REPORT

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Colonization of the Hawaiian Archipelago via Johnston Atoll: a characterization of oceanographic transport corridors for pelagic larvae using computer simulation

Abstract Larval transport between Johnston Atoll and the Hawaiian Archipelago was examined using computer simulation and high-resolution ocean current data. The effects of pelagic larval duration and spawning seasonality on long-distance transport and local retention were examined using a Lagrangian, individual-based approach. Retention around Johnston Atoll appeared to be low, and there appeared to be seasonal effects on both retention and dispersal. Potential larval transport corridors between Johnston Atoll and the Hawaiian Archipelago were charted. One corridor connects Johnston Atoll with the middle portion of the Hawaiian Archipelago in the vicinity of French Frigate Shoals. Another corridor connects Johnston Atoll with the lower inhabited islands in the vicinity of Kauai. Transport appears to be related to the subtropical countercurrent and the Hawaiian Lee countercurrent, both located to the west of the archipelago and flowing to the east. A new analytical tool, termed CONREC–IRC is presented for the quantification of spatial patterns.

Keywords Oceanography · Settlement · Recruitment · Metapopulation · Dispersal · Retention

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Introduction

Johnston Atoll is an extremely isolated coral atoll at 16°45′N, 169°31′W, approximately 1,325 km southwest of the Hawaiian Island of Oahu (Fig. 1). The nearest island, French Frigate Shoals, in the middle of the Hawaiian Archipelago, is 865 km to the north–northeast, and Kingman Reef in the northernmost portion of the Line Islands is 1,385 km to the southeast. The fauna of Johnston Atoll is relatively well documented (e.g., Kosaki et al. 1991; Lobel 2003), with biogeographic ties to both the Hawaiian Islands and the Line Islands (Springer 1982; Robertson et al. 2004; Mundy 2005), and has a relatively low rate of endemism.

Several, recent scientific findings across a wide group of taxa have given rise to compelling evidence that Johnston Atoll is a stepping stone to species colonization in the Hawaiian Archipelago. A genetics study of the Hawaiian grouper, *Epinephelus quernus*, has shown that the greatest genetic diversity of this species occurs in the middle of the Hawaiian Archipelago (Rivera et al. 2004). Based on this spatial pattern, it was hypothesized that *E. quernus* colonized the archipelago via Johnston Atoll and subsequently radiated to the north and south portions of the archipelago. Corals of the genus *Acropora* in and around the Hawaiian Archipelago have been the subject of extensive biogeographic study (Grigg 1981; Grigg et al. 1981). Despite the ability of *Acropora* to reproduce in the Hawaiian Archipelago (Kenyon 1992), it is thought that *Acropora* initially arrived and may be primarily maintained by long-distance larval transport from Johnston Atoll. This is based on the distribution and abundance of adult colonies. These spatial patterns and likely colonization routes are also exhibited by other coral species, such as *Montipora tuberculosa* (Maragos et al. 2004). Recent genetics work on vermetid gastropods has also yielded evidence of a Johnston Atoll link for the colonization pathway of these species (Faucci, personal communication). These findings suggest that
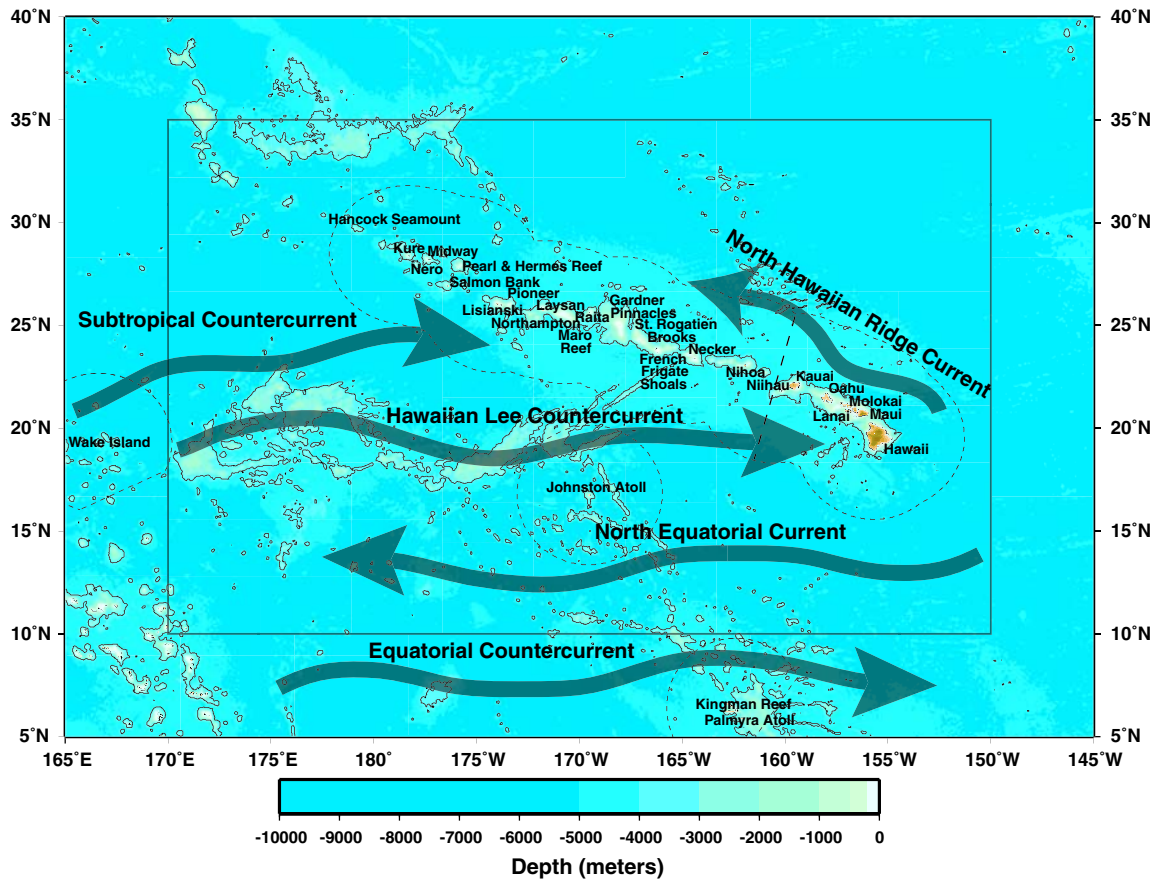
Fig. 1 Reference map of study area and general pattern of surface currents. *Circular and oblong dashed lines* represent US Exclusive Economic Zone. *Straight dashed line* represents boundary between Northwestern Hawaiian Islands (NWHI) and Main Hawaiian Islands (MHI). *Solid interior rectangle* denotes data grid for NLOM ocean current data

