

1 Running head: Larval transport modeling

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3 Natal retention mediated by diel vertical migration:
4 Larval transport modeling in the Hawaiian Archipelago
5 with layered current fields¹

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24 **Keywords:** Recruitment; Settlement; Metapopulation; Connectivity; Simulation

26 **Abstract**

27 Lagrangian transport modeling was used to simulate the effects of diel vertical migration in
28 selected areas of the Hawaiian Archipelago. Shallow and deep current fields were used in a factorial
29 design to examine the effects of year, month, release site, pelagic larval duration, and a measure of diel
30 vertical migration behavior. Generalized additive modeling was used to evaluate the effects of diel
31 vertical migration on retention. The results showed that diel vertical migration, i.e. intermediate
32 residency in both current strata, could enhance natal retention in pelagic larvae. This finding was
33 robust over a range of conditions. This study provides quantitative evidence that diel vertical migration
34 could be an adaptive mechanism to enhance natal retention and thereby minimize advective propagule
35 losses in a patchily distributed metapopulation structure.

36
37 **Introduction**

38 The distributions of marine pelagic larvae are often found to be heterogeneous over time and
39 space. Spatial distributions are manifested in both horizontal and vertical patterns (Ahlstrom, 1959;
40 Leis and Miller, 1976). Vertical patterning in the water column is often related to diel vertical
41 migration (henceforth DVM), whereby organisms change their vertical position in some repeatable
42 pattern over a 24-hour time period. DVM is a phenomenon that is first observed in the deep scattering
43 layers of the ocean and involves pelagic species such as euphausiids and myctophids (Johnson, 1948).
44 Further studies have shown that meroplanktonic organisms display DVM as well (e.g., Rawlinson et
45 al., 2004). DVM has been observed in both marine and freshwater ecosystems and is exhibited by a
46 wide variety of taxa and life-history stages. The proximate mechanisms for DVM are relatively well
47 understood, e.g., responses to light levels, sensory/orientation capability, swimming ability, and
48 buoyancy regulation. In contrast, the ultimate, i.e., underlying selective advantages, are less
49 understood, but are thought to be related to issues such as predator avoidance (Bollens and Frost,
50 1989), prey capture (Sims et al., 2005), metabolic advantages (Winder et al., 2003), and horizontal

51 retention/transport (Smith et al., 2001). This last category of horizontal movement mediated by DVM
52 is of particular interest to meroplanktonic larvae of coastal or insular species, because suitable habitat
53 for settlement is geographically restricted. The type of vertical current shear (differential movement of
54 adjacent water layers) required for this to take place is frequently observed in the field (e.g., Firing,
55 1996) or predicted in ocean circulation models for a particular time and space, yet this alone does not
56 ensure that DVM is robustly associated with retention since each larval propagule occupies portions of
57 a large window of time and space over the course of its trajectory. Larval connectivity and retention
58 are key issues for species with patchy adult habitats, i.e., metapopulations. There are a large number of
59 such geographically separated islands, coral atolls, seamounts, and banks throughout the Hawaiian
60 Archipelago (Fig. 1). Most of the benthic or island-associated species in this region do not routinely
61 cross the large expanses of deep ocean between habitats as adults; however pelagic egg and larval
62 stages can easily traverse these boundaries and even longer distances (Robertson et al., 2004). Despite
63 the importance of these early life history stage towards understanding population dynamics and
64 effectively managing these species or areas (e.g., Crowder et al., 2000; Valles et al., 2001), larval
65 connectivity in this region is relatively unknown. Such information will also be extremely important
66 towards understanding the impact of the Papahānaumokuākea Marine National Monument¹ which was
67 recently established in the archipelago. The purpose of this study is to examine the effect of DVM on
68 pelagic larval natal retention in the Hawaiian Islands using computer simulation and high-resolution
69 ocean current data.

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Materials and Methods

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Surface currents used in this study were monthly (January 1993 through December 2003) 0.5°
x 0.5° latitude/longitude resolution gridded flow fields from the Ocean Surface Current Analyses—
Real Time (OSCAR) project at NOAA Earth and Space Research, henceforth referred to as OSCAR

¹ June 15, 2006 proclamation by President George W. Bush.

75 currents. These surface flow fields are a composite of altimetry-derived geostrophic components and
76 satellite-derived wind components, tuned to 15-m depth drogue trajectories; thusly capturing both the
77 large-scale geostrophic motion as well as the surface, wind-driven, Ekman transport. This approach is
78 documented in Lagerloef et al. (1999). Deep currents used in this study were monthly (January 1993
79 through December 2003) 0.5° x 0.5° latitude/longitude resolution gridded geostrophic flow fields
80 calculated from satellite altimetry obtained from CNES/AVISO/SSALTO (CLS Space Oceanography
81 Division, France), henceforth referred to as AVISO currents. The AVISO currents come from the next
82 generation of satellite altimeters, such as JASON-1, which replaced the earlier TOPEX/Poseidon
83 satellite altimeters. Geostrophic currents typically represent large-scale water movement throughout
84 the mixed layer in the Hawaii region ranging from 30-m to 100-m depths depending on the season and
85 location (Flament et al., 1998). The OSCAR and AVISO currents were simultaneously applied in the
86 larval transport simulation by allowing individual larvae to differentially access the two strata and
87 mimic the consequences of DVM.

