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# Modelling regional and local-scale larval seeding strategies for abalone (H. midae) ranching in South Africa

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1	Modelling regional and local-scale larval seeding strategies for abalone ( <i>H. midae</i> )
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19	Highlights
20	Multi-scale modelling to optimise larval release for ranching, stock enhancement
21	• First high-resolution model of dispersal in a shallow, rocky, high-energy setting
21	• This might condition model of dispersar in a shallow, focky, high-energy setting
22	<ul> <li>Regionally, large embayments act to block connectivity</li> </ul>

23 • Locally, optimised release locations maximise residence time in settlement habitats

## 24

# 25 Keywords

- 26 Larval connectivity, Delft3D, XBeach, hydrodynamic modelling, abalone ranching, stock
- 27 enhancement, larval seeding.
- 28

ABSTRACT

Understanding connectivity between abalone populations and residence times for pelagic larvae 31 32 within suitable settlement habitats is critical for sustainable management of wild abalone stocks 33 and ranching schemes. In the Eastern Cape region of South Africa, poaching has severely 34 depleted wild abalone Haliotis midae populations. Re-building stock through larval seeding is 35 being considered as a potentially viable method, though is hampered by a limited understanding of abalone habitat connectivity through larval dispersal, both at a regional and local scale. To 36 37 address this shortcoming, we apply a multi-scale approach to investigate potential larval dispersal along the coastline of Eastern Cape, South Africa, examining both intra- and inter-site 38 39 connectivity, with the primary focus at the local nearshore scale (< 40 m water depth) where 40 surf zone processes have a strong influence. Delft3D is applied at a regional scale (400-km 41 domain) and XBeach is used at a local scale (2.5-km domain) to model a known abalone habitat 42 at Cape Recife at high-resolution (5-m cell size). Models were validated using field observations. Complex topo-bathymetry data for the local-scale model domain around Cape Recife were 43 44 obtained using a state-of-the-art low-cost multi-method surveying approach. At a regional scale, sites with abalone habitat have the potential to be connected across distances of 50-100 km. 45 However, a large sandy embayment (Algoa Bay; 100-km arc length) is likely to present an 46 obstacle to larval transport in all but the most extreme and sustained wind and wave forcing 47 conditions. The central Cape Recife abalone ranching area has the potential to act either as a 48 49 self-seeding or meta-population connected site, depending on forcing conditions. At the local 50 scale around Cape Recife, a zone of shallow gullies, under lower-energy waves, was determined 51 to be the optimal release point to maximise residency times within the preferred rocky, shallow subtidal habitat of H. midae. Competent larvae released in this zone are predicted to have an 52 53 order of magnitude greater residency than randomly seeded larvae. This study provides site-54 specific connectivity and residence time information for the Eastern Cape abalone fishery, but more generally it provides a novel multi-scale method to aid in planning and managing of 55 abalone larval seeding for ranching and stock enhancement programs that could be applied in 56 other locations. 57

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#### 62 1. Introduction

Population connectivity in sedentary organisms, understood as the exchange of individuals among 63 marine populations (Cowen and Sponaugle, 2009), is fundamental to understanding ecological 64 65 processes such as population regulation and gene flow, and is essential for management and 66 conservation strategies, including designation of protected habitats (Storlazzi et al., 2017). For 67 abalone (mollusca gastropoda, genus Haliotis), the potential for dispersal and exchange between spatially separated meta-populations is limited to the brief pelagic larval stage (Miyake et al., 2000), 68 typically on the order of 1 week, though little is known of the early stages of recruitment (Prince et 69 70 al., 1987; Robins et al., 2013; Rogers-Bennett, 2016). Globally, many abalone populations are under 71 threat from overfishing, including illegal poaching (Raemaekers and Britz, 2009; Cook, 2019), and an 72 understanding of population connectivity is required to assist in re-establishing overfished habitats 73 and the sustainable management of fisheries.

74 The ongoing development of sophisticated hydrodynamic models, such as Delft3D (Lesser et al., 75 2004), has led to an increase in larval dispersal modelling (e.g., Erftemeijer et al., 2009; Storlazzi et 76 al., 2017) to investigate population connectivity. Local populations range from being fully-open, 77 where abundant seeding occurs between a neighbourhood of meta-populations (Cowen and 78 Sponaugle, 2009), to fully-closed, where only local recruitment (self-seeding) occurs. Biological 79 factors that affect connectivity include spawning cues and timing, larval duration, vertical behaviours 80 (swimming) and pre-settlement mortality (Miyake et al., 2000), and these may be modulated by 81 tides and day-night cycles (Counihan et al., 2001, Robins et al., 2013). Physical forcing controls are 82 also important, with higher wind, waves and currents resulting in increased dispersal distances 83 (Stephens et al., 2006; Robins et al., 2013) and evidence of climatological controls, such as ENSO 84 cycles (Rogers-Bennett, 2006) and upwelling/downwelling events (McQuaid and Phillips, 2000) 85 impacting on dispersal. This area of cross-disciplinary research is still new, with a lack of methodological uniformity between studies (Ross et al., 2020), resulting in the potential for 86 87 significant differences in dispersal estimates, depending on model choice and input assumptions. 88 Field data are therefore essential for validating these hydrodynamic models, but it is often challenging and costly to obtain them (Ross et al., 2020). 89

In high-velocity and turbulent flows, abalone are thought likely to act as passive particles that will settle in response to an inducer (Boxshall, 2000), such as crustose coralline algae (Daume et al., 1999; Day and Branch, 2000; Williams et al., 2008; O'Leary et al., 2017). Larvae needing to settle in rocky shallow subtidal environments must be able to enter the surf zone, and/or remain there long enough to successfully metamorphose. The surf zone is a high-energy environment, with breaking waves and wave-generated currents (e.g., Castelle et al., 2016). Yet, despite the importance of surf

96	zone processes to larval dispersal, few studies have examined this region (Fujimura et al., 2014 is	
97	one exception), and no studies have modelled abalone larval transport due to surf zone processes,	
98	at high resolution, in the complex rocky environments that abalone larvae typically require in order	
99	to settle.	
100	The Eastern Cape region of South Africa, where the endemic abalone species is Haliotis midae, is a	
101	site where further understanding of connectivity of abalone populations is critical. These abalone	
102	live within the shallow sub-tidal (typically 0–12 m below low water; Witte, 2017) on rocky outcrops,	
103	with adults 80-150 mm in shell width and juveniles < 30 mm (Wood and Buxton, 1996a,b). Adult H.	
104	midae feed on select species of attached seaweed and drift algae. H. midae is an asynchronous	
105	broadcast spawner, highly fecund, dioecious and iteroparous, with a breeding season from March to	
106	October, peaking from April to June (Wood and Buxton, 1996b). As for all abalone species, H. midae	
107	go through a pelagic, multi-phase larval process (Miyake et al., 2000; Pang et al., 2006; Takami et al.,	
108	2006). Post-fertilisation, the larvae are free swimming (trochophore stage), then, after a period of	
109	~5–7 days (Sales and Britz, 2008), the larvae become competent (veliger stage), being able to attach,	
110	settle and metamorphose on substrata, when a suitable algal inducer is present. The larval period of	
111	H. midae is inversely correlated with water temperature, reaching only 5 days at 20°C, extending to	
112	7 days at 17.5°C (Genade et al., 1988). The full natural distribution of <u>H. midae extends across the</u>	_
113	west, south and east coasts of South Africa (Bester-van det Merwe et al., 2011; Rhode et al., 2017),	
114	with a likely genetic divide at Cape Agulhas, and a potential secondary barrier to gene flow at Algoa	
115	Bay.	

116 Abalone fisheries are of economic importance in many countries, including in South Africa (Kaiser et 117 al., 2017; Rhode et al., 2017), where small-scale-fisheries play a significant role in supporting livelihoods and food security in rural coastal communities. Commercial fishing targeting wild abalone 118 119 in South Africa originated in 1949 (Sales and Britz, 2001), with cultivation and farming commencing 120 in 1981 (Genade et al., 1988). Natural populations of H. midae in the Eastern Cape have come under 121 pressure from overharvesting and ecological changes (Rhode et al., 2017). In particular, illegal 122 poaching of abalone has had a major impact on the fishery in the region (Raemaekers and Britz, 123 2009). Large-scale illegal fishing of H. midae in the Eastern Cape Province began in 1997 and by 2005, the illegal fishery comprised 30 vessels, harvesting 1000-2000 tons, valued at 35-70 million 124 125 USD. The rampant illegal take has been attributed to the high product value and low operational costs of poaching abalone, combined with state failure to issue fishing rights and enforce compliance 126 127 (Raemaekers and Britz, 2009). Uncontrolled fishing has significantly reduced abalone average size and density; yet, despite the scale of poaching, recruitment of young abalone continues to be 128 observed at one of the primary sites, Cape Recife, near Port Elizabeth (Witte, 2017). The impact of 129

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poaching has led to suspension of all commercial and recreational fishing of wild abalone in theEastern Cape (Moriarty, 2019).

