



**Modelling transport of chokka squid (*Loligo reynaudii*)
paralarvae off South Africa: reviewing, testing and
extending the 'Westward Transport Hypothesis'**



Journal:	<i>Fisheries Oceanography</i>
Manuscript ID:	Draft
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	<p>Martins, Rodrigo; Instituto Oceanográfico, Universidade de São Paulo, Departamento de Oceanografia Biológica; Oceans and Coasts (formerly Marine and Coastal Management), Department of Environment Affairs; University of Cape Town, Marine Reserach Institute, Department of Zoology</p> <p>Roberts, Michael; Oceans and Coasts (formerly Marine and Coastal Management), Department of Environment Affairs</p> <p>Lett, Christophe; UMI IRD 209 UPMC UMMISCO, Centre de Recherche Halieutique Méditerranéenne et Tropicale</p> <p>Alves Gonzalez Vidal, Erica; Centro de Estudos do Mar, Universidade Federal do Paraná</p> <p>Moloney, Coleen; University of Cape Town, Marine Reserach Institute, Department of Zoology</p> <p>Chang, Nicolette; CSIR, Centre for High Performance Computing</p> <p>Garcia de Camargo, Maurício; Centro de Estudos do Mar, Universidade Federal do Paraná</p>
Keywords:	chokka squid, paralarvae, larval transport, Agulhas Bank, recruitment < biological dynamics, IBM < model, biophysical < model, generalized linear model < statistics

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Modelling transport of chokka squid (*Loligo reynaudii*) paralarvae off South Africa: reviewing, testing and extending the ‘Westward Transport Hypothesis’

Rodrigo S. Martins^{1,2,*}, Michael J. Roberts¹, Christophe Lett³, Erica A.G. Vidal⁴, Coleen L. Moloney², Nicolette Chang⁵ and Maurício G. de Camargo⁴

¹ *Marine and Coastal Management (MCM), Private Bag X2, Rogge Bay 8012, Cape Town, South Africa*

² *Zoology Department and Marine Research Institute, University of Cape Town, Private Bag X3, Rondebosch 7701, Cape Town, South Africa*

³ *UMI IRD 209 UPMC UMMISCO, Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet, BP 171, 34203 Sète cedex, France*

⁴ *Centro de Estudos do Mar (CEM), Universidade Federal do Paraná (UFPR), Cx. Postal 50.002, Pontal do Paraná, PR, 83.255-000, Brazil*

⁵ *CSIR, Centre for High Performance Computing, PO Box 320, Stellenbosch 7599, Cape Town, South Africa*

* *Present address: Laboratório de Ecossistemas Pesqueiros (LabPesq), Departamento de Oceanografia Biológica, Instituto Oceanográfico, Universidade de São Paulo, Praça do Oceanográfico, 191, São Paulo, SP, 05508-900, Brazil. rodrigo.plei@gmail.com*

Running title suggested: Modelling chokka squid paralarvae transport

Abstract

Annual landings of chokka squid (*Loligo reynaudii*) fluctuate greatly, and this is believed to be related to the success of recruitment. The ‘Westward Transport Hypothesis’ (WTH) attributes recruitment strength to variability in transport of newly-hatched paralarvae from spawning grounds to a ‘cold ridge’ region some 100–200 km to the west, where oceanographic conditions sustain high productivity, ensuring a suitable nursery ground for the paralarvae. We used an individual-based model coupled with a 3-D hydrodynamic model to test the WTH and to assess four factors that might influence successful transport. The effects of four variables (*Release Area*, *Month*, *Specific gravity* and *Diel Vertical Migration – DVM*) were tested in numerical experiments that estimated successful transport of squid paralarvae to the cold ridge. A multifactor ANOVA was used to identify the primary determinants of transport success in the various experimental simulations. Among these, release area was found to be the most important, implying that adult spawning behaviour (i.e., birth site fidelity) may be more important than paralarval behaviour in determining paralarval transport variability. However, specific gravity and DVM were found to play a role by retaining paralarvae on the shelf and optimizing early transport respectively. Upwelling events seem to facilitate transport by moving paralarvae upwards and thus exposing them to faster surface currents. Future field studies should concentrate sampling efforts for paralarvae near and to the west of the spawning grounds at a range of depths in the water column.

Key words: chokka squid, paralarvae, larval transport, Agulhas Bank, recruitment

Introduction

The South African *Loligo* fishery is based on a single species, locally known as ‘chokka’ squid (*Loligo reynaudii*) (Augustyn *et al.*, 1992). Directed exploitation began in 1984, when hand-jigging fishing methods were introduced, establishing the chokka squid as an important target species and replacing their previous ‘minor by-catch’ status in the demersal trawl fishery (Augustyn, 1990, 1991; Sauer *et al.*, 1992). Because of the improvement in fishing methods and resulting profitable catches, a specialized squid boat fleet flourished, basing their efforts mostly off the south coast of South Africa. The fishery targets squid that aggregate and spawn on sandy and low profile reef bottoms located inshore between Plettenberg Bay and Port Alfred (Fig. 1; Sauer *et al.*, 1992; Roberts and Sauer 1994). Although landings show great variability, historical annual yields reported for the species average at around 7 000 mt (Augustyn *et al.*, 1994).

Adult chokka squid distribution over the species’ habitat range and their aggregation on the spawning grounds are relatively well studied and thought to be largely influenced by environmental variables, such as dissolved bottom oxygen, temperature and turbidity (Sauer *et al.*, 1991; Roberts and Sauer 1994; Roberts 1998). However, the causes of the annual variability in the squid fishing yields are poorly known, although they are likely to be related to recruitment variability because of the short-life span of squid. Recruitment will be influenced by environmental conditions over the Agulhas Bank (Fig. 1), which affects both embryonic development and paralarval nourishment (see Roberts, 2005).