88 Larvae movement was simulated using the individual-based, lagrangian techniques outlined in
89 Polovina et al. (1999). These techniques are also known as biased random-walk models (e.g., Codling
90 et al, 2004). The modeling uses a daily time step while accessing the monthly current fields for the
91 nearest pixel of data. Operationally, the location of individual larvae in Cartesian space was calculated
92 with the following equations:

$$93 \quad \begin{aligned} x_{t+\Delta t} &= x_t + \left[u_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t} \right] / \cos(y_t) \\ y_{t+\Delta t} &= y_t + \left[v_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t} \right] \end{aligned}$$

94 where x represents longitude, y represents latitude, t represents time in days, u represents the zonal
95 East-West component of the current speed, v represents the meridional North-South component of the
96 current speed, $\cos(y_t)$ adjusts distance by latitude to account for the spherical coordinate system, and

97 D is the diffusivity coefficient ($500 \text{ m}^2 \text{ sec}^{-1}$). Simulated larvae at the end of their pelagic larval
98 duration (PLD) and in the 140 km radius of a suitable habitat were scored as settled. Orientation and
99 horizontal swimming were not part of the model structure, nor was the capability of early or delayed
100 settlement. A factorial experimental design was applied (Table I) to examine the results of the five
101 following different categorical effects. (1) Interannual variability was examined by releasing larvae
102 from 1993 to 2002, with releases in 2002 extending into 2003 depending on the PLD. (2) Uniform
103 releases were conducted over the 12 months of each year to examine seasonal effects. (3) Release sites
104 were chosen along the Hawaiian Archipelago, including Midway Island, Maro Reef, Necker Island,
105 Oahu, and Johnston Atoll (Fig. 1). (4) PLDs ranging from 1 month to 12 months were examined,
106 which brackets most of the known PLDs of vertebrate and invertebrate species in the region., (5) The
107 vertical occupancy index (VOI), a measure of DVM, was used to quantify the differential use of
108 vertical current strata. The VOI is a simple linear measure of shallow vs. deep exposure to respective
109 currents. Therefore, a VOI of 1 signifies exposure exclusively to shallow OSCAR currents, and a VOI
110 of 5 signifies exposure exclusively to deep AVISO currents. The intermediate VOI levels of 2, 3, and 4
111 signify 75%:25%, 50%:50%, and 25%:75% of shallow:deep exposure, respectively. The intermediate
112 VOI values were intended to simulate DVM, i.e., some manner of active swimming or buoyancy
113 control to vertically navigate to a different current stratum. In all, there were 10 release years, 12
114 release months, 5 release sites, 4 PLDs, and 5 VOIs. For each combination of the five effects (12000
115 unique sets), 500 larvae were released and individually tracked. Natal retention was scored if the larva
116 was within the 140-km radius around the release site at the end of the PLD. Average retention was
117 tabulated for each suite of values within each potential effect. Generalized additive models (GAMs,
118 Hastie and Tibshirani, 1990) were used to further delineate relationships between retention and the
119 examined variables. GAMs have been shown to be useful tools for understanding patterns in simulated
120 larval retention and transport (Kobayashi and Polovina, 2006). Mapping of spatial distributions was
121 performed using the software package called Generic Mapping Tools (Wessel and Smith, 1998).

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Results

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Nonzero retention was observed in 75% of the strata examined (9016 out of 12000 total combinations). Retention varied from 0 to 500 (100% retention observed in 13 strata). Across all strata, retention averaged 17% (86.35 larvae retained out of 500 total). Retention appeared to be related to all experimental factors in the simulation.

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Discussion

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The findings of this analysis indicate that a relatively simple oceanographic mechanism can be related to retention, which could be utilized by the appropriate behavioral or physiological adaptations. Such adaptations would be more energy efficient than having to traverse great horizontal distances or swim against an unfavorable current. This notion of “efficient swimming” (Armstrong, 2001) to save energy, time, or any resource in limited supply is critically important towards understanding survival

147 strategies and adaptations in the multi-dimensional pelagic environment. Even miniscule survival
148 advantages can translate into a plausible mechanism for selective pressure to influence appropriate
149 adaptations over evolutionary time. Vertical current shear has been observed in the Hawaiian
150 Archipelago (Firing, 1996) and elsewhere (e.g., Tomczak et al., 2004).

151 Bartsch (1988), Armsworth (2001), Cowen (2002), and others have discussed or theoretically
152 shown the possibility of larvae using different vertical strata to affect horizontal position. However,
153 empirical evidence is scant. Smith et al. (2001) and Emsley et al. (2005) showed that DVM-mediated
154 horizontal transport for zooplankton was a plausible mechanism to explain observed population
155 abundance dynamics. Cowen et al. (2003) showed that adding active larval orientation in the vertical
156 plane was necessary for their simulations to match field observations of fish recruitment dynamics.
157 Roughan et al. (2005) suggested that crab larvae exhibiting DVM in the lee of a peninsula could be
158 retained by current shear associated with wind-driven flow. Presently, DVM in insular fish species is
159 poorly understood because of extreme rarity in samples and/or sampling difficulties. Some of the more
160 extensive reef fish larval surveys using stratified sampling (e.g., Boehlert et al., 1992; Leis, 1991;
161 2004) showed much variability in depth distribution in both early-stage and late-stage reef fish larvae;
162 in both stages, pronounced interspecific variability was shown, as well as changes over small
163 geographic scales. However, because DVM has been well documented in a variety of zooplankton
164 taxa, it is logical to assume that similar selective advantages would also apply to fish larvae. With the
165 advent of better sampling devices and *in-situ* observations (e.g., De Robertis and Ohman, 1999), it will
166 be useful to explore DVM in a wider range of insular and pelagic fish species.