long-distance, pelagic larval transport from Johnston Atoll may be biogeographically significant and, at least for the corals mentioned above, may additionally be important for present-day population maintenance in the Hawaiian Archipelago. Both the transporting of pelagic propagules and rafting of benthic organisms (Jokiel 1989) may be important in dispersal, and these mechanisms depend critically on the spatial and temporal patterns in the local oceanography. The purpose of this analysis was to address the following two questions based on computer simulation and high-resolution ocean current data: (1) can larvae reach the Hawaiian Archipelago from Johnston Atoll, and how is this related to larval duration and spawning season? (2) Are there identifiable larval pathways for such long-distance transport so that certain parts of the archipelago are more likely to receive Johnston Atoll propagules?

Materials and methods

Ocean current data

The US Naval Research Laboratory (NRL) operates a global, six-layered ocean model at a resolution of 1/16°

(0.0625°) latitude by 45/512° (0.0879°) longitude (Rhodes et al. 2002; Wallcraft et al. 2003). This mesoscale model, henceforth termed NLOM, is eddy-resolving and thermodynamic; the density structure of the modeled ocean can be modified by physical processes. The NLOM is atmospherically forced using data from the Navy Operational Global Atmospheric Prediction System (NOGAPS). It also assimilates remotely sensed, sea surface height data (GFO, JASON-1, and ERS-2 satellites) and sea surface temperature data (NRL/MODAS SST). Daily NLOM output is an operational product from NRL that is available from many cooperating data servers. One of these is the Asia-Pacific Data-Research Center (UH/SOEST/IPRC/APDRC—http://www.apdrc. soest.hawaii.edu/). One of the daily output layers routinely archived is the upper 100 m, henceforth termed surface layer. For this study, 365 days of daily surface layer data (31 January 2003 to 30 January 2004, these dates were not chosen but reflected availability at the time) spanning the region 170°E to 150°W longitude, 10°N to 35°N latitude were obtained from the APDRC. The daily surface-layer data included estimates of u (zonal East–West) component and v (meridional North–South) component for current vectors. The spatial grid (Fig. 1) covered 457×401 pixels.

Modeling of transport

The movement of larvae was simulated using the individual-based, Lagrangian techniques outlined in Polovina et al. (1999). These are also known as biased random-walk models (e.g., Codling et al. 2004). The following modifications to the Polovina et al. (1999) approach were used. Firstly, the daily, higher-spatial-resolution NLOM data was used rather than the 10-day, 0.5° latitude/longitude resolution, TOPEX/Poseidon geostrophic current fields. Secondly, the detection radius for successful settlement was reduced from 140 to 25 km. Thirdly, suitable settlement habitat was defined using a 2-min, high-resolution bathymetric database (Smith and Sandwell 1997) rather than the previously used, four isolated locations along the archipelago. The bathymetric grid was screened to only include 2-min pixels ranging in depth from 0 to 100 m. A latitudinal summary of habitat pixels is shown in Fig. 2 using 0.1° bins. In all other respects, the modeling approach was identical to Polovina et al. (1999), using an eddy-diffusivity coefficient of 500 m^2 s^{-1} and a daily time step. This value of eddy-diffusivity was qualitatively based upon drifter buoy observations (Polovina et al. 1999). The modeling refinements of this study primarily reflect better data availability for ocean currents and habitat definition, as well as further scientific research that is resolving the sensory and swimming capabilities of pre-settlement fish larvae (reviewed by Kingsford et al. 2002). For example, Fisher and Wilson (2004) found that sustainable swimming speeds were on the order of 30 cm s^{-1} for large, ready-to-settle larvae. The 25-km radius used in this study could be traversed in 1 day at these speeds, assuming continuous swimming and directional orientation. While the cues available on the high seas are poorly understood, the "Island Mass Effect" (Gilmartin and Revelante 1974) can have significant, visually detectable effects out to this radius

(e.g., Palacios 2004). Elevated levels of chlorophyll *a*, because of proximity to islands, banks, and sea-mounts, are also apparent at this spatial scale in the Hawaiian Archipelago (Kobayashi, unpublished data). Some larvae do not have well-developed swimming abilities, and appear to behave as passive drifters (corals, lobster, etc.). These larvae may require a more accurate "hit" on suitable substrate for successful settlement to occur. However, the 25-km radius was used in all simulations as a compromise to yield some settlement at a manageable level of larval release magnitude; i.e., the radius could be made smaller but would require more releases to attain non-zero settlement, requiring excessive computer time. By using these methodological improvements, 1,000 simulated larvae were released on every calendar day of the year and tracked for varying pelagic larval durations (PLDs) ranging from 10 days to 6 months. The sample size of 1,000 was chosen as a compromise because of computational speed and data storage concerns. This range of PLDs encompasses the known values for a wide variety of vertebrate and invertebrate species in the Hawaiian Archipelago, including commercially important species such as deepwater bottomfish and lobster, as well as coral reef inhabitants. Because the data spanned a discrete 365-day time block, data were allowed to "wrap around" for simulations initiated in the latter portions of the data. In other words, any larvae still at large on 30 January 2004 would next encounter currents from 31 January 2003, and carry on from that point forward. This would allow a symmetrical analysis of possible seasonal effects. One undesirable consequence of this approach is that it imposes a discrete "jump" in the data stream at the end of January; however, this approach was used to make best use of all available data for the widest range of PLDs possible. Operationally, the location of larvae in Cartesian space was calculated with the following equations:

Fig. 2 Tabulation of successfully settling larvae at latitudinal bins of 0.1° for a 90-day pelagic larval durations (PLD) from Johnston Atoll to the Hawaiian Archipelago (*solid line*). The *vertical line* represents the latitudinal breakpoint separating the Northwestern Hawaiian Islands (NWHI) and Main Hawaiian Islands (MHI). Habitat pixel counts (0–100 m depth) at each 0.1° of latitude are also shown for reference (*dashed line*)
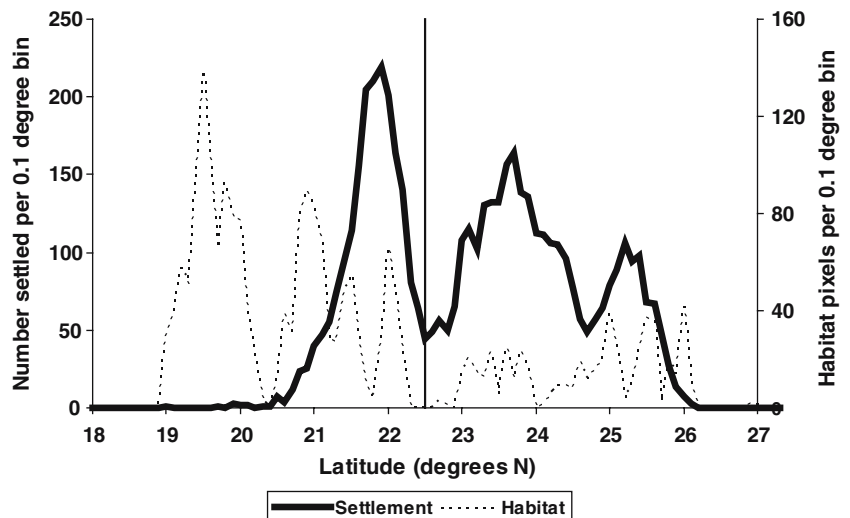
$$x_{t+\Delta t} = x_t + \frac{[u_{(x_t,y_t,t)}\Delta t + \varepsilon\sqrt{D\Delta t}]}{\cos(y_t)}$$

$$y_{t+\Delta t} = y_t + [v_{(x_t,y_t,t)}\Delta t + \varepsilon\sqrt{D\Delta t}]$$

where x represents longitude in degrees, y represents latitude in degrees, t represents time in days, u represents the zonal East–West component of the current speed in degrees day^{-1}, v represents the meridional North–South component of the current speed in degrees day^{-1}, ε is a normal random variate (mean 0 and standard deviation 1), $\cos(y_t)$ adjusts longitudinal distance by latitude to account for the spherical coordinate system, and D is the diffusivity coefficient (500 m^2 s^{-1}, 0.0035 degrees^2 day^{-1}, Polovina et al. 1999). The full-resolution, daily 1/16° latitude by 45/512° longitude u and v arrays were sampled depending on the location in time and space of individual simulated larvae. Simulated larvae at the end of the PLD and in the 25 km radius of any habitat pixel were scored as settled. Orientation and swimming were not implicitly part of the model structure, nor was the capability of early or delayed settlement/metamorphosis. However, it was assumed that competent larvae were able to successfully navigate the last 25 km at the end of the pelagic duration, loosely based on the 30 cm s^{-1} of Fisher and Wilson (2004), coupled with 24 h of swimming. The tabulation of settled larvae includes a range of individuals from directly on the habitat pixel up to 25 km distant; therefore, the actual mean PLD within this grouping may slightly exceed the index value PLD due to variable final transit time among individuals.

Experimental simulations

In the first set of releases, a range of PLDs was used to investigate the threshold of PLD for larvae to reach the Hawaiian Archipelago from Johnston Atoll. For each day of the year, 1,000 larvae were released and tracked individually. Settlement was tabulated to either long-distance transport to the Hawaiian Archipelago or retention back to Johnston Atoll. PLDs ranging from 10 to 180 days at 5-day intervals were examined. The percent of larvae settling in the two locations was evaluated as a function of PLD. The overall spatial pattern of larval abundance was examined for 1-, 3-, and 6-month PLDs.