The impact of environmental conditions on the Agulhas Bank on recruitment of chokka squid has been the subject of directed research. Roberts (2005) carried out a comprehensive review of the environmental conditions believed to be important for

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2
3 recruitment. These include the influence of environmental temperatures on embryonic
4 development and hatching success (Oosthuizen *et al.*, 2002; Oosthuizen and Roberts
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6 2009), temperature influences on yolk utilization and paralarval growth (Vidal *et al.*,
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8 2005; Martins *et al.*, 2010a) and the role of paralarval transport in recruitment. Studies
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10 have been carried out using Acoustic Doppler Current Profiler (ADCP) measurements
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12 (Roberts and van den Berg, 2002, 2005), satellite-tracked drifters (Hancke, 2010) and
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14 models, linking an application of the Regional Ocean Modelling System (ROMS) to an
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16 individual-based model (IBM) (Roberts and Mullon, 2010). More recently, the role of
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18 post-hatching paralarval specific gravity (density) in dispersal has been assessed
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20 (Martins *et al.*, 2010b).
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27 All the above studies aimed to verify the validity of the so-called 'Westward
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29 Transport Hypothesis' (hereafter referred to as WTH), which postulates that paralarvae
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31 hatched on the spawning grounds on the eastern Agulhas Bank would be transported
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33 westward to nursery areas over the central part of the Bank, where an oblique cross-
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35 shore, quasi-permanent upwelling tongue (the 'cold ridge', Swart and Largier, 1987)
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37 boosts local productivity, ensuring a suitable nursery ground for the paralarvae
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39 (Roberts, 2005). In general, the studies tend to support the WTH, by confirming a
40
41 general net westward transport and retention over the Agulhas Bank (Roberts, 2005;
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43 Martins *et al.*, 2010b). However, the physical environment was also shown to be
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45 complex, with variable current patterns that could potentially cause paralarvae to be
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47 advected from the ecosystem or transported to unsuitable areas. Only one of these
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49 approaches (Martins *et al.*, 2010b) considered the role of biological characteristics of
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51 the paralarvae, by including information on paralarval specific gravity. Nonetheless,
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53 those studies provided useful insights into the fate of paralarvae after hatching and the
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55 role of currents on larval transport and recruitment.
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3 The aim of this study is to supplement and extend the results obtained by
4 previous modelling studies of chokka squid paralarvae in the region (Roberts and
5 Mullon, 2010; Martins *et al.*, 2010b). Computer-based Lagrangian transport simulations
6 are used to test the WTH and to investigate the relative contributions of different
7 environmental and biological variables to successful transport of squid paralarvae from
8 spawning grounds to the cold ridge region. ROMS model output is coupled with an
9 IBM of ‘virtual paralarvae’ hatched on inshore and offshore spawning grounds off the
10 south coast of South Africa. The study aims to simulate different transport scenarios and
11 link these to biological scenarios that consider changes in specific gravity and diel
12 vertical migration of chokka squid paralarvae. Thus the study aims to understand how
13 biologically-mediated changes in vertical position in the water column might affect
14 horizontal transport of chokka squid paralarvae in the Agulhas Bank ecosystem.
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34 **Material and Methods**

35 *Hydrodynamic model*

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43 A configuration of the ROMS hydrodynamic model (Shchepetkin and
44 McWilliams, 2005), called the Southern African Experiment (SAfE, Penven *et al.*,
45 2006), was developed for the African shore between 2.5°W–54.75°E longitude and 4.8–
46 46.75°S latitude. Horizontal resolution ranges from 19 km in the south to 27.6 km in the
47 north. Vertical resolution is high in the surface layer (0.37 to 5.70 m) and coarser (11 to
48 981 m) in the bottom layer, with 32 s-coordinate levels. However, simulations were run
49 using a higher resolution (three times finer) child grid extracted from the SAfE parent
50 grid, covering the area from 11.58–27.42°E longitude and 27.73–38.83°E latitude (Fig.
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3 1). GEBCO (General Bathymetric Chart of the Oceans) data were used for bottom
4 topography. The model started from rest and was forced at the surface using the
5 comprehensive ocean-atmosphere dataset (COADS) monthly climatology (da Silva *et*
6 *al.*, 1994) and the WOA (World Ocean Atlas) temperature and salinity data (Conkright
7 *et al.*, 2002). As the model took 2 years to reach statistical equilibrium, only output data
8 from years 3–10 were used. Further information on the structure, functioning and
9 validation of the model used in this study can be found in Chang (2009).
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19 20 21 22 *Individual-based model* 23 24 25