167 This study showed the apparent, low retention rates around Johnston Atoll, a region considered
168 to be an important biogeographic stepping stone for colonization of the Hawaiian Archipelago, as well
169 as for reverse transport towards the Indo-West Pacific (Mundy, 2005). Larval transport corridors
170 between Johnston Atoll and the Hawaiian Archipelago have been documented using computer
171 simulation (Kobayashi, 2006). While such corridors may be important for population maintenance at

172 this remote location, it is plausible that DVM-mediated retention may be particularly important in such
173 an isolated location for species unable to complete the long-distance transport.

174 The simulations in this study examined the potential role of DVM as it relates to horizontal
175 retention. This requires active or passive depth control on hourly time scales. Another type of vertical
176 migration may occur more slowly over the course of an organism's development, for example starting
177 at a shallow depth when young then progressively moving deeper as the organism develops, or vice
178 versa. This is similar to DVM but will have different consequences because of the spatial and temporal
179 dynamics of the current fields. Stenevik et al. (2003) have shown that sardine larvae can enhance their
180 retention by exhibiting stage-specific vertical distribution. Paris and Cowen (2004) suggested that such
181 ontogenetic vertical migration (OVM) manifested as a downward migration trend, coincident with
182 development in damselfish larvae, could be a mechanism for enhanced retention in the Caribbean.
183 More studies are needed, particularly on species with pelagic eggs, to document the locations of egg
184 release, egg stage duration, and buoyancy profiles. These potential effects of OVM on horizontal
185 transport in the Hawaiian region will be examined in a forthcoming study.

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189 versions of this manuscript.

190

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Table Legends

307 Table I. Summary of factors examined in simulated spawning releases. For each unique combination of
308 the five factors (total = 12000), 500 simulated larvae were released and tracked, and natal retention
309 tabulated.

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Figure Legends

312 Fig. 1. Location of release sites in the Hawaiian Archipelago. Stars indicate positions of Midway
313 Island, Maro Reef, Necker Island, Oahu, and Johnston Atoll, from North to South, respectively.

314 Contours are shown at 2000 fathoms using the Smith and Sandwell (1997) bathymetric database.

315

316 Fig. 2. Average larval retention rate as a function of larval release year across all simulation. Error bars
317 indicate 95% parametric confidence bounds.

318

319 Fig. 3. Average larval retention rate as a function of larval release month across all simulation. Error
320 bars indicate 95% parametric confidence bounds.

321

322 Fig. 4. Average larval retention rate as a function of larval release site across all simulation. Error bars
323 indicate 95% parametric confidence bounds.

324

325 Fig. 5. Average larval retention rate as a function of pelagic larval duration across all simulation. Error
326 bars indicate 95% parametric confidence bounds.

327

328 Fig. 6. Average larval retention rate as a function of larval vertical occupancy index across all
329 simulation. Error bars indicate 95% parametric confidence bounds.

330

331 Fig. 7. Additive component of vertical occupancy index (VOI) towards retention using generalized
332 additive models on subsets of data defined by common pelagic larval durations (PLDs) or release sites.
333 Confidence bounds represent ± 2 standard errors.

334

335 Fig. 8. Additive component of vertical occupancy index (VOI) towards retention using generalized
336 additive models on all data pooled. Confidence bounds represent ± 2 standard errors.

337

338 Fig. 9. Example larval spatial distributions after 90-day PLD from a June 1998 spawning at Necker
339 Island for either a shallow (upper), mixed shallow and deep (middle), or deep (lower) configuration.
340 The stars denote the location of the release site Necker Island.

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348 Table I.

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Year (<i>n</i> = 10)	Month (<i>n</i> = 12)	Site (<i>n</i> = 5)	PLD ^a (<i>n</i> = 4)	VOI ^b (<i>n</i> = 5)
1993	January	Midway	1 month	1 (100% shallow, 0% deep)
1994	February	Maro	3 months	2 (75% shallow, 25% deep)
1995	March	Necker	6 months	3 (50% shallow, 50% deep)
1996	April	Oahu	12 months	4 (25% shallow, 75% deep)
1997	May	Johnston		5 (0% shallow, 100% deep)
1998	June			
1999	July			
2000	August			
2001	September			
2002	October			
	November			
	December			

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351 Notes:

352 ^a Pelagic larval duration.

