the training and testing data, respectively

Species	N	AUC _{TRAIN}	AUC _{TEST}
<i>Argyrosomus inodorus</i>	35	0.959	0.916
<i>Argyrosomus japonicus</i>	26	0.984	0.986
<i>Diplodus capensis</i>	34	0.972	0.952
<i>Engraulis encrasicolus</i>	64	0.931	0.861
<i>Heteromycteris capensis</i>	39	0.956	0.895
<i>Sardinops sagax</i>	37	0.951	0.847

Table 3. Relative variable importance in modelling species distributions, quantified by the estimated percentage contribution of each variable to the training models, per species. The most important predictor for each species is highlighted in **bold**

	<i>Argyrosomus inodorus</i>	<i>Argyrosomus japonicus</i>	<i>Diplodus capensis</i>	<i>Engraulis encrasicolus</i>	<i>Heteromycteris capensis</i>	<i>Sardinops sagax</i>
Temperature (max)	6.0	3.1	1.7	1.3	2.8	1.8
Temperature (min)	27.2	6.2	10.0	11.2	13.9	8.2
Temperature (mean)	0	0.3	6.3	3.5	4.8	4.2
Temperature (range)	0	0.5	27.0	1.1	2.8	0
Turbidity (max)	0.7	0	0	0	0	0.2
Turbidity (min)	8.1	21.9	5.1	2.4	3.4	5.3
Turbidity (mean)	14.3	7.2	23.4	14.4	25.4	33.7
Turbidity (range)	2.8	5.1	0.3	0	0.4	1.6
Salinity (max)	3.5	0.1	7.6	2.6	1.7	0.3
Salinity (min)	0.6	19.2	5.3	1.0	0.6	4.0
Salinity (mean)	1.1	4.1	0.2	5.6	0.2	0.3
Salinity (range)	4.8	7.7	4.9	1.7	7.9	9.5
pH (max)	1.2	0	0	5.0	3.3	0
pH (min)	1.3	5.9	3.2	0.6	1.4	0.2
pH (mean)	0	0	1.1	30.4	1.1	3.6
pH (range)	2.7	0.9	0.2	0.1	7.0	3.7
Wind speed (max)	0.1	0.3	0	0.5	2.1	3.9
Wind speed (min)	19.1	15.9	2.5	7.9	14.3	9.4
Wind speed (mean)	6.0	0	1.2	9.2	6.8	6.9
Wind speed (range)	0	1.5	0	1.5	0.1	3.3

monly used abiotic factors that explain the larval distribution of these species. These new techniques are providing much needed insight into fish reproduction and important areas for larval accumulation, retention and grow-out.

The maximum dispersal distances of passive eggs and early-stage fish larvae from a point source in the Algoa Bay nearshore have been calculated in a previous study using progressive vector plots (Patrick et al. 2013). These data included estimates of seasonal dispersal, modelling displacement for 3 month periods. Predictions of net displacement of almost 300 km from a fixed central point in the nearshore during spring and early summer were obtained. These trends suggested that eggs and preflexion larvae would be transported out of Algoa Bay based on passive particle trajectories. The present study, however, took into consideration PLD, which for most coastal fish species occurring in Algoa Bay consists only of a few days to less than 2 wk (Connell 2007). This also allowed for more accurate estimates of dispersal to be calculated. Using RPVPs, the location of spawning areas could be determined. The results indicate several locations of spawning areas for species whose larval stages occur in the bay.

The greatest abundance of all study species occurred between September and February. The majority of teleost marine fishes are seasonal breeders, while a few breed continuously with peaks in breed-

ing activity (Heemstra & Heemstra 2004). Marine temperate fishes spawn predominately during spring and early summer. At the onset of spring, an increase in sea water temperatures is observed with associated higher productivity which ensures better feeding conditions for larvae (Heath 1992, Pörtner et al. 2001). Results indicated that temperature variation, rather than temperature per se, was a better predictor of *Diplodus capensis* larval distribution. Environmental variables that describe both the average conditions experienced by the early developmental stages of fishes, and the variability in those conditions, are important in model development (Francis et al. 2005).