Abalone ranching is now seen by the South African government as a potential pathway to boost the 132 blue ocean economy and provide social uplift (DAFF, 2010; DAFF, 2011). The government has 133 134 ambitious plans to establish small-scale fishing cooperatives throughout the Eastern Cape, including 135 abalone ranching. While seeding of juvenile abalone from large aquaculture farms has proved successful at Cape Recife (Witte, 2017; Moriarty, 2019), this approach may not be viable for regional 136 137 expansion due to the high cost and infrastructure required.- Larval seeding could provide a solution 138 since it bypasses the need for more extensive on-growing facilities. The relative costs and benefits of 139 larval seeding compared to juvenile seeding require further investigation.- Ranch-based cultivation presently occurs in the region and experimental larval seeding of sites in the Eastern Cape with farm-140 141 grown larvae that have reached settling phase are planned. These seeding initiatives are significantly 142 hampered by a lack of understanding of larval transport pathways and residence times, with no 143 insights into optimal seeding conditions and locations. Additionally, any seeding program should 144 account for genetic considerations (Roodt-Wilding, 2007), for example, related to the potential or 145 partial barrier to gene flow around Algoa Bay (Bester-van der Merwe et al., 2007).

To maximise the efficacy of a larval seeding program and assist in the management of the abalone 146 147 fishery, an understanding of larval dispersal is required at two spatial and temporal scales. First, at a 148 regional scale (up to 100's of km, days to weeks), the potential for connectivity must be understood 149 to select locations and timing of larval seeding to optimise the potential benefit, either in regard to 150 local dispersal (self-seeding of a site) or non-local (regional) dispersal (transport to another viable 151 site). It is also critical to identify regions where larval seeding could potentially be most beneficial 152 (larval supply-limited). Second, once a site is selected, at a local scale (100's of m, hours), the chance 153 of seeding success will be a function of retention rates within viable habitat zones. This knowledge 154 could influence method (e.g., boat/land based), location (e.g., specific gulley in the inter-tidal zone), 155 and timing (e.g., optimal wave conditions) of larval deployments. Accordingly, we present a novel approach to address this multi-scale question, using Eastern Cape, South Africa as an example. A 156 157 regional Delft3D model is used to provide a limited, first-pass estimate of the potential for 158 connectivity during the pelagic larval phase. Subsequently, a high-resolution XBeach model is applied 159 to Cape Recife to address retention rates within a complex, rocky surf zone, surveyed using novel low-cost mixed-method techniques, to aid in larval seeding strategies. The latter model-component 160 constitutes the primary contribution of this work. 161

#### 163 2. Site Description

The study location is Eastern Cape, South Africa, with larval dispersion examined at two spatial scales. First, at a regional scale (Fig. 1a) along a ~400-km stretch of coastline extending west past St Francis Bay and east beyond Algoa Bay, past East London. Second, at a local scale (Fig. 1b,c), the primary site is Cape Recife, near the city of Port Elizabeth where a ranching concession designated as EC1 has been declared by the government (DAFF, 2010; DAFF 2011). Additional *H. midae* habitats have been identified on rocky reef areas throughout the region (Witte, 2017; Fig. 1a,d).

170 The Eastern Cape coastline is highly exposed, with sandy beaches interspersed with cliffs and rock 171 platforms in shallow embayments. Longer sandy beaches occur in the two large bays, St Francis and 172 Algoa. The continental shelf is wider to the WSW (>100 km) and narrower to the ENE (<50 km). The 173 Eastern Cape is a high-energy environment, with an annual significant wave height over 3 m (Fig. 2, 174 WAVERYS Global Reanalysis). Prevailing wind and waves (Fig. 2) come from the WSW or ENE. The 175 dominant mode is combined wind and wave forcing from the WSW (Fig. 2c, "W forcing"), with less 176 frequent forcing occurring from the east (Fig. 2c, "E forcing"), and an additional mixed directional mode with SW waves and ENE winds (Fig. 2c, "Mixed forcing"). The geostrophic Agulhas Current 177 runs from ENE to WSW, generally offshore of the shelf. Upwelling and downwelling events 178 179 frequently occur across Algoa Bay (Goschen et al., 2012, 2015; Weidberg et al., 2015), forced by wind and also by meanders of the Agulhas Current. Tides are semi-diurnal and micro-tidal, with a 180 maximum 2 m spring range at Port Elizabeth. 181



Figure 1. Field site. (a) Eastern Cape region of South Africa, red line is Delft3D model boundary; (b) Cape
Recife, red line is XBeach model domain, green line is <u>SBES single-beam bathymetry bathymetric survey</u> extent
and blue line is <u>UAV (drone)</u> based photogrammetric survey coverage; (c) zoom-in on Cape Recife, *in-situ*instrument locations indicated, including pressure transducers (PT), acoustic doppler velocimeter (ADV) and
Aquadopp current profiler (AQD); (d) 1-m resolution DEM around Cape Recife, with locations of abalone

189	monitoring sites indicated (Witte, 2017). Elevations relative to mean sea level. Google Earth images used as
190	background in (b, c).



Figure 2. Marginal distribution and scatter plots of (a) wind speed and direction; (b) significant wave height and direction; and (c) wave and wind direction. Data are from global model output obtained from Copernicus
Marine (details in text), ~100 km south of Cape Recife at Delft3D model boundary (see Fig. 1a). Contours are determined from the fit of a Gaussian mixture model to each variable pair.

#### 197 **3. Methods**

#### 198 3.1 Field measurements

#### 199 *3.1.1. Topo-bathymetric survey*

200 A multi-method survey of the sand apron and complex rocky gullies and outcrops around Cape 201 Recife was undertaken to construct the topo-bathymetry required for the local XBeach model (Fig. 1b-d). Aerial imagery was collected from a DJI P4 RTK unmanned aerial vehicle (UAV) using real-time 202 kinematic Global Navigation Satellite System (RTK-GNSS) positioning on 30<sup>th</sup> Aug 2019, at low water 203 204 (area outlined in Fig. 2b). Ground control points (GCPs) were established across the survey region 205 and were positioned with survey-grade RTK-GNSS, with uncertainty of <3 cm and used for control 206 and validation. Structure-from-Motion and Multi-View Stereo techniques were used (Agisoft 207 Metashape Pro, version 1.5.3) to construct a georeferenced digital elevation model (DEM) from 208 aerial images for terrestrial regions and shallow sub-aqueous zones (<2 m depth), by applying a refraction correction (Woodget et al., 2019), with <10 cm horizontal resolution and elevation error 209 of 5 cm + 10% depth (where sub-aqueous). 210

Bathymetric data were collected on 10<sup>th</sup> Sep 2019 using a low-cost single-beam echosounder (SBES) system (Humminbird HELIX 5 Fishfinder) mounted on a jet-ski, from depths of 2 m to > 20 m, at 200m spaced cross-shore transects throughout the Cape Recife region (area in Fig. 1b). SBES data were exported using ReefMaster software (version 2.0) and processed with local tide-correction and lowpass filtering to remove wave noise ( $H_s < 1$  m). Data were gridded using a natural neighbour method to a cell size of 50-m. Vertical uncertainty is estimated at < 0.5 m.

The combined UAV and SBES survey data covered an area of 6 km<sup>2</sup> extending onshore from the dunes to up to 2 km offshore, at depths > 20 m. The combined UAV and SBES data were transformed to a vertical reference of Mean Sea Level (MSL). The Natural Neighbour method was used to interpolate across gaps in the survey data, with care taken to represent gully morphology. A highresolution (1-m) DEM was produced (Fig. 1d) for the purpose of generating the XBeach model grid.

# 222 3.1.2. In-situ hydrodynamic observations

A 600 kHz Teledyne RDI Workhorse acoustic Doppler current profiler (ADCP) was deployed at Schoenmakerskop to the west of Cape Recife (Fig. 1a) over the period Jan-Mar 2016. The ADCP was deployed in 21 m depth on the bed facing up, with 0.5-m bin spacing and the first bin at approximately 2 m above the bed. Wave and current profile data were collected at hourly intervals in 20-min bursts. A 1-week subset of these data, from 17 to 23 Feb 2016, was used to validate the Delft3D model. During this period, waves were generally S-SSW, with height varying from 1 to 3 m, and depth-averaged currents ranged up to 0.3 m s<sup>-1</sup>, directed toward the east.

230 A cross-shore array of in-situ instruments were deployed off the apex of Cape Recife (Fig. 1c) from 9-231 10 Sep 2019, to observe hydrodynamic conditions within a known abalone habitat, for the purpose 232 of validating the local-scale XBeach model. The instrument array included two RBR pressure 233 transducers (PT1, PT2), used to measure water depth and wave height, a Nortek Vector acoustic 234 Doppler velocimeter (ADV), for measuring currents at a point, and a Nortek Aquadopp ADCP (AQD), 235 measuring the current profile and wave parameters outside the surf zone. The PTs and ADV were 236 deployed in a rocky gully between 0 and 2 m water depth, the AQD was deployed further offshore in 237 7 m depth.

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#### 239 3.2 Regional model and particle tracking methods (Delft3D)

The Delft3D hydro-morphodynamic modelling suite (Lesser et al., 2004) was used to simulate 240 regional scale larval dispersion around the Eastern Cape region of South Africa, coupling the WAVE, 241 242 FLOW and PART components of Delft3D. The regional model is implemented in this study as a first-243 pass assessment (Section 3.3). The goal of the regional model is to approximate the magnitudes and 244 directions of nearshore and inner-shelf wave and wind forced flows, under steady forcing, to 245 estimate the potential range of larval dispersal under representative low and high-energy 246 (wind/wave) conditions, to inform larval seeding strategies, and to provide context for the local scale 247 model (next section), which is the primary focus and novelty of this work. Accordingly, and for simplicity, the complex interactions with the geostrophic Agulhas Current are not included in the 248 boundary conditions, and complex 3D processes such as upwelling and downwelling, known to occur 249 250 in the region (Goschen et al., 2015; Weidberg et al., 2015), are not analysed explicitly. These processes are necessary for a complete understanding of regional larval dispersal but are considered 251 252 beyond the scope of this first-pass assessment and will be addressed in a future study.