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27 Simulations were performed using the public domain software, Ichthyop
28 (version 2.1.1). Ichthyop is an individual-based model (IBM) that uses ROMS offline
29 outputs (i.e. 3D velocity fields) to track Lagrangian movement of particles (Lett *et al.*,
30 2008), which in the present case represent squid paralarvae hatched over the main
31 (inshore and offshore) spawning grounds. Thirty thousand particles were ‘hatched’ over
32 six release areas (5 000 particles release area⁻¹) every first day of every month of all
33 modelled years. Their trajectories were tracked for 40 d to assess their potential
34 transport trajectories over the full period of their planktonic phase. The initial number of
35 particles was chosen based on preliminary tests that indicated it was high enough to
36 ensure robust simulated patterns. The duration of 40 d was chosen because reared
37 *Doryteuthis* (formerly *Loligo*) *opalescens* paralarvae, which size-at-hatching is fairly
38 similar to that of *Loligo reynaudii* incubated at the same temperature (Vidal *et al.*,
39 2005), first start gathering in schools between 35 to 45 days after hatching and with 6.0
40 to 8.0 mm dorsal mantle length (ML) (Yang *et al.*, 1986; Vidal *et al.*, 2009). The
41 formation of schools was assumed to represent the end of the planktonic phase for *L.*
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3 *reynaudii*. The randomness of initial particle positions was a default property of the
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5 Ichthyop tool (Lett *et al.*, 2008).
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8 Six areas for release of particles were used. Three areas represented the shallow
9
10 water spawning grounds (20–50 m) and the remaining three represented the deep water
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12 spawning grounds (60–120 m) (Oosthuizen and Roberts, 2009) (Fig. 1). The areas were
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14 selected based on recorded hydroacoustic signals of spawning aggregations, records of
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16 chokka squid egg pods from trawls in research surveys and observations from SCUBA
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18 divers (Sauer *et al.*, 1992; Sauer, 1995, Roberts *et al.*, 2002). Release areas were named
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20 according to the geographical reference on the shore and were: Plettenberg–
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22 Tsitsikamma inshore (P-T_in), Plettenberg–Tsitsikamma offshore (P-T_off), St Francis
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24 inshore (SF_in), St Francis offshore (SF_off), Algoa Bay inshore (AB_in) and Algoa
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26 Bay offshore (AB_off). Because the ROMS bottom layer resolution is coarse and the
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28 bathymetric gradient in the release areas is steep, a single release depth was chosen as
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30 representative for all release areas according to their location; inshore, particles were
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32 released at 35 m whereas offshore they were released at 90 m. These depths were
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34 chosen because they are the average depths of the shallow and deep spawning grounds
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36 (Oosthuizen and Roberts, 2009).
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43 Simulations were run with virtual paralarvae that were neutrally buoyant or that
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45 had a specific gravity of 1.048 g cm^{-3} , this being the average specific gravity found for
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47 chokka paralarvae (Martins *et al.*, 2010b). In test simulations, individuals with specific
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49 gravity changing with time have been used, in which specific gravity decreased
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51 according to an exponential model. This model was based on yolk utilization and
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53 specific gravity data collected during a seven day experiment (for details, see Martins *et*
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55 *al.*, 2010b). The comparison of mean dispersal distances covered by individuals with
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57 changing specific gravity and individuals with constant specific gravity showed no
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3 significant differences (Students $t = 0.834$, $p = 0.401$, $n = 25\ 411$). Therefore a single
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5 value of specific gravity was used in the simulations, for simplicity.
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10 *Transport scenarios*

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15 Because vertical behaviour of chokka squid paralarvae is poorly known, two
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17 simple transport scenarios were used, based on information from the literature. These
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19 were:
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22 1. Passive Lagrangian transport

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29 In this scenario, the virtual paralarvae are assumed to behave as passive
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31 particles, seeded in each of the release areas and tracked for the duration of the
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33 simulation. This scenario represents the null hypothesis of no ability to change vertical
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35 position in the water column. Simulations for this scenario were run with (1) neutrally-
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37 buoyant particles and (2) particles with a specific gravity of 1.048 g cm^{-3} .
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43 2. Diel vertical migration (DVM)

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48 This scenario is based on the diel vertical migration (DVM) behaviour described
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50 for *Doryteuthis opalescens* off the southern California coast (Zeidberg and Hamner,
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52 2002) and *Loligo vulgaris* off the westward Iberian Peninsula (Moreno *et al.*, 2009).
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54 Zeidberg and Hamner (2002) found *D. opalescens* paralarvae to be concentrated at 30 m
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56 in the daytime and 15 m at night. Moreno *et al.*, (2009) found *L. vulgaris* paralarvae at ~
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58 50–75 m during the day and surfacing at night. Thus, loliginid paralarvae seem to
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3 display Type-1 DVM (Forward, 1988). Such behaviour can have important implications
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5 for larval transport (Forward, 1988; Forward *et al.*, 1999). In the present study, DVM
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7 was mimicked using Ichthyop default vertical migration scheme (Lett *et al.*, 2008),
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9 which allows setting different depths for individuals during day (07h00 to 19h00) and
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11 night (19h00 to 07h00). For individuals released in the inshore release areas, depth
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13 during night (resp. day) was set to 10 m (resp. 30 m), whereas in the offshore release
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15 areas three depth changes scenarios were used: between 10 and 30 m, 10 and 60 m, and
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17 10 and 90 m. These two later additional depth shifts were used only for the offshore
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19 release areas due to the deeper water column to access the response in transport
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21 variability due to further depth shifts. In all DVM simulations individuals were assumed
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23 to have neutral buoyancy.
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32 *Assumptions*

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36 Because there are some current gaps in the knowledge of biological and
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38 oceanographic processes involved in chokka squid paralarval transport, a number of
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40 implicit and explicit assumptions were made in applying the models:
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- 45 • The resolution, forcing and topography employed in the SAfE model resulted in
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47 realistic circulation patterns;
- 48 • The subdivision of spawning grounds into six areas was adequate to capture the
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50 spatial variability of paralarval transport;
- 51 • The cold ridge is a permanent feature;
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53 • Paralarvae have a specific gravity of 1.048 g cm^{-3} ;
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- Diffusion and active horizontal swimming are negligible for paralarvae in the model;
- The planktonic phase ends after 40 d, because data recorded in rearing conditions shows that paralarvae are able to hold the position against a current at around this age (Yang *et al.*, 1986; Vidal *et al.*, 2009);
- The release of 5 000 particles per release area during each run was sufficient to ensure stability in the model outputs.