In the second set of releases, a 3-month PLD was targeted for more detailed spatial analyses. This PLD was chosen based on evidence for coral and fish larvae. Harrison et al. (1984) found that planula larvae of *Acropora hyacinthus* could survive for up to 91 days prior to settling. Similarly, many of the insular deepwater snappers appear to have PLDs of this magnitude (Leis and Lee 1994). Since the biogeographic evidence for the Johnston Atoll link is strongest for *Acropora* corals (Grigg 1981; Kenyon 1992; Maragos et al. 2004) and the deepwater, insular fish species *E. quernus*

(Rivera et al. 2004), potential transport corridors for 3-month PLD larvae were investigated. For each day of the year, 1,000 larvae were released and tracked individually. Successful settlement was tabulated into 0.1° latitudinal bins for spatial analysis (Fig. 2). Larval settlement was tabulated to two arbitrary regions after a successful long-distance transport to the Hawaiian Archipelago. These regions were identified by coincident breakpoints in the latitudinal analysis and the geography of the archipelago (habitat pixel analysis). A northward region was defined as habitats north of 22°−30′N latitude, and a southward region was defined as habitats south of 22°−30′N latitude (Fig. 1). This latitudinal breakpoint separates the populated Main Hawaiian Islands (henceforth MHI) from the more remote and uninhabited Northwestern Hawaiian Islands (henceforth NWHI). The overall spatial patterns of larval abundance were examined separately for these two subsets of larval trajectories. The seasonal effect was examined by tabulating successful settlement, either long-distance or retention, to the day of spawning. Daily data were binned into seasonal (3-month) strata for statistical comparison. Temporal patterns were examined as well as a general comparison between long-distance transport to the Hawaiian Archipelago and retention to Johnston Atoll.

Spatial analyses

One method of summarizing spatial data is by using data contours, which are lines representing a constant set of values in the data of interest (termed z-levels). For studies of larval retention, standard contouring techniques will not be informative because density contours by themselves do not necessarily answer the important question "Where are most of the larvae?" Contouring of simulated pelagic larval abundance in this study was accomplished using a new technique, CONREC–IRC (Appendix). This is based on CONREC (Bourke 1987), a standard contouring technique that uses a triangulation algorithm to recognize pixels that should be contoured. CONREC–IRC has the ability to iteratively refine the contouring z-level to encompass a user-defined percentage of the total data points, i.e., an "Iterative Region of Containment". This methodology is useful for situations in which the total sample sizes may differ from other simulations; hence, contouring at a constant z-level does not allow meaningful comparison of spatial patterns. In the simulated abundance data of this study, the data are aggregated at various levels, with different resultant sample sizes. Similarly, a variable such as PLD can effectively increase the sample size because there are more days per individual in the aggregated data. Such data can be binned into cells of latitude and longitude, and then standardized, yet the resultant contours are still not useful for describing a "region of containment" because standard contouring does not take into account the global distribution of data, only the very local scale

of a few adjacent pixels of information. CONREC–IRC was used to define regions of 95% containment for selected simulation results. This approach may be generally useful in other applications such as mapping pollutants, invasive species, rare species, etc., in which it is desirable to know the location of most individuals.

Results

Based on transport by NLOM currents averaged over all seasons (Fig. 3), there appeared to be a critical PLD of approximately 40–50 days for successful pelagic transport to the Hawaiian Archipelago from Johnston Atoll. Larvae with PLD less than 40 days did not reach the Hawaiian Archipelago. Shorter PLDs were conducive to local retention, however. Because of these offsetting patterns, mortality—as a result of loss from the system—peaks at the 40–50 day range (Fig. 4). CONREC–IRC was used to identify the regions of 95% containment of all larvae for 1-, 3-, and 6-month PLDs (Fig. 5). The containment regions are similar in shape but vary in size depending on the PLD. The oblong and diagonal features of the IRCs reflect prevailing zonal patterns of ocean currents. As an example, Fig. 6 shows the July 2003 NLOM ocean currents averaged over 0.5° latitude and longitude for graphical presentation (temporal and spatial averaging). The latitudinal breakpoint of 22°–30′N separating the MHI and NWHI also corresponded to a break in the tri-modal settlement data and in habitat pixels along the archipelago (Fig. 2).

The 3-month PLD larvae were examined in more detail (Figs. 7, 8). These results suggest the possibility of larval transport corridors to both the mid-archipelago (e.g., French Frigate Shoals) and the northern portion of the main island group (e.g., Kauai). The seasonal timing of spawning was significant. For example, spawning earlier in the year appears to enhance both long-distance transport and local retention (Fig. 9). The local minimum in transport at the end of January may be related to the data wrap around; however, there is no obvious reason why this discontinuity in the data stream would be associated with lower transport and/or retention. When examined in more statistical detail, seasonal differences are observed (Fig. 10). As seen in the first set of simulations, long-distance transport exceeds local retention at the longer PLDs, such as the 3-months used in these simulations.