A Cartesian coordinates rectilinear model grid was used for Delft3D WAVE and FLOW (Fig. 1a) with 1-km resolution, aligned ENE-WSW, extending approximately 150 km southwest of Cape Recife, 300 km northwest and 100 km offshore. GEBCO 15-arc-second global bathymetry was used to generate the depth grid, using the Delft Dashboard utility.

The 3D FLOW model used 10 depth levels with higher resolution near the bed. The three open boundaries were forced with tidal harmonics obtained from the TPXO 8.0 global inverse tidal model. Initial analysis indicated that tidal flows were minor relative to wave and wind-forced flows, and therefore tidal effects were not included as a focus of the analysis and discussion. Wind forcing was applied with a time-space varying grid, obtained from satellite scatterometer data from Copernicus Marine, pressure data were from the NOAA CFSv2 Forecast. Physical parameters used default

settings where possible. For bottom friction, the 'Chezy' formulation was applied, with a setting of 55 m<sup>1/2</sup> s<sup>-1</sup> determined through calibration. The WAVE model was forced with parametric boundary conditions, extracted from the WAVERYS (MFWAM) Global Reanalysis model. WAVE and FLOW were coupled with a 1-hour communication interval.

267 The Delft3D WAVE-FLOW model was validated over the period 17-24 February, February 2016, against the Schoenmakerskop ADCP (Fig. 3, left column). Wind forcing was observed to be the 268 269 primary control on nearshore currents throughout the domain. Mean absolute error (MAE) is used 270 to assess model skill, with MAE  $\leq$  0.08 m s<sup>-1</sup> for observed and modelled currents up to 0.3 m s<sup>-1</sup>. The 271 model captures the magnitudes and direction of currents in the validation region and therefore 272 satisfies our stated requirement for a first-pass estimate of potential larval dispersion ranges, 273 acknowledging that a more sophisticated model will be required in future to capture complexities of 274 upwelling/downwelling and interactions with the Agulhas Current.

275 To determine representative high and low energy boundary forcing conditions, a Gumbel copula 276 joint probability model (Arns et al., 2020) was fitted to the historical global reanalysis (1993-2018) of 277 wind and wave conditions (Fig. 2) obtained from the Copernicus Marine site (IFREMER Global 278 Blended Mean Wind Fields; WAVERYS Global Ocean Waves Reanalysis). Four representative 279 scenarios were determined (Table 1) at 90% (low energy) and 10% (high energy) joint probability 280 exceedance from the prevailing westerly (dominant) and easterly (secondary) wave-wind forcing 281 directions. The four scenarios are named (Table 1) by forcing direction (E, W) and energy level ('Lo', 282 'Hi'). A mixed-direction scenario with westerly waves and easterly winds was also found to occur 283 (Fig. 2c) but was omitted from analysis as we seek only to determine a low and high estimate 284 potential larval transport under steady forcing.

285 The Delft3D-PART model was used to simulate larval dispersion based on the outputs from the 286 WAVE-FLOW model. The PART model applies an advection-diffusion model (Postma et al., 2013) and allows for prescribed larval behaviour such as periods of upward/downward motion or neutral 287 buoyancy. Default settings were used for diffusion rates. Particles were released from each abalone 288 289 site (n = 10,000 per site, as per Robins et al., 2013). Based on currently limited data on H. midae larval behaviour (Genade et al., 1988; Grubert 2005; Courtoise de Vicose et al. 2007; Sales and Britz, 290 2001; Visser-Roux 2011), the behaviours outlined in Table 2 were applied over a 9-day period. This 291 includes an initial day of hatching and upward swimming, a 5-day planktonic stage, followed by a 292 293 downward swimming and settling phase. A duration of 9-days is near the upper limit of laboratory results (Tong et al. 1992; Roberts and Nicholson 1997; Roberts and Lapworth 2001), allowing an 294 assessment of an upper limit to connectivity distances. Once the settling phase begins, particles are 295

'caught' and removed from further tracking analysis if they come within a fixed radius (3 km) and
depth (<12m) of a designated settlement site, informed by local knowledge and available literature</li>
(Wood, 1993; Proudfoot, 2006). Twelve designated release/catchment sites were specified between
St Francis Bay and east of Algoa Bay, centred around Cape Recife (Fig. 1a), based on existing expert
knowledge and mapping of abalone habitats (Witte, 2017).

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Figure 3. Hydrodynamic model validation. Delft3D validation period (left column) includes: (a) astronomical
water level; (b) wind speed and direction; (c) significant wave height; (d) mean wave direction; (e) easterly
current velocity; (f) northerly current velocity. XBeach (right column) observation-model comparisons across
the in-situ array (PT1, ADV, PT2, AQD; Fig. 1c) are provided for: (g) significant wave height; (h) peak wave
direction; (i) flow velocity; and (j) flow direction. For (c - j), mean absolute error (MAE) between observed

(grey) and modelled (red) variables is given.

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# 311 Table 1: Boundary conditions for regional (Delft3D) and local (XBeach) models

	Wave			Wind	
	Height	Period	Direction	Speed	Direction
Scenario	( <i>H</i> <sub>s</sub> ; m)	$(T_{\rho}; s)$	(Drn)	(U <sub>wind</sub> ; m/s)	(D <sub>wind</sub> )
Delft3D bounda	ry conditions				
1. E-Lo	2.5	10.5	64°	7.6	70°
2. E-Hi	3.9	11.6	64°	16.5	70°
3. W-Lo	2.6	10.9	227°	5.5	253°
4. W-Hi	5.6	12.6	227°	16.2	253°
XBeach bounda	ry conditions				
1. E-Lo	1.6	10.4	96°	7.6	70°
2. E-Hi	3.7	8.9	95°	16.5	70°
3. W-Lo	2.2	10.6	219°	5.5	253°
4. W-Hi	4.7	12.2	223°	16.2	253°

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# Table 2: Delft3D-PART particle tracking larval behaviour settings

	Stage	Total time (days)	Stage duration (days)	Larval behaviour	
	1	0.5	0.5	Pre-hatch, particles are released in bottom/bed layer and are neutrally buoyant.	
	2	1	0.5	Post-hatch, upward swimming at 1 mm/s <a href="https://www.stage">trochophore stage</a> ). Most particles will arrive at the surface at the end of this period.	Formatted: Highlight
	3	6	5	Planktonic for 5 days, neutrally buoyant <mark>(veliger stage).</mark>	Formatted: Highlight
	4	7	1	Downward swimming at 1 mm/s. Most larvae will reach the bottom layer within a day.	
	5	9	2	Settling phase. Downward swimming ceases. Settling occurs when particles come within a fixed radius (3 km) and depth ( <12 m) of a designated settlement site.	
15					
16					
17					

#### 318 3.3 Local model particle tracking methods (XBeach)

319 XBeach (Roelvink, 2009) is a 2D-horizontal, depth-averaged, hydro-morphodynamic model suited to event-scale scenarios, capable of resolving wave-group (infragravity) motions and surf zone currents. 320 321 A local, high-resolution XBeach model was setup around Cape Recife (Fig. 1b-d) to assess residence times under steady forcing. The model was run in 'surf-beat' mode, resolving individual wave-322 groups. XBeach does not include 3D-layers (it is depth averaged) and therefore cannot be used to 323 324 investigate downward/upward larval swimming behaviours or residence within a particular layer, 325 e.g., offshore directed bed return flow or surface layer onshore flow due to wave breaking, as 326 explored by Fujimura et al. (2014). However, XBeach is generally preferred over Delft3D for surf zone 327 simulations, and has been demonstrated to be effective in assessing flows and particle residence 328 time in rocky coast environments (e.g., Castelle and Coco, 2013; Scott et al., 2016). Given these 329 factors, the analyses of residence time are indicative of a generic, neutrally buoyant tracer, which is considered suitable to represent abalone larvae during the planktonic veliger stage. 330

Analysis was conducted to evaluate optimal locations and conditions for releasing competent larvae, 331 332 to maximise the chance of settling in a suitable habitat, in this case defined by water depth and 333 presence of rocky substrate. In future work this will be modified to incorporate specific data on habitat suitability when this becomes available. The model domain is 5-by-5 km, with a maximum 334 resolution of 5-m around the apex of the cape. The local XBeach model was one-way nested within 335 336 the regional Delft3D model (Figure 1), with XBeach boundary conditions (Table 1, bottom) extracted from the Delft3D results (Table 1, top). Wind was applied uniformly across the domain with the 337 338 same settings as for Delft3D.

A simple particle advection model was applied (e.g., Castelle et al., 2015; McCarroll et al., 2015). 339 340 Particles were released across a 2.5-km square that covered the tip of Cape Recife (Fig. 4) at a 10-m spacing (n = 62,500). Particles were advected at the rate predicted by the nearest grid cell of the 341 342 XBeach output. A 1-h time varying ('surf-beat') XBeach simulation was looped to drive a 6-h particle 343 advection simulation for each of the four scenarios (Table 2, bottom). The 6-h limit was chosen based on initial analysis, as the majority of particles exited the domain within this time, and 344 345 processes trapping particles for longer periods (e.g., persistent eddies) could be easily identified within this time frame. Velocities were linearly interpolated across isolated dry regions (rocky 346 347 outcrops), to prevent particles stopping when advected into an isolated region with no data. This effectively assumes that if a particle is washed onto a rock surrounded by water, it will quickly be 348 349 washed off again, and be free to advect with the flow.