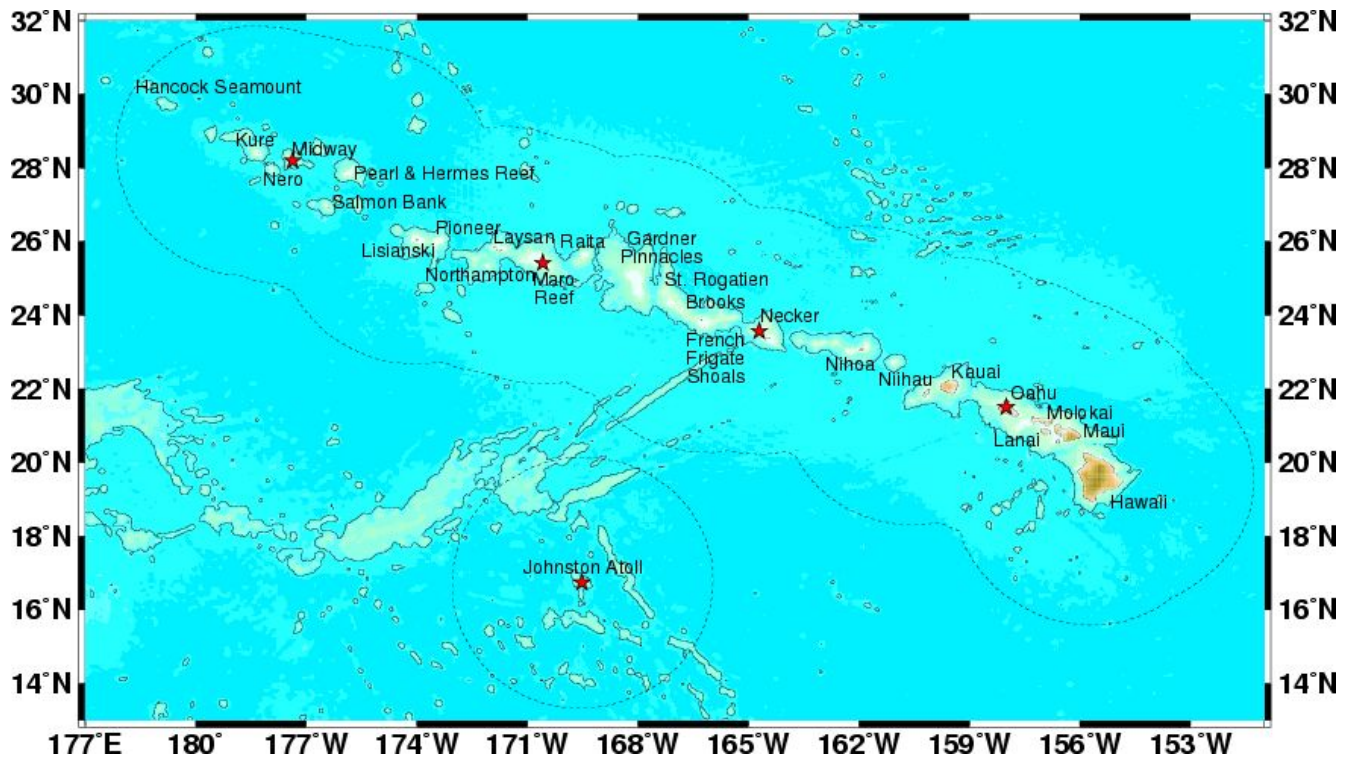
353 ^b Vertical occupancy index.

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357 Figure 1.