The socio-economic important scieanid species, *Argyrosomus japonicus* and *A. inodorus*, revealed different distributions in their larval locations. *A. inodorus* had a close association with St Croix Island in the western sector of Algoa Bay. The probability of occurrence of *A. inodorus* larvae was also high at Bird Island and Woody Cape in the far eastern sector. Bird Island supports breeding Cape gannets *Morus capensis* (Aves: Sulidae), 1 of only 6 locations in the world. The highest probability of larval areas of *A. japonicus* included locations associated with the Alexandria Dune Field in the eastern sector and areas between the Sundays and Swartkops estuaries and St Croix Island. Groundwater seeps from the land into the sea through the Alexandria Dune Field

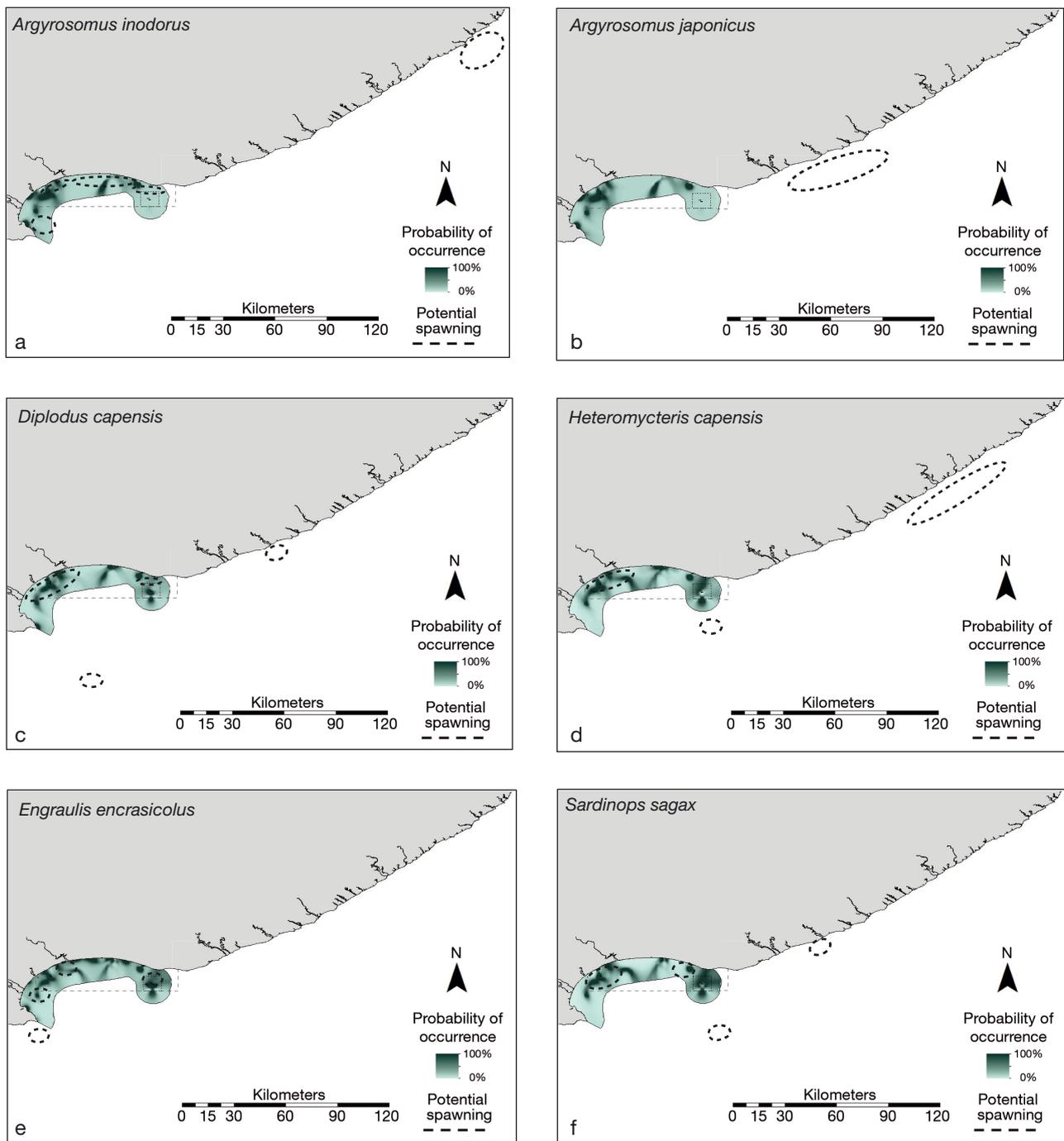


Fig. 4. Distribution models showing the origin of spawning and the probability of occurrence of (a) *Argyrosomus inodorus*, (b) *A. japonicus*, (c) *Diplodus capensis*, (d) *Heteromycteris capensis*, (e) *Engraulis encrasicolus* and (f) *Sardinops sagax* larvae in the study area of the coastal nearshore of Algoa Bay

in aquifers. This groundwater is discharged in large volumes and contains very high nutrient levels (Campbell & Bate 1991). However, origins of spawning locations of *A. japonicus* consistently indicate spawning occurring outside of Algoa Bay, specifi-

cally in a north-easterly direction which would place spawning in the proximity of Port Alfred. Upwelling of colder water has been detected in this area along a strip of coastline approximately 100 km long and is known to enhance the nutrient concentrations of the

surrounding waters substantially (Lutjeharms et al. 2000, Lutjeharms 2006, 2007).

Pelagic fish species which occur in the Algoa Bay region include the sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. Adult anchovy are known to spawn during mid-summer (November to December) on the Agulhas Bank (Hutchings et al. 2002). However, since 1994 there has been a distinct eastward shift in the spawning distribution to the east-central Agulhas Bank, with anchovy known to spawn on the shelf on the east coast (Armstrong et al. 1991, Beckley & Hewitson 1994) and in Algoa Bay (Patrick & Strydom 2008). The majority of sardine spawning is known to occur on the west coast, with less spawning intensity occurring on the central and eastern Agulhas Bank. However, sardine spawning does occur on the east coast (Hutchings et al. 2002), and postflexion larvae are regularly encountered in coastal areas of Algoa Bay (Strydom 2003b, Patrick & Strydom 2008). In the present study, the RPVPs indicated an origin of spawning of *S. sagax* within Algoa Bay, specifically in the nearshore region, and this was supported in the distribution modelling of the