Fig. 3 Percent of total larvae retained at Johnston Atoll (*solid*) and transported to Hawaiian Archipelago (*dashed*) as a function of pelagic larval durations (PLD) using NLOM data. Data from all 365 calendar-day releases combined
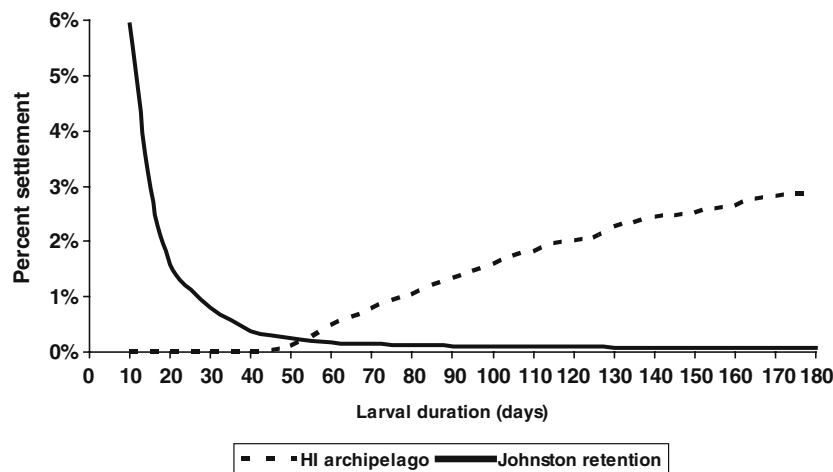
Fig. 4 Estimated larval mortality due to physical loss as a function of pelagic larval durations (PLD), using NLOM data. Data from all 365 calendar-day releases combined. Larvae with PLD less than 40 days do not reach the Hawaiian Archipelago
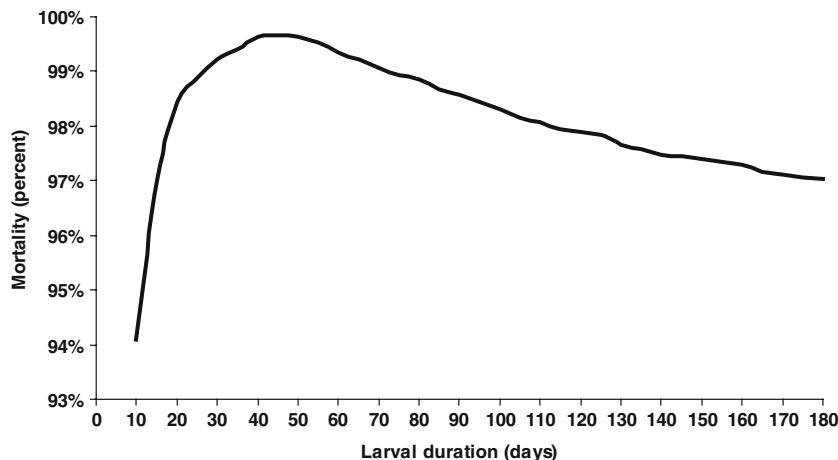
Fig. 5 Regions of 95% larval
containment using CONREC–
IRC for 1-month, 3-month, and
6-month pelagic larval
durations (PLDs), using
NLOM ocean current data.
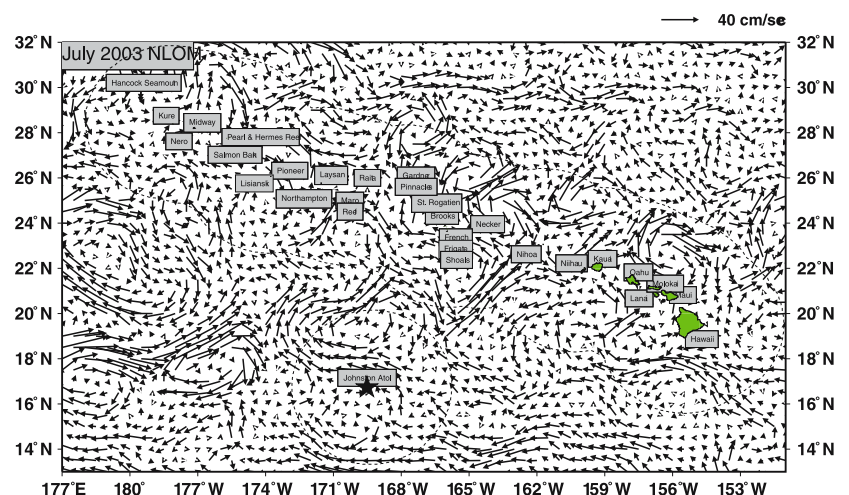Data from all 365 calendar-day
releases combined
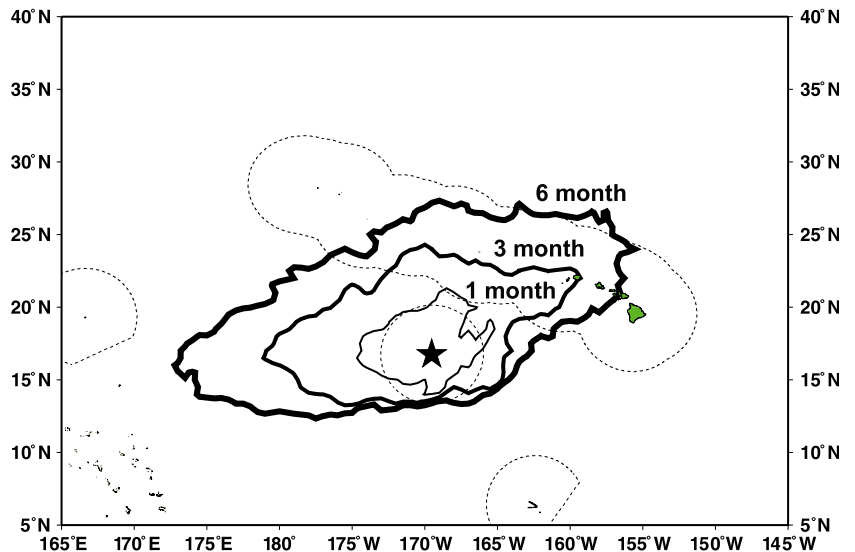
Discussion

Ocean currents that could facilitate larval transport
from Johnston Atoll to the Hawaiian Archipelago in-
clude the subtropical countercurrent (SCC; Yoshida and
Kidokoro 1967) and the Hawaiian Lee countercurrent
(HLCC; Qiu et al. 1997). Both the SCC and the HLCC
generally flow in the eastward direction at latitudes
between 19° and 25°N. The dynamics of the SCC and
the HLCC are not well understood, although it is
thought that the HLCC is a result of a large-scale, island
wake effect in the prevailing wind field (Xie et al. 2001).
Dynamics of the SCC have been found to be important
in the recruitment dynamics in other portions of the
Hawaiian Archipelago (Polovina and Mitchum 1992).
Further study is necessary to understand the relation-
ships of these important currents to pelagic larval ecol-
ogy. Comparing other ocean current data will allow a

better understanding and validation of the NLOM-dri-
ven simulations. As a start, the NLOM current fields
(Fig. 6) closely resembles the composite flow field pre-
sented by Qiu et al. (1997), which was estimated from a
large dataset of surface drifter tracks. Both general
features and overall magnitude of current speed match
well for the region around the Hawaiian Archipelago
and Johnston Atoll.