Modelled transport success

According to the WTH, the cold ridge is the nursery area for chokka squid paralarvae. Thus, ‘virtual paralarvae’ (particles) in the model were considered to have successfully been transported if (1) they were located in this area at the age of ≥ 3 d and (2) they were located between the surface and 80 m in the passive Lagrangian transport scenarios and ≤ 30 m in the DVM scenarios (hereafter referred to as depths of ‘recruitment’). The former depth of ‘recruitment’ criterion was based in test runs that showed that Lagrangian transport success was very sensitive to depth (data not show), whereas the later one (DVM) was chosen because in the real world the most suitable feeding environment for paralarvae are distributed throughout the top 30 m of the water column (Verheye *et al.*, 1994). Model outputs were analysed using orthogonal multifactor ANOVA that related the percentage of successfully transported individuals to a number of explanatory variables: release area, month, depth of ‘recruitment’ (which were different for Lagrangian and DVM scenarios, see above) and depth range of DVM. The factor ‘year’, although included in the simulations, was excluded from this analysis to avoid the risk of Type-I error (Underwood, 1997). Because the percentage success

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3 data were heteroscedastic, they were transformed using a $\log_{10}(x + 1)$ transformation.
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5 Normality of residuals was visually evaluated using quantile-quantile (Q-Q) plots and
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7 plots of mean and variance of residuals against observed values for each variable were
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9 also evaluated for trends.
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12 13 14 15 **Results**

16 17 18 19 *Overall patterns*

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24 Univariate analyses were used to investigate the roles of each explanatory
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26 variable and transport scenario in determining the success of transport to the cold ridge
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28 area, expressed as percentage of individuals reaching the cold ridge area at an age of ≥ 3
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30 d (Appendix 1). Transport success decreased from the release area in the west
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32 (Plettenberg-Tsitsikamma) to the east (Algoa Bay). There was little interannual
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34 variation in transport success for all transport scenarios and slight seasonality, with
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36 transport success generally reduced from April to July. The depth of arrival into the
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38 nursery area tended to occur between 10 and 50 m for inshore release of particles and
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40 between 20 and 80 m for offshore release. DVM apparently had a massive impact for
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42 particles released inshore. For instance, for the P-T_in release area, transport success
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44 increased from 24% for passive Lagrangian particles to nearly 89% for DVM-
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46 undergoing particles, and this pattern was consistently reflected in all other variables
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48 investigated (Appendix 1). DVM transport scenarios also had a significant impact for
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50 those particles released offshore, with transport success 4–5 times higher than for the
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52 passive Lagrangian scenario in the west-east release areas (Appendix 1). However,
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3 because the 'recruitment' depth criterion was different between Lagrangian and DVM
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5 simulations, these scenarios are not directly comparable.
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10 *Passive Lagrangian and specific gravity transport scenarios*

14 1. Inshore release areas

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20 Results of analyses of multiple factors affecting transport success of neutrally-
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22 buoyant particles are shown in Appendix 2. Of the three significant main effects,
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24 recruitment depth and release area together explained most of the variability, with a
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26 significant interaction between these two variables. In general, transport success tended
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28 to be greater for particles released in the P-T_in area than for the SF_in area, and those
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30 from the AB_in area had smallest transport success (Fig. 1a). Most of the particles
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32 reached the nursery area at 10 to 50 m depth (Fig. 1b), with shallow recruitment depths
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34 being more important for eastern than western release areas (Fig. 1c). There was a clear
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36 seasonality in transport success throughout the year (Fig. 1d), with smallest values in
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38 winter months (Fig. 1e).
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43 For transport success of passive particles with a specific gravity of 1.048 g cm^{-3} ,
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45 release area was the most important factor affecting variability, followed by the
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47 month \times recruitment depth interaction (Appendix 2). Most of the particles that
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49 successfully transported to the nursery area were the ones released from the P-T_in area
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51 (Fig. 3a), which partly overlaps with the cold ridge (Fig. 1). This indicates that there is
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53 more retention than transport in this scenario. Similar to the results for neutrally-
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55 buoyant particles, most of the successfully transported particles with a constant specific
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57 gravity were $< 50 \text{ m}$ deep (Fig. 3b), the recruitment depth \times release area interaction
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3 decreases from west to east and with depth (Fig. 3c) and there was a clear seasonality
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5 (Fig. 3d).
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10 2. Offshore release areas 11 12 13 14

15 The passive Lagrangian transport scenario for neutrally-buoyant particles
16 released offshore showed that release area and recruitment depth were the most
17 important factors, with the interaction between those two factors also being significant
18 (Appendix 2). In spite of the considerable variability, transport success for particles
19 released in P-T_off and SF_off was similar, followed by the AB_off release area (Fig.
20 4a). In terms of recruitment depth, most particles arriving in the nursery area were > 40
21 m deep (Fig 6b). Again, the recruitment depth×release area interaction was more
22 important for P-T_off than the remaining areas, increasing with depth (Fig. 4c). Overall
23 transport success showed a clear seasonality, with the lowest transport success observed
24 in autumn-winter months, and the highest transport success observed during spring-
25 summer (Appendix 1, Fig. 4d).
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41 Particles with a specific gravity of 1.048 g cm^{-3} had different factors affecting
42 transport success than neutrally buoyant particles. Month and recruitment depth were
43 the most important factors, followed by release area (Appendix 2). Transport success for
44 this scenario was higher for all parameters investigated in relation to their neutrally-
45 buoyant counterparts (Appendix 1). Transport success also decreased from west to east.
46 As for their neutrally-buoyant counterparts, transport success was similar for P-T_off
47 and SF_off release areas (Fig. 5a). Most particles arriving in the nursery area were > 40
48 m deep (Fig. 5b). The recruitment depth×release area (Fig. 3c) interaction was also
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3 similar to the situation found for neutrally-buoyant particles. There was a clear
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5 seasonality in transport success (Fig. 5d).
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10 *Diel vertical migration (DVM) transport scenarios*

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20 Most of the variability in transport success for the DVM transport scenario was
21 explained by release area (Appendix 2). Transport success decreased from west to east
22 (Fig. 6a). There was a weak seasonality (Fig. 6b).
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29 2. Offshore release areas

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34 Release area and month were also the most important factors affecting transport
35 success for the DVM scenario with offshore release, accounting for most of the variance
36 (Appendix 2). The three different DVM depth ranges explained little of the total
37 variance. As in all previous scenarios, transport success decreased from west to east
38 (Fig. 7a). There was no discernible seasonality in transport success (Fig. 7b). The 10–90
39 m DVM scenario yielded a slightly higher transport success than its shallower
40 counterparts (Fig. 7d).
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Discussion