larvae. Inshore distribution of spawning of *S. sagax* has been observed off the southern and central California coastline (Brewer & Smith 1982, Lynn 2003). Sardines in Japan and in the Humbolt and California Current systems have been observed to spawn in coastal waters when population levels and biomass are low, only expanding their spawning range significantly into oceanic mixing areas when population levels are high (Cury et al. 2000).

Heteromycteris capensis spawns in the marine environment, with larvae and juveniles recruiting into estuarine nursery areas (Whitfield 1998). RPVPs indicate that spawning of *H. capensis* is occurring locally in Algoa Bay, particularly in the western sector. The distribution of *H. capensis* larvae was confined to the nearshore of Algoa Bay. Postflexion *H. capensis* larvae are commonly observed in surf zones (Cowley et al. 2001, Strydom 2003a, Watt-Pringle & Strydom 2003, Strydom & d'Hotman 2005), where they accumulate before recruitment into estuarine habitats. Two permanently open and smaller estuaries are located in the western sector of the bay. The close proximity of the estuarine nursery areas could play a role determining the distribution of larvae of these marine-estuarine dependent species within the nearshore.

D. capensis lays pelagic eggs, typical of all other species within the Sparidae family in South Africa, excluding Steentjie seabream *Spondyliosoma emarginatum*. Spawning origins and larval distributions of

D. capensis follow similar patterns in distribution to potential reef areas identified by Chalmers (2011) in Algoa Bay. Shallow, subtidal bays associated with rocky shores function as preferred nursery habitats for mid- to late-stage larval and newly settled juvenile *D. capensis* (Strydom 2008). These rocky shores occur exclusively at Woody Cape in the eastern sector, and in the western sector of the bay.

It should be noted that the measurements from the RPVPs used in the current study should be used as a guideline for potential dispersal of eggs and preflexion larvae, as information on the vertical distribution of larvae in temperate coastal waters is limited. Furthermore, limited information exists on taxon-specific vertical distribution of preflexion larvae in coastal waters. Therefore, efforts to understand dispersal of larvae by ocean currents are difficult. Studies conducted on tropical larvae indicate that specific patterns in vertical distribution occur for related taxa, with strong vertical structure occurring during the day and weak structure at night, with most taxa occurring deeper during the day (Leis 1986, 1991b). The depth intervals used in the present study, although having been represented in the literature as common areas of accumulation for preflexion larvae and eggs, are still estimates.