The 40–50-day PLD required to transit from John-
ston Atoll to the Hawaiian Archipelago is consistent
with the *Acropora* pattern, because their planula larvae
can be competent for up to 91 days (Harrison et al.
1984). *Epinephelus quernus* larvae appear to have PLD
exceeding this threshold as well (DeMartini, personal
communication). In other species, PLD has been shown
to be strongly related to genetic differentiation and,
hence, biogeography. Riginos and Victor (2001) found
that PLD for three blennioid species in the Gulf of
California inversely correlated with the degree of genetic

Fig. 6 Example plot of July
2003 NLOM ocean currents.
All daily data of July 2003 were
averaged into 0.5° bins of
latitude and longitude for
graphical presentation. The
original NLOM data are at a
resolution of approximately
sevenfold spatial increase in
data points as shown here and
daily

Fig. 7 Larval abundance from northern trajectories successfully reaching Hawaiian Archipelago from Johnston Atoll using NLOM currents and 3-month pelagic larval durations (PLD). Data from all 365 calendar-day releases combined
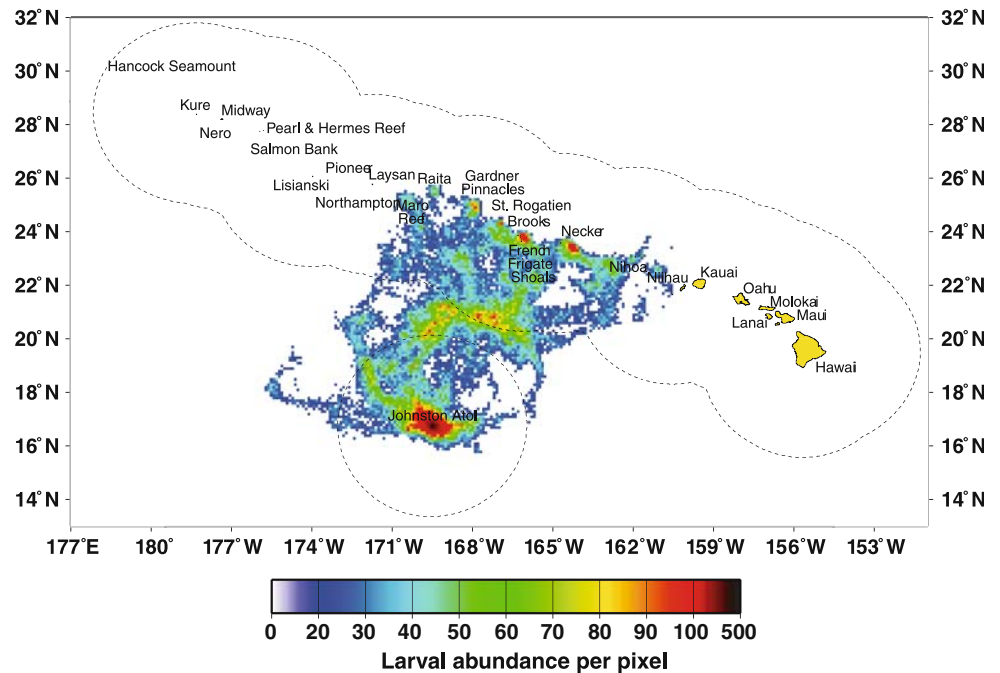

partitioning in the population. The spacing of biogeographic "stepping stones" will thusly serve to filter species colonization, depending on their reproductive strategy. Further simulations will examine this process in more detail for the Hawaiian Archipelago, using an approach similar to Dytham (2003). Taxa with relatively long PLDs or capable of delayed settlement/metamorphosis (e.g., Leis 1983; Victor 1986) are more likely to complete the transit on a routine basis.

Lobel (1997) found that the PLD for the damselfish *Plectroglyphidodon imparipennis* was approximately 40 days, according to samples collected at Johnston Atoll and Hawaii. He concluded that this PLD was insufficient to successfully traverse the distance between the Hawaiian Archipelago and Johnston Atoll, hence populations were locally self-sustaining. Given the results of this study, it remains conceivable that this species could make the crossing. A follow-up study will