For visualisation and analysis, the region of interest was divided into 10 sectors, with 5 divisions 350 counter-clockwise alongshore ('A' to 'E'), and two depth zones ['1' - from 3 to 6 m; and '2' - from 0 351 352 to 3 m]. E.g., 'C2' is the third sector alongshore, in the shallow depth band (Fig. 4). The choice of depth bands is informed by preliminary research on seeding strategies (Moriarity, 2019), suggesting 353 high-recruitment rates in shallow depths (up to 2 m) and significantly lower recruitment as deep as 7 354 355 m. The lower depth band in the modelling analysis has been capped at 6 m to avoid interaction with 356 boundary effects in the model (extending the analysis to greater depths would require a 357 substantially larger model domain). Residence times and connectivity were analysed based on initial 358 sector and starting position, final sector (at various time intervals) and time within each depth band.

359



360

Figure 4. Example of particle advection in the local-scale XBeach model around Cape Recife. (Left) initial
 particle positions, and (right) after 60 min. Sectors used for analysis are labelled [A-E] alongshore and [1-2]
 cross-shore, e.g., "C2".

364

365 The local XBeach model was calibrated against data collected by the cross-shore in-situ array 366 (Section 3.1.2), running the model for 2 h, then excluding 1 h spin-up, for an average wind-wave condition observed during the first mid-tide during the deployment. Wind forcing was obtained from 367 368 Copernicus Marine scatterometer data, wave conditions were taken from the nearshore ADCP (AQD 369 in Fig. 1c), assuming minimal wave dissipation between the boundary and the instrument. Default settings were used where possible. Flow bed friction was calibrated to 35 m<sup>1/2</sup> s<sup>-1</sup> (Chezy 370 formulation, default 55 m<sup>1/2</sup> s<sup>-1</sup>, lower values equate to higher friction) and wave bed friction was 371 372 increased to 0.25 (dimensionless; default 0, maximum 1), to achieve optimal agreement with 373 observations. High friction values are unsurprising due to the rugose, complex rocky outcrops, reefs

and gullies that predominate across the domain. Comparison with the field observations suggests wave height dissipation is well-modelled within the observed gully (Fig. 3g; MAE = 0.2 m). Flow speed is well modelled (MAE = 0.04 m/s) and flow direction is accurate outside the inner-gully (AQD, Fig. 3j). Given the extremely complex nature of the morphology in this region, the validation is satisfactory and the model is considered suitable for estimating particle residence times around Cape Recife.

#### 380 **4. Results**

#### 381 4.1 Regional larval dispersion modelling

#### 382 4.1.1 Regional: Full larval cycle

Larval tracking results from the regional-scale Delft3D model (Fig. 5) indicate potential larval 383 transport distances under steady-forcing. In general, particles remain near the coast. Particle 384 385 transmission rates are ~50 to 100 km after 9 days for the low energy scenarios (Fig. 5, Rows 1 and 3) 386 and >100 km for the high energy scenarios (Fig. 5, Rows 2 and 4). Using the two large bays for 387 reference (Algoa and St Francis, labelled in Fig. 5, Row 3), under low-energy forcing, it is predicted 388 that larvae could be transported the extent of one of these bays, within the larval stage of the abalone (settling from day 7 to 9). For example, for the 'E-Lo' condition (Fig. 5, Row 1), Site 9 389 390 particles travel west to east across the extent of Algoa Bay. Whereas under sustained high-energy 391 wind and waves, the model suggests particles could traverse the extent of both bays. Sensitivity testing (not shown) indicates wind is the primary control. For example, for the 'W-Hi' scenario (Fig. 392 5, Row 4), Site 1 particles are transported east to west, across St Francis then across Algoa Bay, as far 393 as Site 9. The sustained high-energy conditions represent the most extreme possible transport 394 395 distances (sustained 10% exceedence conditions), with more typical larval transport ranges better 396 represented by the lower energy scenarios (sustained 90% exceedence conditions).

Releases from abalone habitat sites that are on the coast produce an elongated cloud of particles; this is due to some particles being washed-up on shore, slowing or preventing further transport. By comparison, for the only offshore site (Fig. 5, Site 9-orange, 'Bird Island'), particles tend to be transported within a ~10-km wide cloud (e.g., Flg. 5, Row 1, 'E-Lo'), unless and until the cloud is transported near to shore, in which case it begins to spread out (e.g., Fig. 5, Row 2). These results suggest that Bird Island (Site 9) has the potential to source Cape Recife and sites east of Algoa Bay, acting as a key source community and linking point across the Algoa Bay.

Despite the large transport distances (Fig. 5), and the apparent potential for connectivity, in some instances the number of particles reaching potential sites is very low or zero. For instance, for 'E-Hi' conditions (Fig. 5, Row 2), it appears that Site 12, east of Algoa Bay, may potentially seed Sites 5-8, west of Cape Recife. However, closer inspection reveals particle trajectories several km offshore of the abalone habitat 'catchment' region (not shown).

409 Connectivity within and between sites is important in order to assess whether sites are potentially 410 'self-seeding' or connected, and whether sites are supply-limited. The extent of connectivity 411 between sites varies significantly under the different scenarios. Potential connectivity rates are 412 summarised in Figure 6. Under easterly, low-energy forcing (Fig. 6b) catchment sites are typically to

the west of the release site, indicated by a dominance of coloured squares to the left of the dashed line. The western St Francis Bay sites (Fig. 6b, Sites 1–2), are self-seeding, and also receive a large amount of seeding (20–50% of particles caught) from the eastern St Francis Bay sites (Sites 3–5). The eastern St Francis Bay sites along to Cape Recife (Sites 5–8) are also self-seeding, under lower energy forcing. Larvae from Cape Recife (Site 8) are simulated to reach as far as Site 3, but do not traverse fully westward across St Francis Bay. The east Algoa Bay sites (Sites 10–12) are self-seeding under easterlies, with little or no seeding of sites west of Algoa Bay.

For high-energy easterlies (Fig. 6c), a similar overall pattern is observed, with westward transport occurring, but over larger distances. For example, Cape Recife (Site 8) now seeds as far as Site 1, and Site 9, the offshore site east of Algoa Bay, is predicted to seed as far west as Site 3. Overall, levels of self-seeding are reduced under the higher energy scenario.

Westerly forcing (Fig. 6d,e) produces an eastward trend in transport (coloured squares now lie to the right of the dashed line). Low rates of seeding may potentially occur across St Francis Bay (Site 1–2 releases are caught by Site 3–4). Under lower energy (Fig. 6d) a greater amount of self-seeding or seeding of adjacent sites occurs, e.g., Sites 3–8 and Sites 10–12 form separate clusters. For highenergy conditions (Fig. 6e), releases from east St Francis Bay to Cape Recife (Sites 3–8) are predicted to cross Algoa Bay and potentially seed the far eastern sites (Sites 10–12).

In summary, the regional scale model results suggest a significant amount of seeding may occur across St Francis Bay, even in low energy conditions (e.g., Fig. 6b, Site 1 receives seeding from Sites 3–5). Seeding across Algoa Bay appears less likely in low-energy conditions (Fig. 6b,d), but may be possible in sustained high-energy conditions (e.g., Fig. 6e, Sites 9–12 receive seeding from Sites 3–8). Cape Recife (Site 8) is predicted to be mostly self-seeding under easterlies (Fig. 6b,c), but may receive larvae from adjacent regions (Sites 3–7) during westerlies (Fig. 6d,e). The simulations suggest the majority of sites within the sub-regions are interconnected under modal conditions.



438

Figure 5. Regional larval dispersion using the large-scale Delft3D model, showing 5 of the 12 sites (for clarity),
after 5 days (left column) and 9 days (right). Rows are model simulations: (Row 1, E-Lo) easterly low-energy
wind and waves; (Row 2, E-Hi) easterly high-energy; (Row 3, W-Lo) westerly low-energy; and (Row 4, W-Hi)
and westerly high-energy. Five of the 12 larval catch/release sites are shown.



Figure 6. Regional connectivity, total particles 'caught' after 9-days. (a) Map of abalone habitats 1 to 12; (b-e)
connectivity plots, colour indicates percentage of particles from each release site (y-axis) that are caught and
retained within the catch site (x-axis). For (b-e), the title indicates forcing scenario, with direction (E or W) and
energy level ('Lo' or 'Hi'), details in Table 1.

#### 451 4.1.1 Regional: Dispersal after 24-hours

The previous section explored the potential for regional connectivity, or alternatively for selfseeding, of abalone larvae released naturally through spawning, with a catchment period of 5 to 9 days after release. We now test the potential for connectivity and self-seeding of sites after a period of 24-h, simulating potential outcomes if ranch-grown abalone larvae were released at the point of competency, when ready to settle. This is an intermediate step between the regional scale dispersal over the whole larval stage (section 4.1.1) and the local scale, high-resolution modelling at a single site over a period of hours, to determine specific release points (section 4.2).

One day after release, in lower energy conditions (Fig. 7, left column), most sites are self-seeding, 459 460 with higher retention rates in sites 1 to 7 (see map in Fig. 6). Under higher energy conditions (Fig. 7, 461 right column) there is a high degree of connectivity between adjacent sites 3 to 7, while the sites at the eastern and western edges of the domain are more isolated. Cape Recife (site 8) is potentially 462 463 self-seeding under easterly low energy (Fig. 7a), acts as a feeder site to sites 5 to 7 under high 464 easterly conditions, and may be seeded by multiple sites to the west under high energy westerly 465 conditions (Fig. 7d). This site is therefore an interesting location to investigate larval release 466 strategies at a local-scale.