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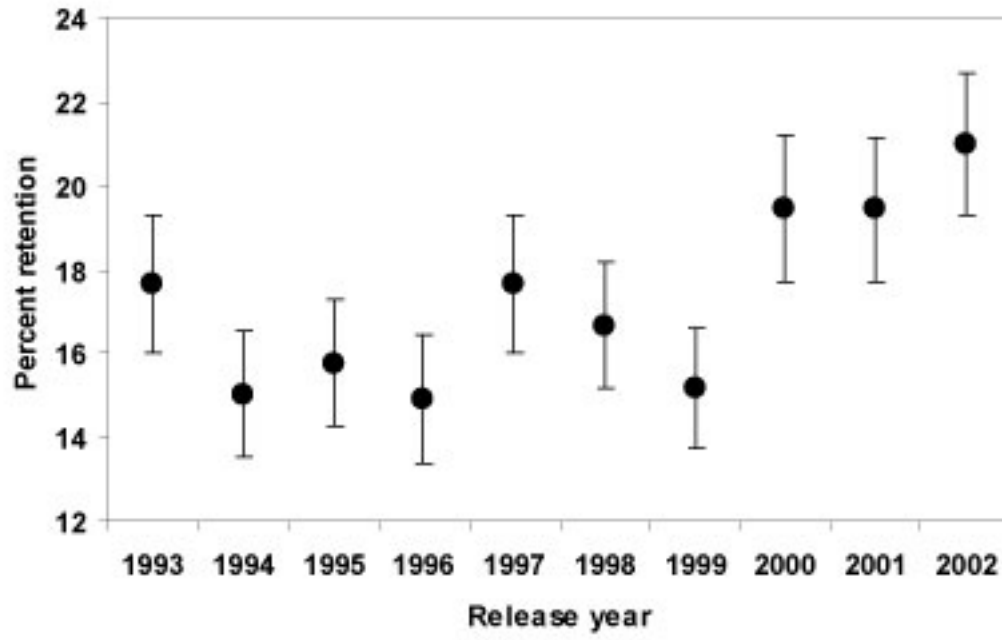
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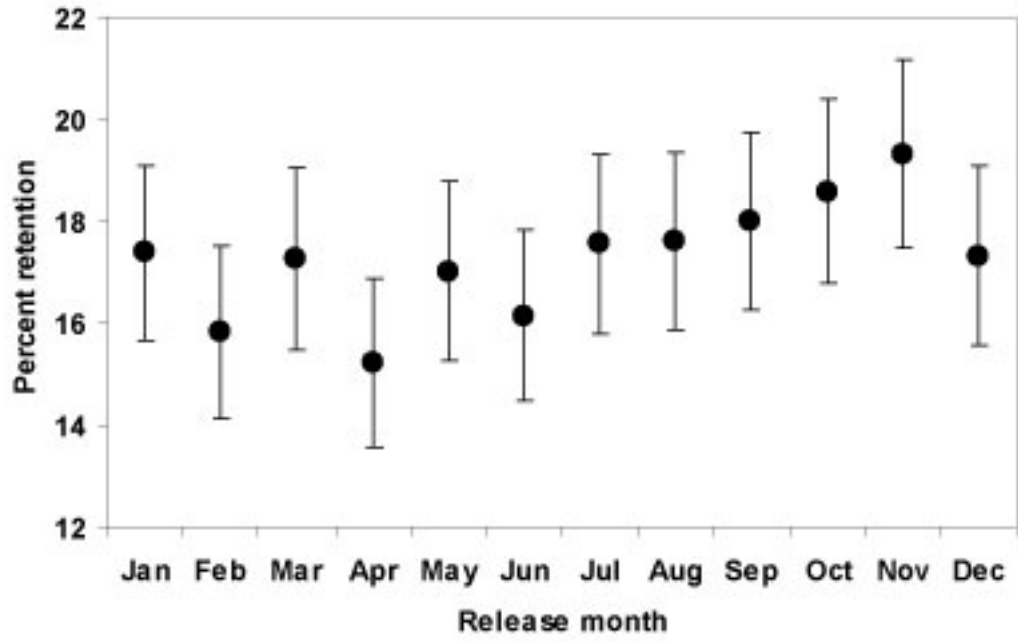
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387 Figure 3.



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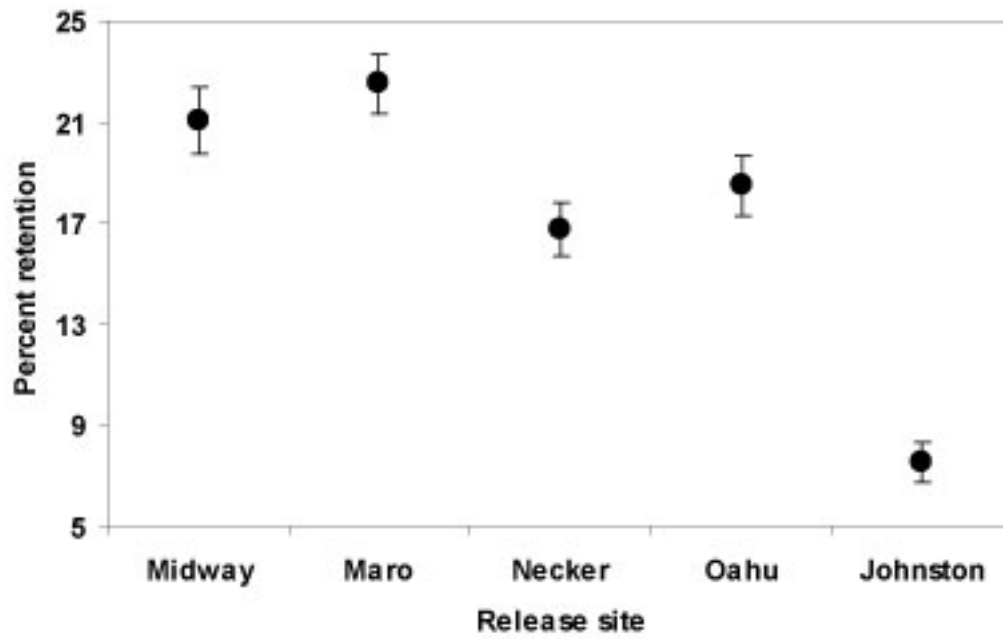
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402 Figure 4.