Fig. 8 Larval abundance from southern trajectories successfully reaching Hawaiian Archipelago from Johnston Atoll using NLOM currents and 3-month pelagic larval durations (PLD). Data from all 365 calendar-day releases combined
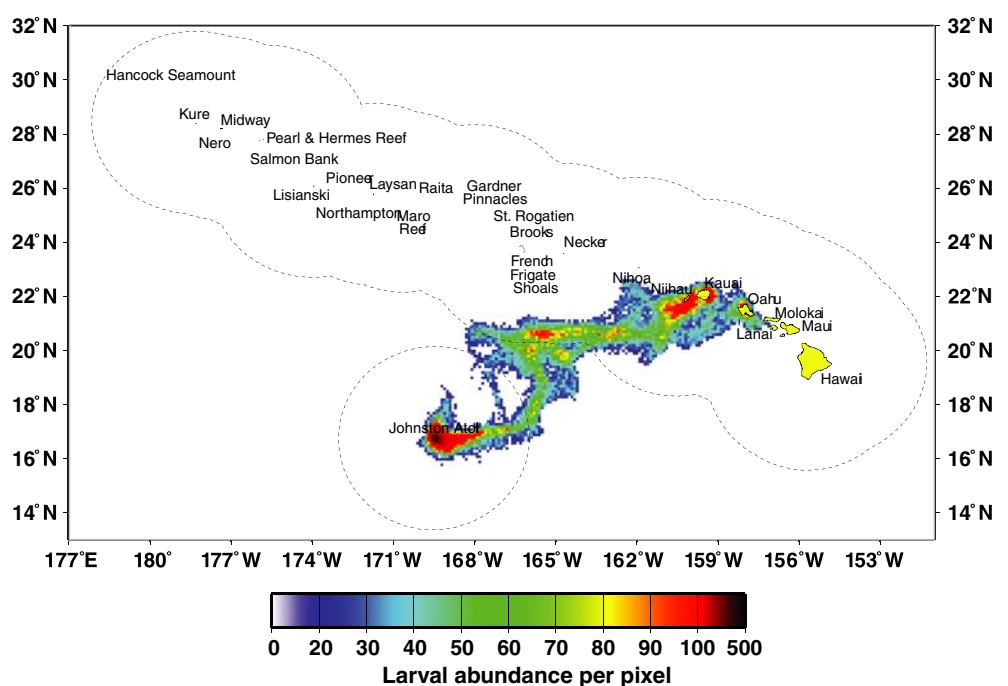
Fig. 9 Seasonal pattern of long-distance transport and local retention using NLOM currents and 3-month pelagic larval durations (PLD). Number of successful settlers (out of 1,000 released) tabulated to day of spawning
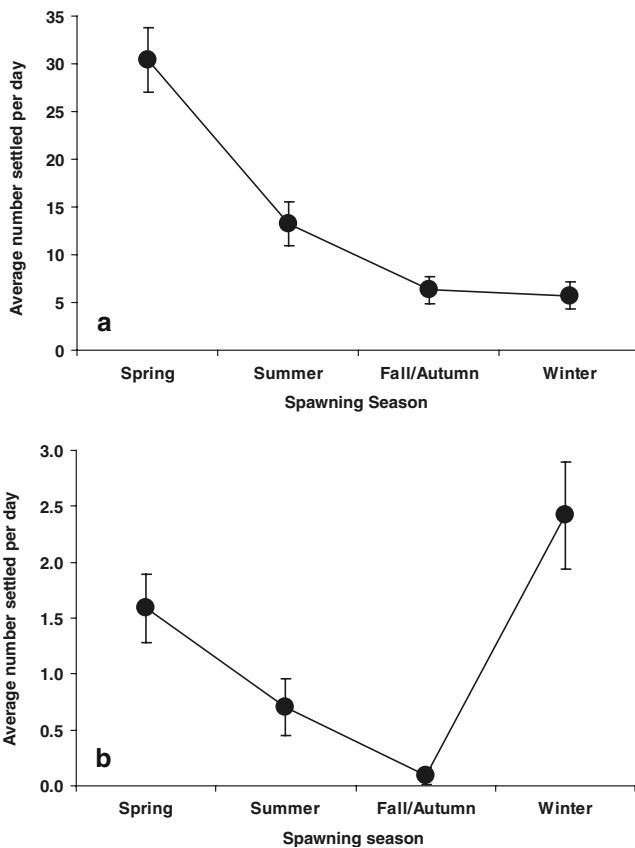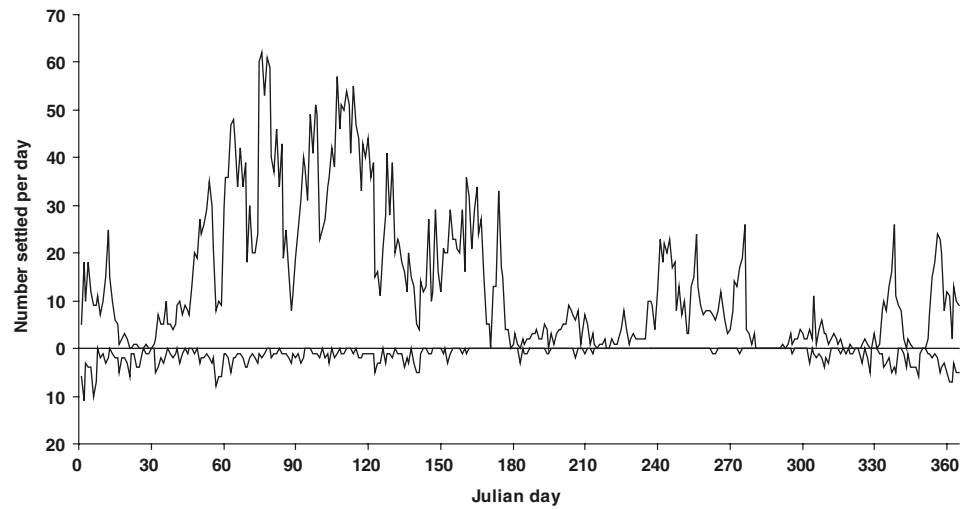
Fig. 10 Comparisons of long-distance transport (**a**) and local retention (**b**) segregated by spawning season using NLOM currents and 3-month pelagic larval durations (PLD). Spring, summer, fall/autumn, and winter seasons are defined as February–April, May–July, August–October, and November–January, respectively. Means and 95% CIs from all daily data for each season are plotted

examine the dynamics of the reverse path, from areas in the Hawaiian Archipelago to Johnston Atoll.

A larval fish survey around Johnston Atoll found indications of a retention zone on the leeward (Western) side of the atoll (Boehlert et al. 1992). This was primarily a result of the distribution of gobiid larvae with very short PLDs. Larvae of island-associated species were also most common in the upper 100 m, which supported the use of that particular NLOM layer of current data in the present study. The NLOM does not describe near-shore or near-bottom currents well and will not be useful for describing retention zones associated with sub-mesoscale oceanographic processes. Results from computer simulation are not intended to replace field sampling. However, the extreme scarcity of larvae of island-associated species in field samples has handicapped many such studies. With better knowledge of the oceanographic conditions, targeted sampling in both space and time could yield more meaningful scientific data, such as sampling areas that are significant to population maintenance and long-distance transport.