Figure 7. Regional connectivity, total particles 'caught' between 24-h and 48-h after release. (a-d) connectivity
plots, colour indicates percentage of particles from each release site (y-axis) that are caught and retained within
the catch site (x-axis). Title indicates forcing scenario, with direction (E or W) and energy level ('Lo' or 'Hi').

#### 471 4.2 Local-scale particle advection modelling

The regional analysis (Sec. 4.1) has a resolution of 1-km, which is incapable of resolving local-scale features such as rocky outcrops and gullies, local wave breaking patterns and high-resolution surf zone currents. Therefore, the regional approach has no capacity to determine if larvae retained in the general vicinity of sites such as Cape Recife (catchment zones in Figs. 6 and 7 use a 3-km radius) will be retained within the shallow, rocky zones that make suitable abalone habitats. That degree of detail is typically absent from larval retention modelling studies and can only be achieved by applying a high-resolution surf zone hydrodynamic model, using high-quality bathymetry.

#### 479 4.2.1 Local-scale: Forcing

This section describes the results of the local model around Cape Recife, where XBeach was used to run-the four scenarios (Table 2, bottom) using inputs from the Delft3D model. Mean wave and flow fields (Fig. 8) indicate that, in general, for lower energy forcing (Fig. 8, rows 1 and 3), inshore currents are < 0.5 m s<sup>-1</sup>, while for high-energy scenarios (Fig. 8, rows 2 and 4), inshore currents range from 0.4 to 1 m <sup>-1</sup>s, with the highest average currents for the 'W-Hi' scenario.

Under easterly forcing ('E-Lo' and 'E-Hi'), waves converge onto the tip of the cape and produce a divergent flow pattern, with northerly currents to the east of the cape, and northwesterly currents to the west. An eddy forms off the tip of the cape at [3200 mE, 2300 mN].

Under westerly forcing (Fig. 8; 'W-Lo' and 'W-Hi'), waves approach the cape from the southwest and break over a shallow offshore reef approx. 1.5 km SSW off the cape tip [2400 mE, 1400 mN], generating northeast flow (> 1 m/s for 'W-Hi'). Waves refract around the cape toward the northwest, but are substantially attenuated. Currents are generally directed counter-clockwise around the cape, coming from the southwest, to the tip of the cape, then around to the northwest.

#### 493 4.2.2 Local-scale: Particle advection

Snapshots of particle advection simulations (Fig. 9), predict that the majority of tracers will be advected away from the region of interest after 4 h (total simulation time was 6 h), even during lower energy conditions.

For the Easterly forcing 'E-Lo' case (Fig. 9, row 1), the divergent flow around the headland sees Sector A particles being advected west, away from Cape Recife, while Sectors E and D are advected to the north. By comparison, tracers in Sectors B and C are maintained within the region for a longer period due to the eddy recirculating off the tip of the cape. After 4 h (Fig. 9, 'E-Lo', 240 min), a small number of tracers remain in the eddy. Under higher energy easterly forcing (Fig. 9, row 2), particles are advected more quickly away to the west and north, with few particles remaining after 120 min.

503	Westerly forcing scenarios (Fig. 9, rows 3 and 4) generate anticlockwise currents from southwest
504	around the cape to NNW, with a similar pattern for 'W-Lo' and 'W-Hi', though with lower residence
505	times for the higher energy case. Sector E1 is $\underline{in}$ the lee of the cape, resulting in a drop in current
506	velocities (Fig. 8, 'W-Lo' and 'W-Hi'). As particles from all sectors are transported counter-clockwise
507	around the cape, longer residence times occur around Sector E1. Eddies are apparent offshore of
508	Sector A1 and north of Sector E2, resulting in some recirculation and increased residence times.





512 Figure 8. Local Cape Recife XBeach model, (left) mean significant wave height and direction and (right) mean

513 current field, for the four scenarios ('E-Lo', 'E-Hi', 'W-Lo' and 'W-Hi'). A local coordinate system is used.



# 

Figure 9. Particle advection for the local-scale Cape Recife XBeach model. Rows are time series' (at 20, 60, 120 and 240 min) of different forcing scenarios (Table 1), with varying direction (E, W) and energy level ('Lo',
'Hi'). The region of interest is divided into 10 sectors (labelled in top-left panel), numbered counter-clockwise alongshore [A to E], and split cross-shore into two depth zones [1 – deep; 2 – shallow]. E.g., 'C2' is the third sector alongshore, in the shallow depth band. To aid in visualisation, particles are coloured by the initial starting sector, and a coloured mesh of sector colour is held fixed in all panels. Particles starting outside the defined sectors are mauve coloured.

#### 524 4.2.3 Local scale: Residence times

A series of residence time 'heatmaps' (Fig. 10) indicate the amount of time a particle is predicted to spend within any sector (Fig. 10, column 1), within the shallow-band sectors (Fig. 10, column 2) or within the deep-band sectors (Fig. 10, column 3). Particles in Figure 10 are *plotted by initial position* and this plot does not explicitly show trajectories. The heatmaps are then summarised (Fig. 11) by applying spatial smoothing (50-m moving average) and extracting the top 2% of residence times, by depth band.

For low energy easterly forcing (Fig. 10, row 1, 'E-Lo'), the dominant feature related to increased residence times is the eddy just south of the tip of the cape (in Sector C1). Particles released in the region of the eddy experience residence times > 4 h, mostly with the deeper band (Fig. 10, 'E-Lo', right). The eddy is still apparent under higher easterly forcing (Fig. 10, row 2, 'E-Hi'), but now maximum residence times, in any sector are < 3 h (Fig. 10, 'E-Hi', left). The eddy is clearly highlighted in the summary map (Fig. 11, top row; Sectors B1, C1).

537 For westerly forcing (Fig. 10, rows 3 and 4), transport is from the southwest counter-clockwise 538 around to north; therefore, longer residence times generally occur for release points to the southwest, including outside the designated sectors (e.g., W-Hi in Fig. 11). An eddy to the southwest 539 540 of Sector A1 is responsible for longer residence times and may be targeted as a location for offshore 541 release (Fig. 10, row 3; Fig. 11, row 2); however, particles released in this eddy are predicted to 542 reside near-exclusively in the deeper band. This is demonstrated by the eddy being clearly defined in 543 the deep band (Fig. 10, row 3, right), while it is near-absent from the shallow band (Fig. 10 row 3, 544 middle).

545 A consistent pattern across all scenarios is that releases from all shallow-band sectors (A2, B2 in 546 particular) are likely to result in longer residence times within the shallow-band (Fig. 10, middle 547 column; Fig. 11, blue shaded areas). This indicates that larvae released in the protected bay and gully areas near the shoreline are more likely to stay within these zones, as opposed to particles released 548 549 further offshore, for example from a boat. For comparison, if particles are randomly seeded at any 550 location (Fig. 4 contains the initial spatial distribution), then the 80<sup>th</sup> percentile residence time in the shallow band is 9 min, i.e., 4 out of 5 randomly seeded particles will spend less than 9 min in the 551 targeted habitat zones. By comparison, if seeding selectively occurs in sectors A2 and B2 under 'W-552 Lo' conditions, the mean residence time is > 2 h, an order of magnitude increase over random 553 554 seeding. Indeed, the only release points predicted to have residence times > 1 h within the shallow 555 band are within the shallow gullies (Fig. 10, middle column; Sectors A2-E2) or potentially within the eddy predicted to occur south of the cape during easterlies (Fig. 10, row 1; Sectors B1,C1). 556

557	In summary, residence times for neutrally buoyant tracers off Cape Recife are predicted on the order
558	of just a few hours, for all simulated scenarios. Under low-energy conditions, maximum (top 2%)
559	residence times are on the order of 3 h (Fig. 9, bottom; 'E-Lo', 'W-Lo'), while under high-energy
560	forcing, maximum residency is < 2 h (Fig. 9, bottom, 'E-Hi', 'W-Hi'). West low energy forcing is
561	determined to be the optimum condition as it has the highest shallow water residence times, and
562	sectors A2 to B2 are determined to be the optimal release zones, as they produce the highest
563	residence times in the shallow zone (Figs. 10-11).



566

567Figure 10. Heatmaps for the Cape Recife XBeach advection model output indicating particle residence time568within depth ranges for various forcing scenarios. Rows are the four forcing scenarios ('E-Lo', 'E-Hi', 'W-Lo',569'W-Hi'; Table 1). Sectors are numbered [A-E] alongshore and [1-2] cross-shore (labelled in bottom-left panel).570For all panels, colourmap indicates residence time within a given depth band, for a given starting position. All571particles are plotted and coloured by starting position, i.e., this plot does not show trajectories. Column 1572indicates residence time in any sector based on starting position (0 < d ≤ 6 m); Column 2 indicates time within</td>573the shallower depth band (0 < d ≤ 3 m); and Column 3 indicates time within the deep band (3 < d ≤ 6 m).</td>





#### 587 4.2.4 Local-scale: Connectivity

588 A connectivity analysis was conducted on the local Cape Recife model (Fig. 12). The earlier regional 589 connectivity analysis (Fig. 5) allowed particles to be 'caught' and removed from further analysis if 590 they entered a defined catchment zone. By comparison, the local model connectivity analysis counts particles within a given sector (Fig. 3), at a given time-lag from the initial release, then allows these 591 592 particles to continue advecting to other sectors or beyond the region of interest. In general, the local 593 connectivity analysis indicates that particles are likely to remain within the starting cell or adjacent 594 cells for the first 30 min (Fig. 12, column 1); however, within 6 h, few tracers remain within the system (most values <1% in Fig. 12, column 3). 595

For the easterly forcing scenarios (Fig. 12, rows 1,2), particles are dispersed in both directions by the divergent currents around the cape (see 'E-Lo' and 'E-Hi' in Figs. 6-7). This is evidenced by significant particle concentrations (coloured squares in Fig. 12, rows 1,2) occurring both left and right of the 1to-1 dashed line. For example, for 'E-Hi' after 120-min (Fig. 12, row 2, middle), particles originating in Sectors C1 and C2 have dispersed across all sectors in the domain. This wide distribution is also due to the eddy predicted in that region under easterly forcing (Fig. 7, rows 1-2).