Main findings and limitations

No biological characteristics other than specific gravity and DVM were assigned to the particles. The results therefore indicate the interaction of modelled circulation for different transport scenarios with biologically-mediated vertical position. This is a reasonable approach, because the average swimming velocity of paralarvae of several species, sizes and ages ranges from 0.003 to 0.25 m s⁻¹ (Zuev, 1964; Packard, 1969; O'Dor *et al.*, 1986; Villanueva *et al.*, 1997; Zeidberg, 2004; Vidal *et al.*, 2009), which is slower than typical horizontal current velocities (0.2–3.5 m s⁻¹) found on the Agulhas Bank (Roberts, 2005). Accordingly, at least some of the paralarval dispersal could be the result of passive transport within the current velocity field they are embedded in.

In this study, we simulated a suite of possible transport scenarios interacting with vertical shear in horizontal currents on the Agulhas Bank in order to address Roberts' (2005) WTH. A common feature among all transport scenarios simulated was that particles were transported mainly westward towards the cold ridge area, thus supporting the hypothesis. Nonetheless, it is important to recognize the weaknesses in the modelling approach adopted. First, the currently incomplete information on vertical and horizontal distributions of chokka squid paralarvae prevents validation of the results. A second important limitation is that entire populations of particles were transported at discrete depths in the DVM scenarios, whereas a real planktonic population would likely be distributed above and below a centre of gravity, introducing additional variability in the transport patterns (Leis, 2007). Finally, the time period chosen to represent the end of the planktonic period may not be realistic, as it has

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3 obtained under laboratory rearing conditions, and the capacity to become independent
4 from purely advective Lagrangian transport is likely more related to size than age (Vidal
5 *et al.*, 2009). Thus, this certainly is not a sudden event affecting equally whole cohorts
6 of heterogeneously-growing paralarvae.
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12 The substantial contribution of area of particle release to variability in transport
13 success in most modelled transport scenarios suggests that the location of the spawning
14 grounds favours successful paralarval transport, particularly for those sites located west
15 of Algoa Bay. This, in addition to appropriate bottom substrata for egg pod attachment,
16 water visibility conducive to mating and suitable environmental conditions for
17 embryonic development (Roberts and Sauer, 1994; Roberts, 1998; Oosthuizen *et al.*,
18 2002; Oosthuizen and Roberts, 2009), may partially explain why these areas are
19 repeatedly used every year by spawning chokka squid (Sauer *et al.*, 1992). This implies
20 that variability in adult spawning behaviour (i.e. birth site fidelity – ‘homing’) may be
21 more important than paralarval behaviour in determining paralarval transport success
22 (Edwards *et al.*, 2008).
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41 *Importance of upwelling in the modelled paralarval transport*

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46 Regardless of the transport scenario or release depth, the Plettenberg-
47 Tsitsikamma area had the greatest proportion of successfully transported particles
48 among all release areas. Whereas this may be explained by the partial overlap of this
49 area with the nursery area (cold ridge), transport success was greatest for particles
50 transported at the release depth. In contrast, the greatest transport success for the two
51 other release areas was for particles transported above the release depth. This was
52 reflected by the elevated importance of the release area × recruitment depth interaction in
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3 the passive Lagrangian transport scenarios. This result is consistent with particles
4 moving upwards, which suggests upwelling could be the mechanism underpinning this
5 pattern. In fact, both empirical and modelling studies have shown that coastal upwelling
6 is very common on the eastern Agulhas Bank (Schumann *et al.*, 1982; Lett *et al.*, 2006).
7
8 This may partially explain why relatively high loliginid paralarval concentrations are
9 often found during upwelling and uplifted thermocline events (Rocha *et al.*, 1999;
10 Zeidberg and Hamner, 2002; González *et al.*, 2005; Martins and Perez, 2006; Moreno *et*
11 *al.*, 2009).

22 23 24 *Specific gravity and the WTH*

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29 From a strictly Lagrangian perspective, assigning specific gravity of 1.048 g
30 cm⁻³ to the particles released inshore, making them denser than seawater, introduced a
31 major challenge to the WTH, as the retention in the release areas was elevated, with few
32 particles being transported to the cold ridge (except where the release area merge with
33 the nursery area). However, inshore productivity is relatively high in the study area
34 because of wind-driven intermittent upwelling (Shannon *et al.*, 1984; Probyn *et al.*,
35 1994; Lett *et al.*, 2006), sustaining an assorted plankton assemblage (Verheye *et al.*,
36 1994), which may provide food for paralarvae. Indeed, most chokka paralarvae sampled
37 thus far have been caught inshore, overlapping with the spawning grounds (Sauer, 1995;
38 Roberts and van den Berg, 2002). This suggests that the cold ridge might not be used as
39 a nursery ground by at least part of inshore spawned paralarvae.

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In the offshore release areas, in contrast, approximately 21.2% of the 1.048 g
cm⁻³ particles reached the nursery area between the surface and 30 m (Appendix 1),
where the bulk of the zooplankton (food) is present (Verheye *et al.*, 1994). This

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3 suggests that the transport success strategies for paralarvae hatched inshore and offshore
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5 could be different, with the later tending to use westward current transport (thus
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7 supporting the WTH) to take advantage of the enhanced productivity of the cold ridge.
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10 11 12 *Comparison with field data and other IBMs and implications for the life-cycle* 13 14