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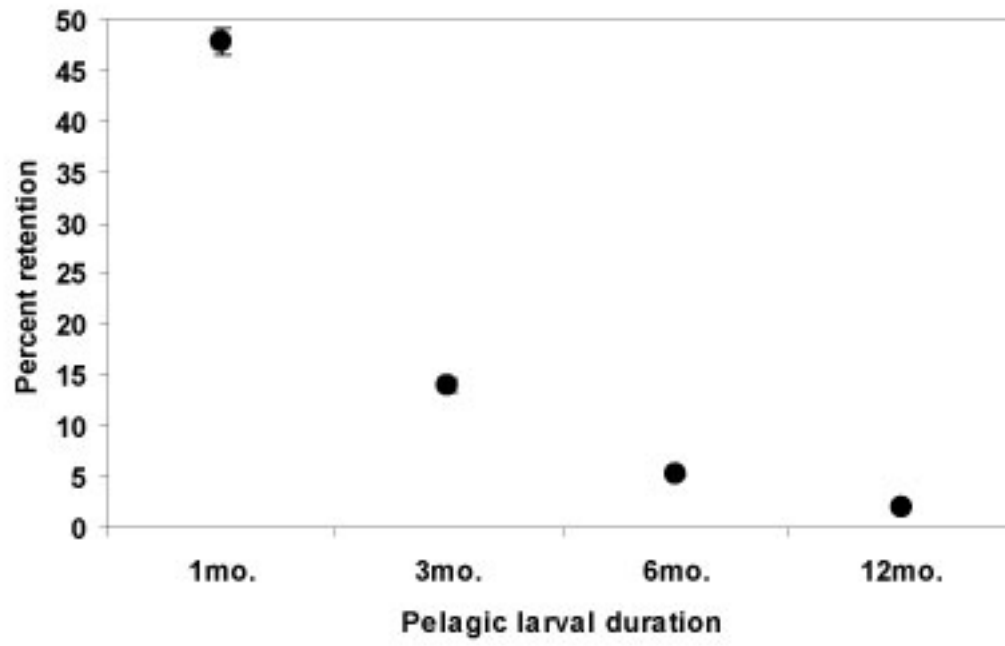
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417 Figure 5.