602 Under westerly conditions (Fig. 12, rows 3,4) transport is more uniformly counter-clockwise around 603 the cape, indicated by high concentrations to the right of the dashed line. High concentrations occur 604 in Sectors E1-E2, as currents bringing particles from the rest of the domain decelerate in this region 605 (e.g., Fig. 12, 'W-Lo' at 120 min; see also Fig. 7, row 3). The protected shallow sectors A2 and B2 are again highlighted as retaining more particles for longer than other sectors, for example for 'W-Hi' 606 (Fig. 12, row 4), where nearly all particles have left the domain, ~1% of particles remain in Sectors A2 607 608 and B2 after 6 h (Fig. 12, bottom right). Particles released from Sectors A2 and B2 also spread widely 609 through all other sectors directed counter-clockwise throughout the domain (e.g., Fig. 12, 'W-Lo' and 610 'W-Hi' at 120 min).





#### 623 5. Discussion

624 The majority of studies of larval dispersal have focused on regional scales (e.g., Robins et al., 2013; 625 Storlazzi et al., 2017). Here, we have examined connectivity and retention rates at both the regional 626 and local scales that are of interest in abalone aquaculture. The regional connectivity projections 627 (Sec 4.1) act as a first-pass estimate of a maximum potential transport range of naturally seeding H. 628 midae during the planktonic larval phase. From the perspective of managed seeding of farmed larvae, the regional model indicates connectivity and self-seeding potential after a 24-h period (Fig. 629 7); however, at this scale there is no indication of larval retention rates within the energetic and 630 morphologically complex intertidal to subtidal habitat of the abalone, which necessitates use of a 631 632 local scale model (Sec 4.2).

633 The regional dispersal model and the local advection model are summarised in Figure 13. Regional 634 pathways (Fig. 13, top and middle rows) under low- and high-energy scenarios have been inferred 635 from Figs 5-6. It is stressed these are potential maximums given sustained uniform forcing, and actual rates of transport given frequent variations in forcing are likely to be substantially less 636 (McQuaid and Phillips, 2000), in particular for easterly forcing which occurs more sporadically (Fig. 637 638 2). It is predicted that St Francis Bay can be crossed in both the east and west directions under 639 sustained low energy, with a high degree of connectivity between Cape Recife and adjacent sites to 640 the west (Sites 5 to 8, Fig. 13), consistent with other studies demonstrating connectivity between nearby Hawaiian islands (Storlazzi et al., 2017) and shellfish populations up to 50 km apart in the 641 642 Irish Sea (Robins et al., 2013).

643 Both St Francis Bay (Fig. 13, top) and Algoa Bay (Fig. 13, middle) can theoretically be crossed in both directions under sustained high energy. Algoa Bay in particular presents a likely impediment to 644 connectivity, in all but the most sustained, high-energy conditions. Bird Island acts as a linking point 645 646 across Algoa Bay (Site 9, Fig. 13), and could be further explored as a potential key natural seeding 647 population. These findings indicate that under dominant westerly forcing, sites to the east of Algoa 648 Bay may be larval supply-limited and may therefore be target regions for larval seeding. Genetic 649 variation studies (Rhode et al., 2017) and drifter-based validation (Storlazzi et al., 2017), are required 650 to determine the extent of cross-bay connectivity of wild populations. Our findings are generally in 651 line with earlier crude estimates of mussel larval transport potential in this region using wind data 652 (McQuaid and Phillips, 2000), predicting gross displacement of 100-200 km over the course of a month, and net transport of 50 to 160 km. 653

The first-pass Delft3D model in this study does not include the Agulhas Current (Goschen et al., 2012, 2015) or 3D forcing at the boundary. An observational study of mussel larvae in the Algoa Bay

656 region (Weidburg et al., 2015), found that high veliger abundances were found close to the coast 657 and inferred that vertical swimming strategies may assist with onshore retention, consistent with 658 studies in other regions (Robins et al., 2013). Periodic meanders from the Agulhas act to vertically homogenise the flow, occasionally pumping mass offshore transport of larvae (Weidburg et al., 659 2015). A simplified vertical swimming procedure has been applied in the present study (Table 2); 660 661 however, a full analysis of the impact of swimming behaviour and the interaction with 3D 662 oceanographic process will be incorporated into the next phase of regional modelling. Aleatoric 663 variability in forcing conditions are expected to produce large variations in larval transport rates 664 (Erftemeijer et al., 2009). Accordingly, in the case of the Eastern Cape, South Africa, it would be 665 interesting to model various typical wind and wave patterns (e.g., a frontal system from the WSW) 666 combined with geostrophic current behaviours (e.g., meanders from the Agulhas current).



Figure 13. Conceptual summary of regional larval dispersal range after a 9-day pelagic stage (top and middle) and suggested strategies for larval release points at Cape Recife to maximise residence times (bottom row). For bottom row, optimal release zones are indicated by 'IN' for the inner, shallower band, and 'OUT' for the outer, deeper band; pink/blue arrows indicate additional zones larvae are likely to disperse to.

675 At the local scale around Cape Recife, the modelling results are now interpreted in the context of 676 planning the release of farmed abalone larvae that are in settling phase (Table 2) to identify the 677 optimal release points to maximise residence times. Unsurprisingly, lower energy conditions are 678 projected to result in higher maximum residence times (Fig. 11), consistent with other works at lower resolution (Stephens et al., 2006; Robins et al., 2013). If performing an inshore release in the 679 680 lower intertidal region, our modelling suggests the ideal release point is from the gullies and small bays just west of the cape ('IN' region in bottom row of Fig. 13). Simulations indicate that particles 681 682 released here will stay locally for longer and in the case of westerlies, also have extended residence 683 times as they are transported through the rest of the system (Fig. 13, blue arrows). Releases under 684 low energy westerlies in these regions are predicted to have the longest residence time in the 685 shallow depth band (>2 h). By contrast, if performing an offshore (boat-based) release, the predicted optimal release location under westerly forcing is at the southwest tip of the domain (Fig. 13, 686 bottom-left, 'OUT'), while just south of the tip of the cape is projected to be best during easterlies 687 (Fig. 13, bottom-right). These findings highlight the importance of high resolution modelling for 688 689 abalone habitats and other shellfish species with a planktonic larval phase, in which residence time 690 in regions of suitable settlement habitat are a key factor in recruitment success (Moss and Tong, 691 1992; Cowen and Sponaugle, 2009), in particular where there is interest in seeding sites with farmed larvae that are ready to settle. Besides location and timing, larval density and habitat suitability are 692 important controls on survival rates (Preece et al., 1997; Boxshall, 2000). The current approach does 693 694 address larval density to some degree (Fig. 12), and habitat suitability is simplified into preferential depth ranges (Fig. 11); however, these factors should be addressed explicitly in future efforts. 695

696 Particles in both shallow and deep regions have the potential to be caught in recirculating eddies, 697 also described as 'boundary rip cells' (Castelle et al., 2016), with subsequent potential for distribution throughout the rest of the system. However, the residence times for passive particles 698 699 around a rocky cape were found generally to be short (a few hours at most). This can be contrasted with hydrodynamic studies examining surf zone retention rates (residence time of passive particles) 700 701 which find that retention rates within the surf zone of a long open coast beach will generally 702 increase with wave height (Castelle et al., 2014) as larger waves trap material in the surf zone, while 703 headlands and rocky coasts can act to substantially increase the exchange of material between the 704 surf zone and nearshore (Castelle and Coco, 2013), as hard rocky boundaries deflect wave generated currents offshore. 705

One significant limitation of the local scale model is use of a depth averaged (2D-horizontal) method.
 This approach cannot resolve 3D processes that may be important for onshore transport of larvae
 such as surface wind generated currents and wave streaming at the bed (Fujimura et al., 2014).