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17 Although these ROMS–IBM results support the WTH, across-shore field data
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19 have been either conflicting or consistent with the hypothesis. Close inshore (off the
20
21 Tsitsikamma coast), ADCP measurements and release of satellite-tracked drifters
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23 revealed a general eastward current flow and leakage of shelf waters into the open sea
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25 near the southern tip of the Agulhas Bank (Roberts and van den Berg, 2002, 2005,
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27 Hancke, 2010). However, drifters are poor simulacra of paralarvae, as they lack
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29 completely the behavioural component (Hare *et al.*, 2007). In addition, their trajectory
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31 can be affected by the roughness of the sea surface and wind conditions. Trajectories of
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33 drifters released offshore, on the other hand, were more similar to these ROMS–IBM
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35 results, suggesting that paralarvae hatched on the eastern Bank would likely be
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37 transported westwards and retained in the ecosystem near the cold ridge.
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44 A comparison of our data with the results of the first chokka squid ROMS–IBM
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46 study carried out by Roberts and Mullon (2010) showed important differences. Whereas
47
48 the transport was mostly westward in our simulations, their results suggest mostly
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50 eastward transport, regardless of the release position, with massive losses of particles to
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52 offshore waters. There are two possible reasons for this difference. (1) They used an
53
54 outdated ROMS model configuration (the PLUME; Penven *et al.*, 2001) with a smaller
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56 domain, which was therefore influenced by boundary effects, particularly on the eastern
57
58 Agulhas Bank, where the main spawning grounds are located (Parada *et al.*, 2003;
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3 Roberts and Mullon, 2010). (2) The previous study modelled the paralarvae as
4 neutrally-buoyant particles only, whereas specific gravity and DVM have been shown
5 here to be important factors determining transport trajectories on the shelf.
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10 Other ROMS–IBM studies have been carried out for anchovy (*Engraulis*
11 *encrasicolus*) and sardine (*Sardinops sagax*) in the southern Benguela, including the
12 Agulhas Bank. These also suggested the cold ridge area was important for recruitment
13 variability of these fish species (Parada *et al.*, 2003; Lett *et al.*, 2006; Miller *et al.*,
14 2006). However, the neutral buoyancy of clupeoid fish eggs and early yolk sac larvae
15 can result in huge advective losses of progeny to offshore waters, mainly on the outer
16 eastern Agulhas Bank (Boyd *et al.*, 1992; Roel *et al.*, 1994; Hutchings *et al.*, 2000;
17 Parada *et al.*, 2003). Those losses can be compensated by high fecundity typical of
18 clupeoid fish (Alheit, 1989; Hutchings *et al.*, 2000; Huggett *et al.*, 2003). In contrast,
19 paralarvae are negatively buoyant and this appears to help in their retention in
20 productive inshore areas and mitigates offshore losses (Martins *et al.*, 2010b). This can
21 partially account for the relative success of chokka squid as a species in a dynamic
22 ecosystem such as on the Agulhas Bank, even though their fecundity is considerably
23 lower than most of their fish competitors.
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46 *Food availability vs. transport*

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50 Extensive plankton surveys on the Agulhas Bank have shown that up to 100–
51 350 plankters L⁻¹ (mostly microcrustaceans) can be found in the chlorophyll maximum
52 layer associated with the thermocline, with most of the remaining planktonic biomass
53 distributed throughout the top 30 m of the water column (Verheye *et al.*, 1994; Roel
54 *et al.*, 1994). Therefore, zooplankton concentrations on the Agulhas Bank can approach
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3 (or even exceed) the minimum threshold feeding concentration (i.e. 50 prey L⁻¹; Vidal
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5 *et al.*, 2002) that allows loliginid paralarval survival and growth, at least in laboratory
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7 conditions.
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10 The criterion for transport success time in the present study was initially based
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12 on data from starvation and recovery experiments carried out with 15 d old *Doryteuthis*
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14 *opalescens*, where paralarvae were found to regain the before-starvation condition if fed
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16 after 3 d of food deprivation (Vidal *et al.*, 2006). Newly-hatched chokka squid
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18 paralarvae, however, can survive up to 1–4 d on their yolk reserves before entering in
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20 irreversible starvation, assuming an exponential yolk utilization rate and depending on
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22 the temperature (Martins *et al.*, 2010a). Complete absence of food, however, is probably
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24 not often the case in the wild. This implies that a demographically meaningful number
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26 of good condition paralarvae could reach the cold ridge area beyond the minimum ‘3 d
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28 deadline’. This would be particularly important for those individuals hatched further
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30 east, i.e., between Algoa Bay and Port Alfred.
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39 *DVM vs. Lagrangian transport scenarios*

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43 In other ROMS–IBM studies of larvae of different organisms, the value of
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45 vertical migration behaviour for larval transport has been (1) particularly important
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47 (Cowen *et al.*, 2006; North *et al.*, 2008), (2) only of secondary importance (Edwards *et*
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49 *al.*, 2008; Parada *et al.*, 2008) and (3) not important (Hare *et al.*, 1999) in relation to
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51 passive Lagrangian transport. Our results are similar to the second case, because
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53 although all DVM transport scenarios improved transport, they explained only a small
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55 amount of the total variance in the models. Nonetheless, transport success of particles
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57 undergoing DVM was much greater than for their passive Lagrangian counterparts for
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3 all variables investigated. This suggests that DVM could be a strategy adopted in the
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5 wild to influence transport to favourable areas.
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8 Although DVM behaviour resulted in enhanced transport success, most DVM-
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10 undergoing particles were transported off the Agulhas Bank and lost to the South
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12 Atlantic after 40 days of transport. This implies poor retention potential for paralarvae
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14 undergoing DVM behaviour on the Agulhas Bank (at least for the depth shifts simulated
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16 in the present study). However, paralarval swimming capability increases with age and
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18 size (Zeidberg, 2004; Vidal *et al.*, 2009) and thus 40-d old (or even younger, depending
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20 on their individual size) paralarvae might be able to use directed horizontal swimming
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22 to remain in the nursery area (cold ridge), as observed in fish larvae (Leis, 2006). Future
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24 modelling studies should investigate the effect of size (i.e. growth) rather than age as a
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26 criterion for transport success (see Miller *et al.*, 2006).
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34 *Transport success and recruitment*