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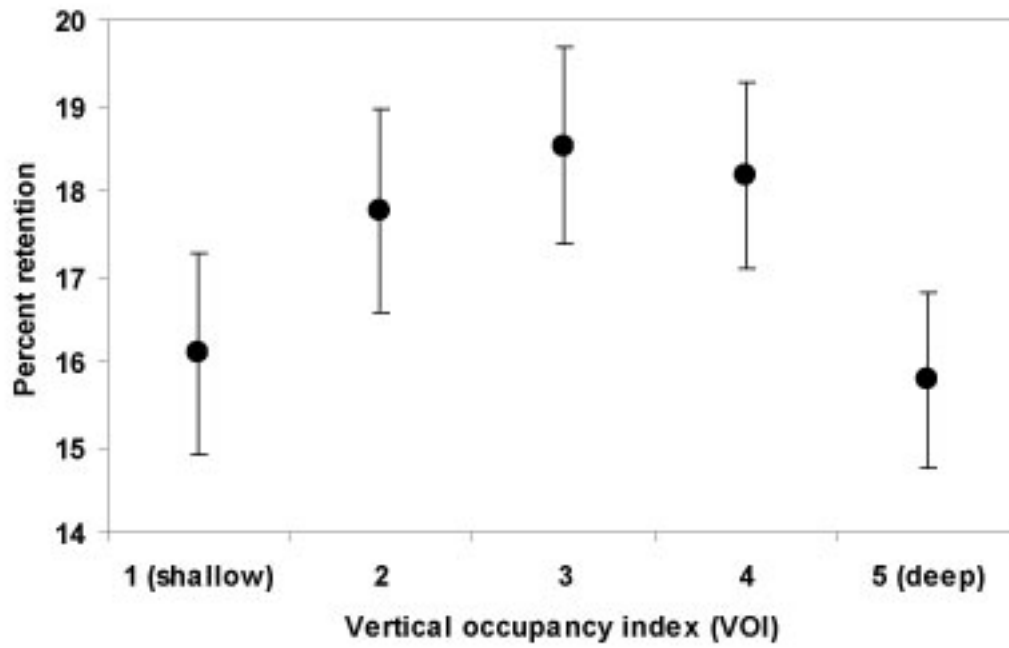
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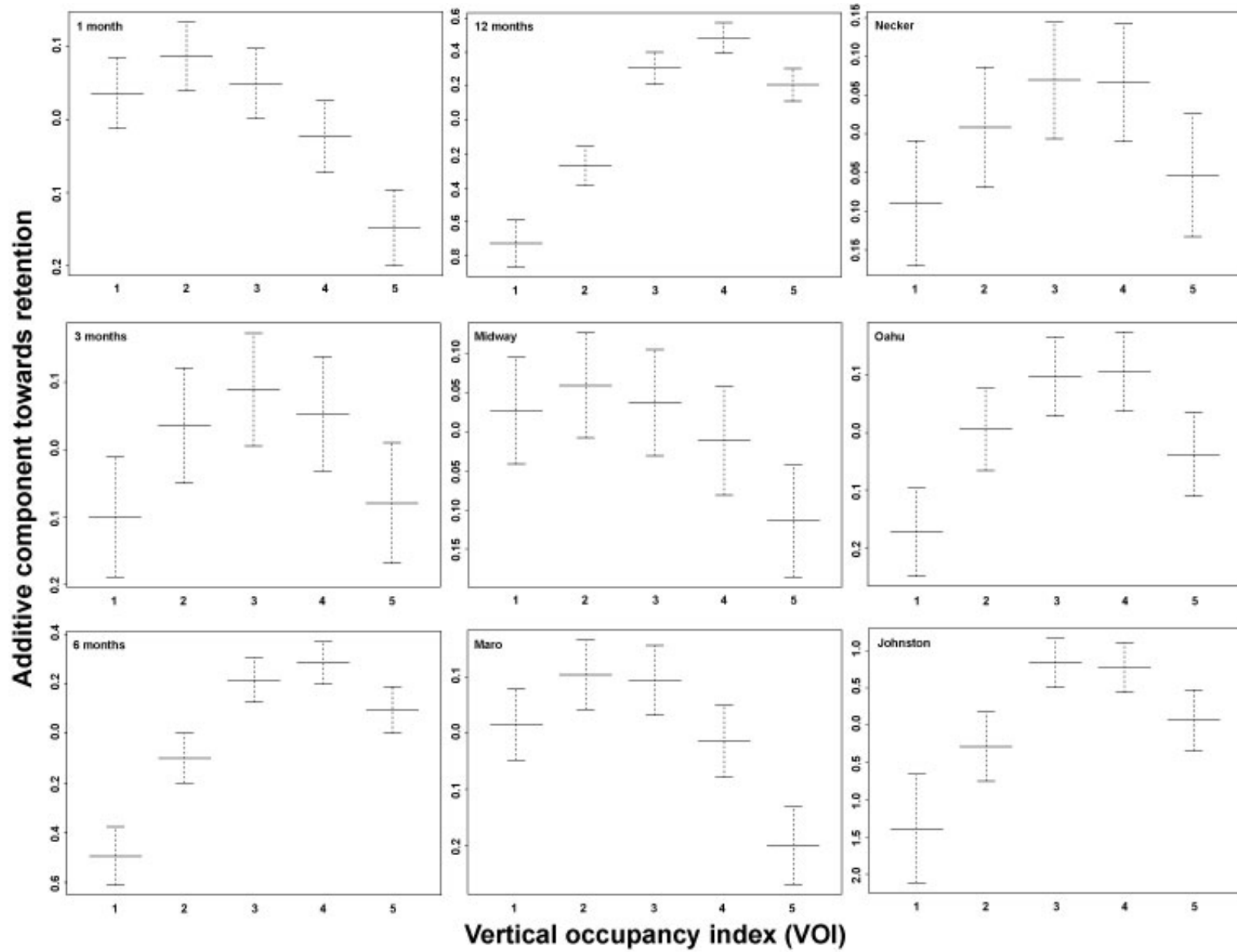
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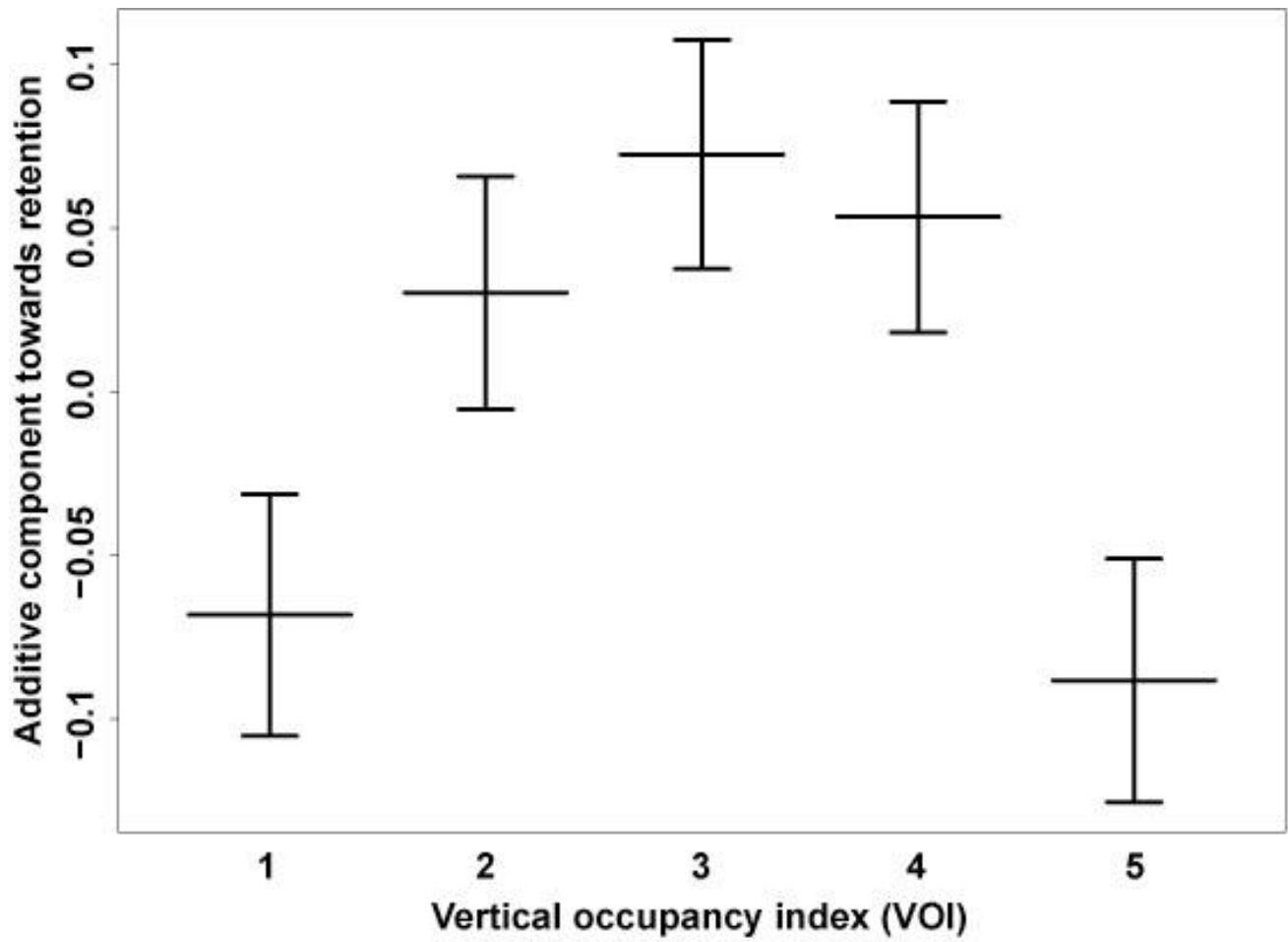
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447 Figure 7.