709 However, in the highly-energetic surf zone, it is anticipated that abalone vertical swimming 710 behaviours will be overwhelmed by turbulent mixing (Koehl and Powell, 1994). At a microscopic 711 scale, water velocities and chemical cues to larvae may also influence behaviour (Koehl and Hadfield, 712 2010). A more sophisticated 3D model is required to resolve these processes in future. 713 In this study, we have investigated the potential for Jarval release in the Eastern Cape region, 714 examining transport pathways and residence times. The choice to examine the seeding of larvae as 715 opposed to juveniles was prompted by the interest of local ranchers in larvae release due to the 716 lower cost and shorter duration of farm-based cultivation. However, no direct comparison of the 717 costs and benefits of larval compared to juvenile seeding has been conducted in this region, and 718 should be the basis of future work. Previous studies have shown that mortality rates for juveniles 719 may be high in some cases, (e.g., >85%; James et al., 2007), though this is highly case-dependent, 720 with Roodt-Wilding (2007) providing an extensive summary of mortality rates ranging from 30% to 721 >95% for various abalone juvenile seeding programs, distributed globally. Rates of mortality for 722 larvae are expected to be even higher (e.g., Preece, 1997), which may be an acceptable trade-off for 723 reduced farming costs, but this is yet to be quantified. 724 Genetic considerations are critical in any reseeding program (Roodt-Wilding, 2007). It is important to 725 maintain high genetic diversity in hatchery-reared stock that will be used for reseeding natural 726 habitats, and the genetic distribution of seeded larvae should be tested to ensure they are 727 genetically representative of wild populations. If such procedures are not followed, genetic 728 contamination may occur (Roodt-Wilding, 2007; Rhode et al., 2012; Rhode et al., 2013), which can 729 present a major risk factor to ranching and stock enhancement. Algoa Bay has been identified 730 through genetic analysis as a potential or partial barrier to gene flow (Bester-van der Merwe et al., 731 2011), this is entirely consistent with our regional modelling results which suggest that Algoa Bay 732 may be crossed by larval abalone, but that this is likely to occur infrequently, only under extreme, 733 sustained wave and wind conditions. These relatively rare events that transmit genetic material 734 across geographic barriers could be a mechanism to explain observed temporal shifts in genetic 735 structure within a single location (Rhode et al., 2017). Given the potential genetic divide to the east 736 and west of Algoa Bay, it may be necessary to conduct ongoing genetic testing to ensure that 737 hatchery-reared larvae are adequately genetically matched to individuals not only in the location 738 they are seeded, but also with populations at downstream locations that our modelling predicts they 739 may be distributed to (Fig. 13-top). 740

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A limitation of the present study is the geographic restriction to the Eastern Cape region of South
Africa, which fails to capture the full distribution of <u>H. midae</u>. A sufficiently robust biophysical model
that includes the major oceanographic processes (e.g., Storlazzi et al., 2017), could be used to assess
connectivity across the full range of <u>H. midae</u>, covering the west, south and east of South Africa.
Such an approach could be used to test large-scale hydrodynamic influences on genetic diversity and
barriers to gene transport (e.g., Bester-van der Merwe et al., 2011; Rhode et al., 2012, 2017).

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## 750 6. Conclusions

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A multi-scale modelling approach was undertaken to better understand abalone larval connectivity and residence times across a section of the Eastern Cape, South Africa, to inform a larval seeding program. A Delft3D model was applied regionally to make a simplified, first-pass assessment of potential transport distances. An XBeach model was applied at high resolution to examine residence times within known abalone habitats at Cape Recife. The latter represents a novel application of this type of surf zone model in relation to larval dispersal, when combined with the complexity of the morphology involved.

758 For the regional model, the initial finding was that abalone sites had potential connectivity across 759 50-100 km ranges. However, the extensive stretch of Algoa Bay is likely to act as a barrier to larval 760 dispersal in all but the most extreme, prolonged forcing conditions. An offshore site, Bird Island, may 761 act as linking point across the bay, and as such may represent a key connection to the potentially 762 larval supply-limited eastern regions. At the local level, specific sites were identified in order to 763 maximise residence times within the rocky, coralline algae encrusted, intertidal habitat suitable for 764 larval settlement. In particular, a zone of protected rocky gullies, with seeding occurring under 765 lower-energy wave conditions, is predicted to increase residence in the target zone by an order of 766 magnitude or more relative to random seeding. This multi-scale approach provides useful 767 information on connectivity and larval seeding strategies for the Eastern Cape region, and Cape 768 Recife in particular. More broadly, these methods could be applied to similar abalone fisheries in 769 other locations.

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#### 782 References

- Arns, A., Wahl, T., Wolff, C., Vafeidis, A. T., Haigh, I. D., Woodworth, P., Niehuser, S. & Jensen, J.
   (2020). Non-linear interaction modulates global extreme sea levels, coastal flood exposure and
   impacts. Nature Communications, 11, 1918.
- Bester-van der Merwe, A. E., Roodt-Wilding, R., Volckaert, F. A., & D'Amato, M. E. (2011). Historical isolation and hydrodynamically constrained gene flow in declining populations of the South-African abalone, Haliotis midae. Conservation Genetics, 12(2), 543-555.
- Boxshall, A. J. (2000). The importance of flow and settlement cues to larvae of the abalone, *Haliotis rufescens* Swainson. Journal of Experimental Marine Biology and Ecology, 254(2), 143-167.
- Castelle, B., & Coco, G. (2013). Surf zone flushing on embayed beaches. Geophysical Research
   Letters, 40(10), 2206-2210.
- Castelle, B., Reniers, A., & MacMahan, J. (2014). Bathymetric control of surf zone retention on a rip channelled beach. Ocean Dynamics, 64(8), 1221-1231.
- Castelle, B., McCarroll, R.J., Brander, R.W., Scott, T., Dubarbier, B., (2015). Modelling the alongshore
   variability of optimum rip current escape strategies on a multiple rip-channelled beach. Natural
   Hazards, 1-24.
- Castelle, B., Scott, T., Brander, R. W., & McCarroll, R. J. (2016). Rip current types, circulation and
   hazard. Earth-Science Reviews, 163, 1-21.
- Cook, P. A. (2019). Worldwide Abalone Production Statistics. Journal of Shellfish Research, 38(2),
   401-404.
- Counihan, R. T., McNamara, D. C., Souter, D. C., Jebreen, E. J., Preston, N. P., Johnson, C. R., &
   Degnan, B. M. (2001). Pattern, synchrony and predictability of spawning of the tropical abalone
   *Haliotis asinina* from Heron Reef, Australia. Marine Ecology Progress Series, 213, 193-202.
- Courtois de Viçose, G., Viera, M.P., Bilbao, A., and Izquierdo, M.S. (2007) Embryonic and larval
   development of Haliotis tuberculata coccinea Reeve: an indexed micro-photographic
   sequence. Journal of Shellfish Research 26, 847–854.
- Cowen, R. K., & Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. Annu.
   Rev. Mar. Sci, 1, 443-66.
- 810 DAFF. 2010. Marine Living Resources Act (Act No.18 of 1998). General Guidelines for Marine
- Ranching and Stock Enhancement in South Africa. Government Gazette No. 33470, Notice R. 728.
   Department of Agriculture, Forestry and Fisheries, South Africa.

813 DAFF. 2011. Marine Living Resources Act (Act No.18 of 1998). Invitation to apply for rights to engage 814 in abalone ranching and stock enhancement pilot projects. Government Gazette No. 34241, 815 Notice R. 353. Department of Agriculture, Forestry and Fisheries, South Africa. 816 Daume, S., Brand-Gardner, S., & Woelkerling, W. J. (1999). Settlement of abalone larvae (Haliotis laevigata Donovan) in response to non-geniculate coralline red algae (Corallinales, Rhodophyta). 817 818 Journal of Experimental Marine Biology and Ecology, 234(1), 125-143. 819 Day, E., & Branch, G. M. (2000). Relationships between recruits of abalone Haliotis midae, encrusting 820 corallines and the sea urchin Parechinus angulosus. South African Journal of Marine Science, 821 22(1). 137-144. 822 Erftemeijer, P. L., van Beek, J. K., Bolle, L. J., Dickey-Collas, M., & Los, H. F. (2009). Variability in 823 transport of fish eggs and larvae. I. Modelling the effects of coastal reclamation. Marine Ecology 824 Progress Series, 390, 167-181. 825 Fujimura, A. G., Reniers, A. J., Paris, C. B., Shanks, A. L., MacMahan, J. H., & Morgan, S. G. (2014). 826 Numerical simulations of larval transport into a rip-channeled surf zone. Limnology and 827 Oceanography, 59(4), 1434-1447. 828 Genade, A. B., Hirst, A. L., & Smit, C. J. (1988). Observations on the spawning, development and 829 rearing of the South African abalone Haliotis midae Linn. South African Journal of Marine Science, 830 6(1), 3-12. 831 Goschen, W. S., Schumann, E. H., Bernard, K. S., Bailey, S. E., & Deyzel, S. H. P. (2012). Upwelling and ocean structures off Algoa Bay and the south-east coast of South Africa. African Journal of Marine 832 833 Science, 34(4), 525-536. 834 Goschen, W. S., Bornman, T. G., Deyzel, S. H. P., & Schumann, E. H. (2015). Coastal upwelling on the 835 far eastern Agulhas Bank associated with large meanders in the Agulhas Current. Continental 836 Shelf Research, 101, 34-46. 837 Grubert, M.A., 2005. Factors influencing the reproductive development and early life history of 838 blacklip (Haliotis rubra) and greenlip (H. laevigata) abalone. Unpublished PhD thesis. University of 839 Tasmania. Australia. 840 James, D. S., Day, R. W., & Shepherd, S. A. (2007). Experimental abalone ranching on artificial reef in 841 Port Phillip Bay, Victoria. Journal of Shellfish Research, 26(3), 687-695. 842 Kaiser, H., Erasmus, B., & Naylor, M. (2017). Behavioural responses of farmed South African abalone 843 Haliotis midae L. to disturbances caused by husbandry procedures. Aquaculture international, 844 25(1), 21-29. 845 Koehl, M. A. R., & Powell, T. M. (1994). Turbulent transport of larvae near wave-swept rocky shores: 846 does water motion overwhelm larval sinking. Reproduction and development of marine 847 invertebrates. Johns Hopkins University Press, Baltimore, 261-274. 848 Koehl, M. A. R., & Hadfield, M. G. (2010). Hydrodynamics of larval settlement from a larva's point of 849 view. Integrative and Comparative Biology, 50(4), 539-551. Lesser, G. R., Roelvink, J. V., Van Kester, J. A. T. M., & Stelling, G. S. (2004). Development and 850 851 validation of a three-dimensional morphological model. Coastal engineering, 51(8-9), 883-915. McCarroll, R.J., Castelle, B., Brander, R.W., Scott, T., (2015). Modelling rip current flow and bather 852 853 escape strategies across a transverse bar and rip channel morphology. Geomorphology 246, 502-854 518. 855 McQuaid, C. D., & Phillips, T. E. (2000). Limited wind-driven dispersal of intertidal mussel larvae: in situ evidence from the plankton and the spread of the invasive species Mytilus galloprovincialis in 856 857 South Africa. Marine Ecology Progress Series, 201, 211-220. 858 Miyake, Y., Kimura, S., Horii, T., & Kawamura, T. (2017). Larval dispersal of abalone and its three modes: a review. Journal of Shellfish Research, 36(1), 157-167. 859