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38 The overall annual average transport success from the release areas to the
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40 nursery area (cold ridge) ranged from 7.4% (worst case scenario, for Lagrangian
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42 transport of particles assigned 1.048 g cm^{-3} specific gravity released inshore) to 51%
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44 (best case scenario, for DVM-undergoing particles released inshore). Natural mortality
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46 of squid paralarvae appears to be much lower than for fish eggs and larvae (O'Dor,
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48 1998), even considering sources of mortality such as advective losses, predation,
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50 starvation and inappropriate environmental conditions. Therefore, it is likely that there
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52 would be sufficient individuals recruiting to the adult population, even in the worst case
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54 scenario. By comparison, a survival rate of only 0.002% of progeny is thought to be
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3 sufficient to maintain the equilibrium of the population of high-fecundity anchovy in the
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5 southern Benguela (Hutchings *et al.*, 1998).
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10 *Conclusions and future directions*

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15 This study represents a step towards predicting squid-stock abundance
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17 fluctuations by providing insights to some processes affecting the early life stages of
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19 chokka squid. The ROMS–IBM models are useful tools for investigating paralarval
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21 transport in the dynamic environment of the Agulhas Bank. Successful transport to the
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23 nursery area (cold ridge) seems to be affected by a number of factors. Although
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25 spawning location was found to be the most important, other factors such as upwelling,
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27 buoyancy of the paralarvae and DVM behaviour were also found to play a role in the
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29 variability of paralarval transport in the model. Upwelling can facilitate transport by
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31 moving paralarvae upwards and thus exposing them to faster surface currents. Specific
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33 gravity, on the other hand, can help retain paralarvae in the productive inshore areas,
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35 preventing offshore advective losses. Finally, DVM behaviour appears to optimize early
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37 transport by allowing paralarvae to take advantage of the vertically stratified flow field.
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43 Improved knowledge is required of the horizontal and vertical distributions,
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45 growth and the swimming abilities of chokka squid paralarvae to validate the results
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47 obtained in the present modelling study. Extensive plankton sampling efforts with
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49 Bongo nets, WP-2, MOCNESS multiple net and hyperbenthos samplers (Zeidberg and
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51 Hamner, 2002; Moreno *et al.*, 2009; Bouali *et al.*, 2009) should be carried out in the
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53 study area to compare the situation in the wild with the ROMS–IBM results. It is likely
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55 that horizontal and vertical distributions of early paralarvae probably coincide with, or
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57 are very close to, the egg beds. Our results suggest that this is the first place to search.
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Acknowledgements

Financial support for this study was provided by Bayworld Centre for Research and Education (BCRE), South African Squid Management Industrial Association (SASMIA) and the Brazilian National Research Council (CNPq – PROÁFRICA Program, Proc. n° 490554/2008-3). The first author was supported by a Brazilian Ministry of Education (CAPES) scholarship (BEX 2045/03-6). This work forms part of a South African–Brazilian–French scientific cooperation initiative.

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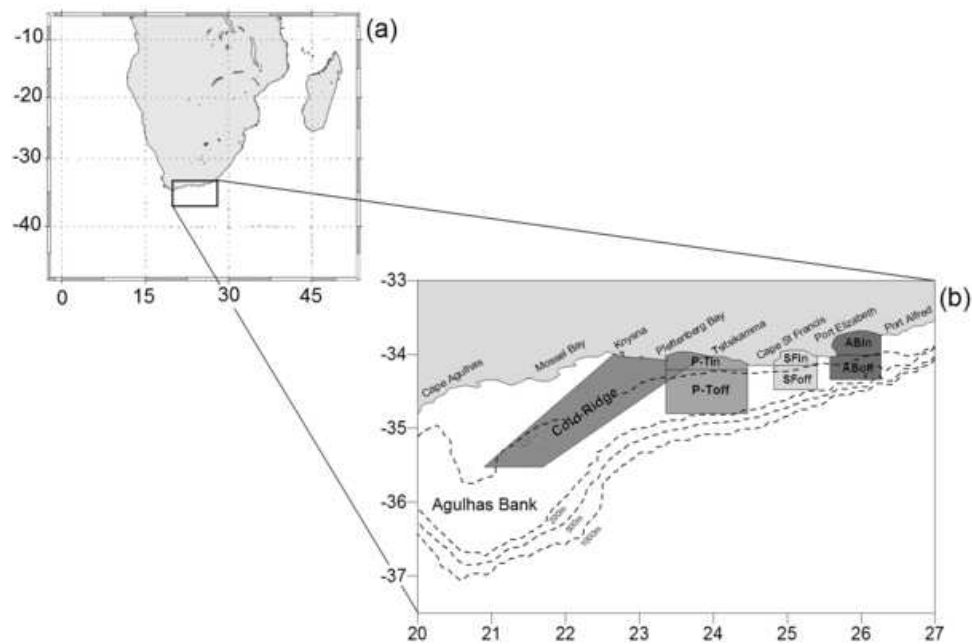


Fig. 1. (a) SAFE domain. (b) Study area off the south coast of South Africa showing the position of the cold ridge and the release areas. P-T_in: Plettenberg-Tsitsikamma inshore, P-T_off: Plettenberg-Tsitsikamma offshore, SF_in: St Francis inshore, SF_off: St Francis offshore, AB_in: Algoa Bay inshore, AB_off: Algoa Bay offshore.
53x35mm (300 x 300 DPI)

Review

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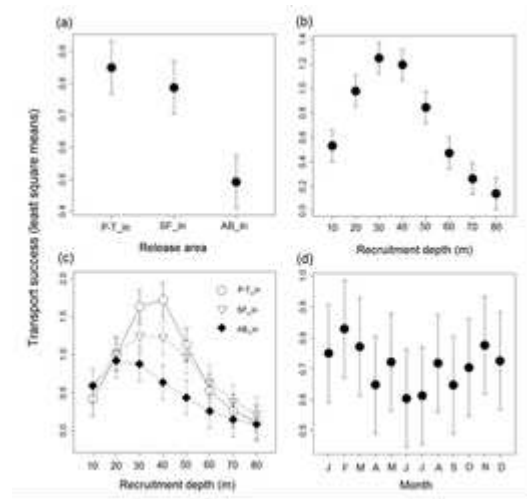


Fig. 2. Simulation results showing transport success for neutrally buoyant passive particles released inshore. The least squares means (\pm 95% C.I.) are shown for different effects and interactions: (a) release area, (b) recruitment depth, (c) release area \times recruitment depth interaction and (d) month.