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449 Figure 8.



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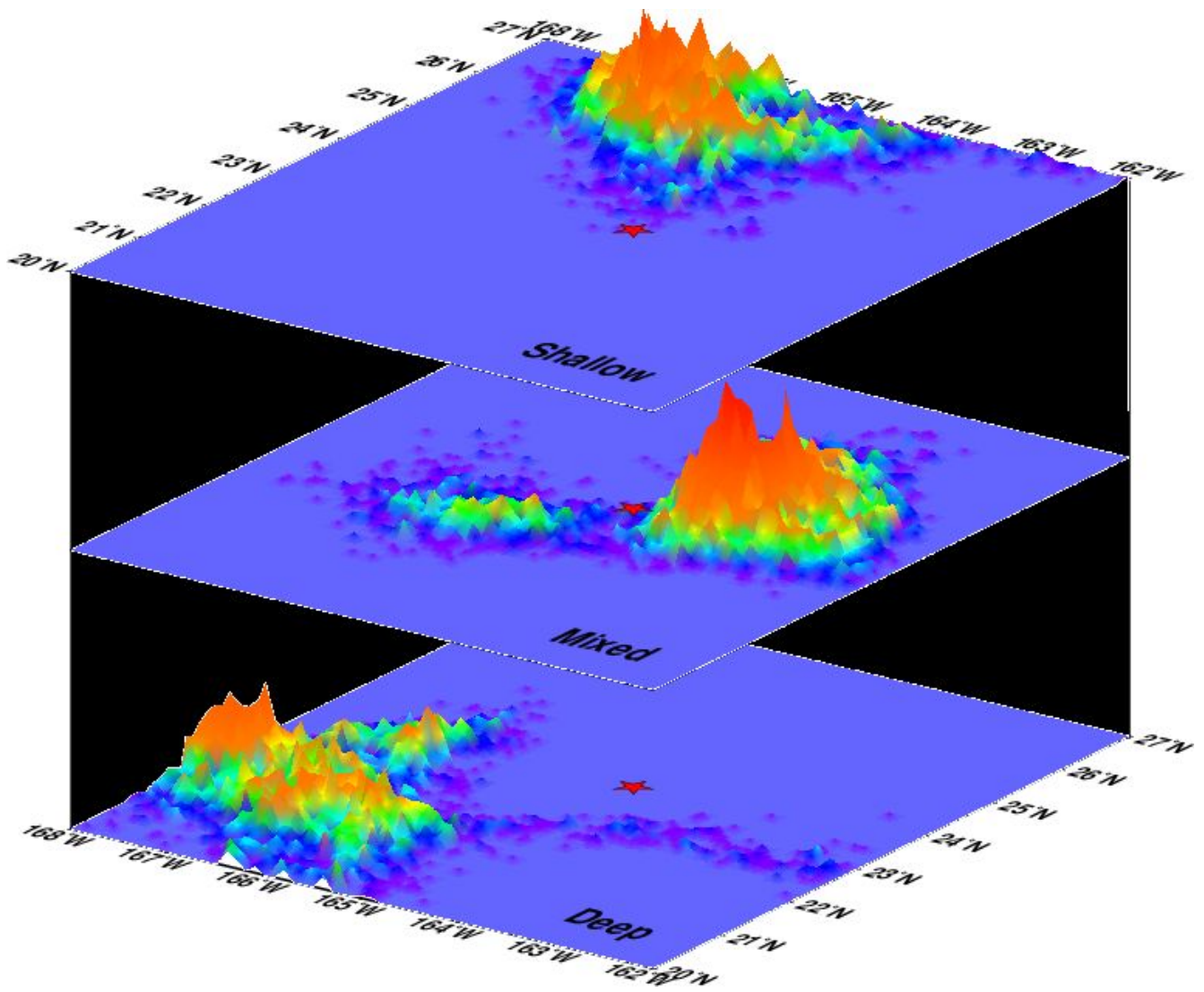
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461 Figure 9.



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