- Moriarty, L. A., 2019, Inshore benthic communities of the Port Elizabeth abalone ranching
   concession area. MSc thesis, Nelson Mandela University.
- Moss, G. A., & Tong, L. J. (1992). Effect of stage of larval development on the settlement of the
   abalone, *Haliotis iris*. New Zealand journal of marine and freshwater research, 26(1), 69-73.
- O'Leary, J. K., Barry, J. P., Gabrielson, P. W., Rogers-Bennett, L., Potts, D. C., Palumbi, S. R., & Micheli,
   F. (2017). Calcifying algae maintain settlement cues to larval abalone following algal exposure to
   extreme ocean acidification. Scientific reports, 7(1), 1-10.
- Pang, S. J., Zhang, Z. H., Bao, Y., & Gao, S. Q. (2006). Settling abalone veliger larvae in a free swimming microalgal culture. Aquaculture, 258(1-4), 327-336.
- Postma, L., van Beek, J.K.L., van den Boogaard, H.F.P., Stelling, G.S., 2013. Consistent and efficient
   particle tracking on curvilinear grids for environmental problems. Intern. J. Numerical Meth.
   Fluids 71: 1226-1237
- Preece, P. A., Shepherd, S. A., Clarke, S. M., & Keesing, J. K. (1997). Abalone stock enhancement by
   larval seeding: effect of larval density on settlement and survival. Molluscan Research, 18(2), 265 273.
- Prince, J. D., Sellers, T. L., Ford, W. B., & Talbot, S. R. (1987). Experimental evidence for limited
  dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). Journal of experimental
  marine biology and ecology, 106(3), 243-263.
- Proudfoot, L., (2006). Population structure, growth and recruitment of two exploited infralittoral
  molluscs (*Haliotis Midae* and *Turbo Sarmaticus*) along the south east coast, South Africa.
  Unpublished MSc thesis, Rhodes University. Pp. 1-144.
- Raemaekers, S., Hauck, M., Bürgener, M., Mackenzie, A., Maharaj, G., Plagányi, É. E., et al. (2011).
  Review of the causes of the rise of the illegal South African abalone fishery and consequent
  closure of the rights-based fishery. Ocean and Coastal Management. 54, 433–445.
- <u>Rhode, C., Hepple, J. A., Jansen, S., Davis, T., Vervalle, J., Bester-van der Merwe, A. E., & Roodt-</u>
   <u>Wilding, R. (2012). A population genetic analysis of abalone domestication events in South Africa:</u>
   Implications for the management of the abalone resource. Aquaculture, 356, 235-242.
- <u>Rhode, C., Vervalle, J., Bester-van der Merwe, A. E., & Roodt-Wilding, R. (2013). Detection of</u>
   <u>molecular signatures of selection at microsatellite loci in the South African abalone (Haliotis</u>
   <u>midae) using a population genomic approach. Marine genomics, 10, 27-36.</u>
- Rhode, C., Bester-van der Merwe, A. E., & Roodt-Wilding, R. (2017). An assessment of spatiotemporal genetic variation in the South African abalone (*Haliotis midae*), using SNPs: implications
  for conservation management. Conservation genetics, 18(1), 17-31.
- Roberts, R. D., & Nicholson, C. M. (1997). Variable response from abalone larvae (Haliotis iris, H.
  virginea) to a range of settlement cues. Molluscan Research, 18(2), 131-141.
- Roberts, R.D., and Lapworth, C. (2001). Effect of delayed metamorphosis on larval competence, and
   post-larval survival and growth, in the abalone *Haliotis iris* Gmelin. Journal of Experimental
   Marine Biology and Ecology 258, 1–13.
- Robins, P. E., Neill, S. P., Giménez, L., Jenkins, S. R., & Malham, S. K. (2013). Physical and biological
   controls on larval dispersal and connectivity in a highly energetic shelf sea. Limnology and
   Oceanography, 58(2), 505-524.
- Roelvink, D., Reniers, A., Van Dongeren, A. P., De Vries, J. V. T., McCall, R., & Lescinski, J. (2009).
   Modelling storm impacts on beaches, dunes and barrier islands. Coastal engineering, 56(11-12),
   1133-1152.
- Rogers-Bennett, L., Dondanville, R. F., Catton, C. A., Juhasz, C. I., Horii, T., & Hamaguchi, M. (2016).
   Tracking larval, newly settled, and juvenile red abalone (*Haliotis rufescens*) recruitment in
   Northern California. Journal of Shellfish Research, 35(3), 601-609.

907 908	Roodt-Wilding, R. (2007). Abalone ranching: a review on genetic considerations. Aquaculture Research, 38(12), 1229-1241.	
909 910 911	Ross, R. E., Nimmo-Smith, W. A. M., Torres, R., & Howell, K. L. (2020). Comparing Deep-Sea Larval Dispersal Models: A Cautionary Tale for Ecology and Conservation. Frontiers in Marine Science, 7, 431.	
912 913	Sales, J., & Britz, P. J. (2001). Research on abalone ( <i>Haliotis midae</i> L.) cultivation in South Africa. Aquaculture Research, 32(11), 863-874.	
914 915 916	Scott, T., Austin, M., Masselink, G., & Russell, P. (2016). Dynamics of rip currents associated with groynes—field measurements, modelling and implications for beach safety. Coastal Engineering, 107, 53-69.	
917 918 919	Serge, J. P. R., & Britz, P. J. (2009). Profile of the illegal abalone fishery (Haliotis midae) in the Eastern Cape Province, South Africa: Organised pillage and management failure. Fisheries Research, 97(3), 183-195.	
920 921 922	Stephens, S. A., Broekhuizen, N., Macdiarmid, A. B., Lundquist, C. J., McLeod, L., & Haskew, R. (2006). Modelling transport of larval New Zealand abalone ( <i>Haliotis iris</i> ) along an open coast. Marine and Freshwater Research, 57(5), 519-532.	
923 924 925	Storlazzi, C. D., van Ormondt, M., Chen, Y. L., & Elias, E. P. (2017). Modeling fine-scale coral larval dispersal and interisland connectivity to help designate mutually-supporting coral reef marine protected areas: insights from Maui Nui, Hawaii. Frontiers in Marine Science, 4, 381.	
926 927	Takami, H., Fukazawa, H., & Kawamura, T. (2006). Delayed metamorphosis by larval abalone in the field. Bull. Fish. Res. Agency, 5, 97-117.	
928 929 930	<ul> <li>Tong, L. J., Moss, G. A., Redfearn, P., and Illingworth, J. (1992). A manual of techniques for culturing paua, Haliotis iris, through to the early juvenile stage. New Zealand Fisheries Technical Report No. 31. (MAF Fisheries, Fisheries Research Centre: Wellington.)</li> </ul>	
931 932	Visser-Roux, A., 2011. Reproduction of the South African Abalone. Unpublished PhD thesis, University of Stellenbosch. Pp 1-88.	
933 934 935	<ul> <li>Weidberg, N., Porri, F., Von der Meden, C. E., Jackson, J. M., Goschen, W., &amp; McQuaid, C. D. (2015).</li> <li>Mechanisms of nearshore retention and offshore export of mussel larvae over the Agulhas Bank.</li> <li>Journal of Marine Systems, 144, 70-80.</li> </ul>	
936 937 938	Williams, E. A., Craigie, A., Yeates, A., & Degnan, S. M. (2008). Articulated coralline algae of the genus <i>Amphiroa</i> are highly effective natural inducers of settlement in the tropical abalone <i>Haliotis asinina</i> . The Biological Bulletin, 215(1), 98-107.	
939 940	Witte, A. D., 2017. Benthic algal communities of shallow reefs in the Eastern Cape: availability of abalone habitat. Unpublished MSc thesis, Nelson Mandela Metropolitan University. Pp 1-183.	
941 942 943	Wood, A. D., (1993). Aspects of the biology and ecology of the South African abalone Haliotis Midae Linnaeus, 1758 (Mollusca: Gastropoda) along the Eastern Cape and Ciskei coast. Unpublished MSc thesis, Rhodes University. Pp 1-161	
944 945 946	Wood, A. D., & Buxton, C. D. (1996). Aspects of the biology of the abalone <i>Haliotis midae</i> (Linne, 1758) on the east coast of South Africa. 1. Feeding biology. South African Journal of Marine Science, 17(1), 61-68.	
947 948 949	<ul> <li>Wood, A. D., &amp; Buxton, C. D. (1996). Aspects of the biology of the abalone <i>Haliotis midae</i> (Linne, 1758) on the east coast of South Africa. 2. Reproduction. South African Journal of Marine Science, 17(1), 69-78.</li> </ul>	
950 951 952 953	Woodget A. S., Carbonneau P. E., Visser F., Maddock I. P. (2015). Quantifying submerged fluvial topography using hyperspatial resolution UAS imagery and structure from motion photogrammetry. Earth Surface Processes and Landforms 40: 47–64.	