22x20mm (300 \times 300 DPI)

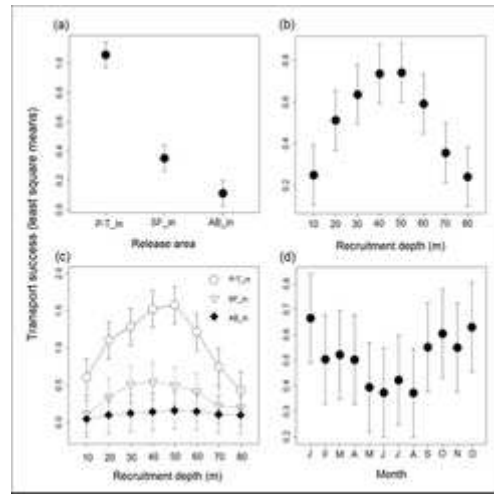


Fig. 3. Simulation results showing transport success for 1.048 g cm⁻³ passive particles released inshore. The least squares means (\pm 95% C.I.) are shown for different effects and interactions: (a) release area, (b) recruitment depth, (c) release area \times recruitment depth interaction and (d) month.

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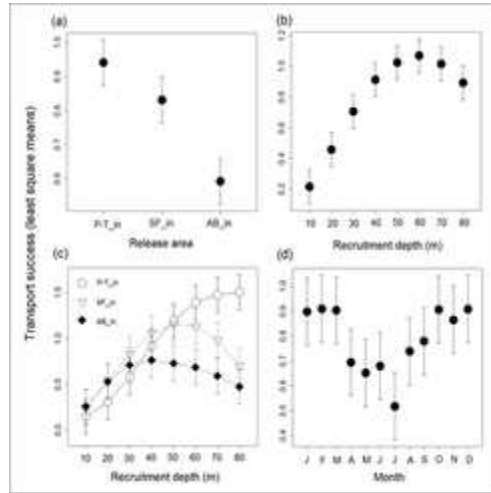


Fig. 4. Simulation results showing transport success for neutrally buoyant passive particles released offshore. The least squares means (\pm 95% C.I.) are shown for different effects and interactions: (a) release area, (b) recruitment depth, (c) release area \times recruitment depth interaction and (d) month.

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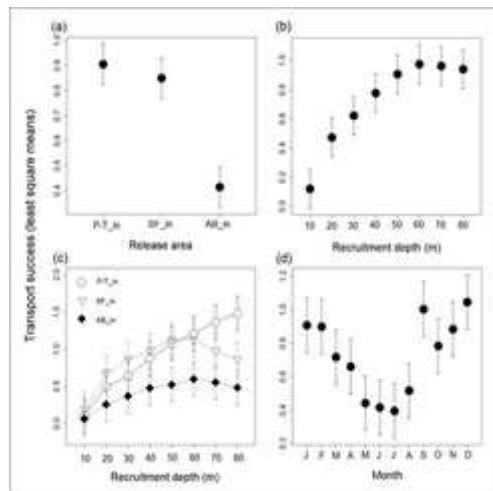


Fig. 5. Simulation results showing transport success for 1.048 g cm⁻³ passive particles released offshore. The least squares means (\pm 95% C.I.) are shown for different effects and interactions: (a) release area, (b) recruitment depth, (c) release area \times recruitment depth interaction and (d) month.

20x20mm (300 x 300 DPI)

Peer Review

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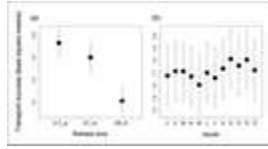


Fig. 6. Simulation results showing transport success for neutrally-buoyant particles released offshore and undergoing DVM. The least squares means (\pm 95% C.I.) are shown for different effects and interactions: (a) release area and (b) month.
11x6mm (300 x 300 DPI)

For Peer Review

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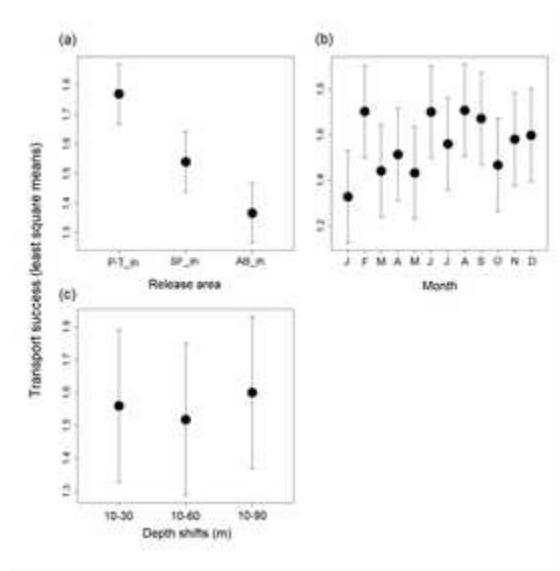


Fig. 7. Simulation results showing transport success for neutrally-buoyant particles released offshore and undergoing DVM. The least squares means (\pm 95% C.I.) are shown for different effects and interactions: (a) release area, (b) month, and (c) DVM scenario.
23x24mm (300 x 300 DPI)