Environmental variables play an important role in determining the distribution of the early life-history stages of fish species. However, biotic processes need to be incorporated explicitly into SDMs as, for a substantial portion of the pelagic larval stage, behaviour influences dispersal (Leis 2006). Therefore, only dispersal of eggs and preflexion larvae was considered, as larvae upon hatching are very small and poorly developed with limited swimming abilities and, with respect to ocean currents, are regarded as close to passive. These predictions are plausible given what is known of the juvenile and adult ecology of each species.

Although the modelling approach employed here may lose precision in assuming that species distributions are dictated by a general and restricted set of environmental variables, the MaxEnt model predictions in the present study have served as a valuable tool to model very complex spatial distributions of fish larvae, for which data and ecological knowledge are often scarce. At the species level, adult spawning behaviour showed individualistic responses to predictors, although consistent models of species distributions were produced. Furthermore, dispersal distances to determine origin of spawning locations proved to be species specific. Species with longer PLD were dispersed over much greater distances

than those with relatively short PLDs. Furthermore, life-history characteristics such as larval vertical and horizontal migration and swimming abilities also differ between species and will influence dispersal.

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Appendix 1. Ranges of 6 environmental variables considered to be important potential drivers or predictors of larval distributions and movement of the study species

	<i>Argyrosomus inodorus</i>	<i>Argyrosomus japonicus</i>	<i>Diplodus capensis</i>	<i>Engraulis encrasicolus</i>	<i>Heteromycteris capensis</i>	<i>Sardinops sagax</i>	Background data
Temperature (min)	12.07–15.86	12.63–15.34	11.64–15.34	11.64–15.86	12.19–15.43	12.07–15.34	11.64–15.94
Temperature (max)	19.34–25.25	19.29–24.67	19.29–25.46	19.29–25.25	19.29–24.05	19.29–22.93	18.74–25.46
Temperature (mean)	16.62–19.11	16.35–18.34	16.36–19.03	16.36–19.20	16.36–18.74	16.36–18.09	16.22–19.20
Turbidity (min)	0–2.60	0–0.58	0–1.57	0–2.99	0–2.99	0–1.31	0–3.63
Turbidity (max)	0.94–22.01	0.40–27.4	0–17.45	0–31.79	0–31.79	0–17.45	0–37.68
Turbidity (mean)	0.30–8.63	0–7.58	0–4.31	0–9.49	0–7.92	0–3.64	0–11.19
Salinity (min)	32.50–35.40	32.50–35.40	32.50–35.40	32.50–35.40	32.50–35.40	32.50–35.40	32.46–35.47
Salinity (max)	35.76–36.37	35.76–36.42	35.76–36.53	35.76–36.53	35.76–36.53	35.76–36.53	35.70–36.61
Salinity (mean)	34.83–35.88	34.86–35.88	34.70–35.88	34.41–35.88	34.84–35.88	35.14–35.88	34.41–35.91
pH (min)	7.27–8.61	7.76–8.69	7.69–8.69	7.12–8.69	7.12–8.69	7.87–8.69	6.97–8.77
pH (max)	8.34–9.10	8.48–9.09	8.09–9.11	8.09–9.11	8.39–9.11	8.34–9.11	8.09–9.22
pH (mean)	8.12–8.84	8.13–8.94	7.90–8.97	7.90–8.97	8.02–8.97	8.20–8.97	7.90–9.08
Wind speed (min)	1.79–2.93	1.68–2.93	1.69–2.93	1.68–2.93	1.79–2.93	1.79–2.93	1.64–2.98
Wind speed (max)	4.53–11.24	4.67–8.89	4.67–9.01	4.53–11.48	4.53–11.48	4.53–7.11	3.38–13.34
Wind speed (mean)	3.25–5.25	3.37–5.02	3.16–5.05	3.16–5.33	3.25–5.33	3.25–4.26	3.13–5.97

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