The findings of this study are relevant to any island-associated species with pelagic larval stages. Various vertebrate, invertebrate, and marine algal species all have pelagic stages with common processes affecting their distribution and survival (e.g., Bradbury and Snelgrove 2001). Further study of this shared environment will be critical towards understanding biogeographic patterns and metapopulation structure. Other critical issues, such as invasive species colonization, could be addressed with these computer simulation tools.

Swimming behavior, especially for fish larvae, may be very important for the larger and older stages near the end of the PLD. Fisher and Wilson (2004), Fisher (2005), and others have shown that larval fish possess great mobility, and if the suitable orientation cues exist, they would be able to traverse many kilometers of ocean in the latter portions of the PLD. The 25-km detection radius used in this study could be traversed in a single day based on the findings of Fisher and Wilson (2004). Conveniently for modeling purposes, this region, where

active swimming may take over, encompasses areas where oceanographic data usually lapse, because of the complexities of bottom topography, coastlines, tides, internal waves, etc. While swimming and orientation are undoubtedly important, the strongest visual, chemical, acoustic or other sensory cues appear to be localized to within a few kilometers of the target habitat (Leis, personal communication), and oceanographic processes remain significant in the transport of passive eggs and pre-flexion larvae as well as bringing older larger larvae close enough to the target habitat to orient and settle. The "Island Mass Effect" (Gilmartin and Revelante 1974), as it relates to larval settlement cues, is an important area of future research.

The effect of spawning seasonality warrants further attention. The simulations indicate that the timing of spawning to be very important for subsequent larval survival, either via long-distance transport or local retention. Spawning seasonality in Hawaiian fishes is highly variable (Walsh 1987), and further work is needed to understand the relationships between biogeography, adult reproductive strategies, and oceanographic variability.

The computer simulation results of this study serve to identify the PLD threshold needed to reach the Hawaiian Archipelago from Johnston Atoll. Additionally, potential oceanographic transport corridors have been charted and are consistent with the existing biogeographic theory for the region. Findings show that both long-distance transport and local retention are strongly dependent on spawning seasonality and pelagic larval duration. The high-resolution NLOM data appears to be a useful new tool for modeling larval transport in this region. A new analytical technique, CONREC–IRC, was introduced in this paper and its application in the quantification of spatial distributions was shown.

Appendix

CONREC–IRC (IRC refers to "Iterative Region of Containment") is an iterative program to objectively enclose a scatter of cartesian data points at a user-defined level of containment using a standard contouring algorithm to define the polygon. It was developed from CONREC, an open-source contouring subroutine originally written in FORTRAN-77 (Bourke 1987). CONREC has been ported to many languages (see http://www.astronomy.swin.edu.au/~pbourke/projection/conrec/), including the Visual Basic version (by James Craig), which was the precursor to CONREC–IRC.

CONREC–IRC is written in QuickBasic 4.5 and takes advantage of the POINT command, which can query an individual pixel on the graphical output screen. This functionality was instrumental to CONREC–IRC by enabling tabulation of raw data points inside or outside of the contoured polygon. While mathematical algorithms exist to determine whether a point is within a polygon or not, the simplest method of plotting points, plotting the enclosing polygon, filling the enclosing polygon with color, then querying each data point's color was the most straightforward technique. The basic step-by-step methodology of CONREC–IRC is as follows:
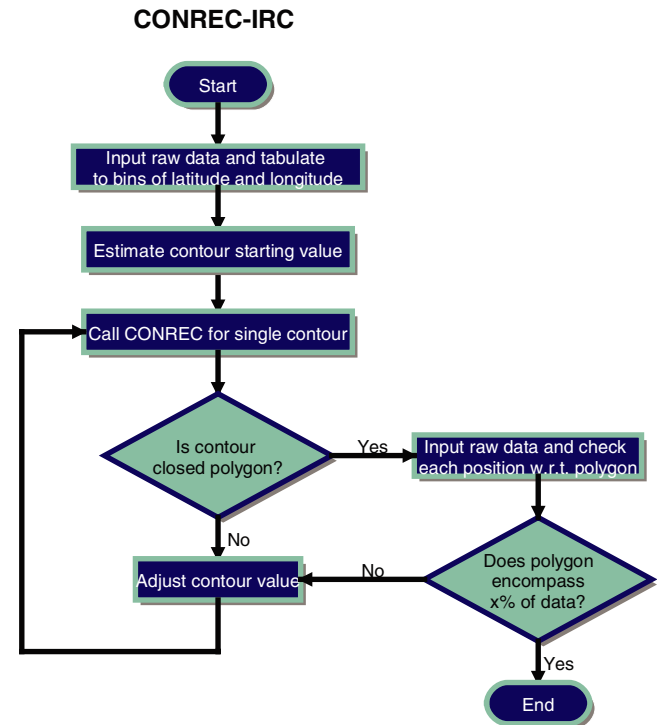

Fig. 11 Flowchart

Because only a single value is being optimized, a simple, direct search algorithm (Hooke and Jeeves 1961) was used to converge on the contouring level that would encompass the specified amount of data points. Proportional adjustments to the contour value were based on residuals from the percentage of data points encompassed. Testing with simulated data indicated that CONREC–IRC was able to quickly find the contouring solution within 10–15 iterations and was not sensitive to starting values. CONREC–IRC is suited for spatial data with a single center of mass with density tapers in all directions. More complex spatial patterns would yield multiple or nested contours and are not amenable to the CONREC–IRC approach since definition of a single mass is problematic. The source code for CONREC–IRC is available on request.

Fig. 12 CONREC–IRC example using Johnston Atoll retained larvae

Plot of Raw Data

Plot of Binned Data

Plot of CONREC - IRC 95% contour
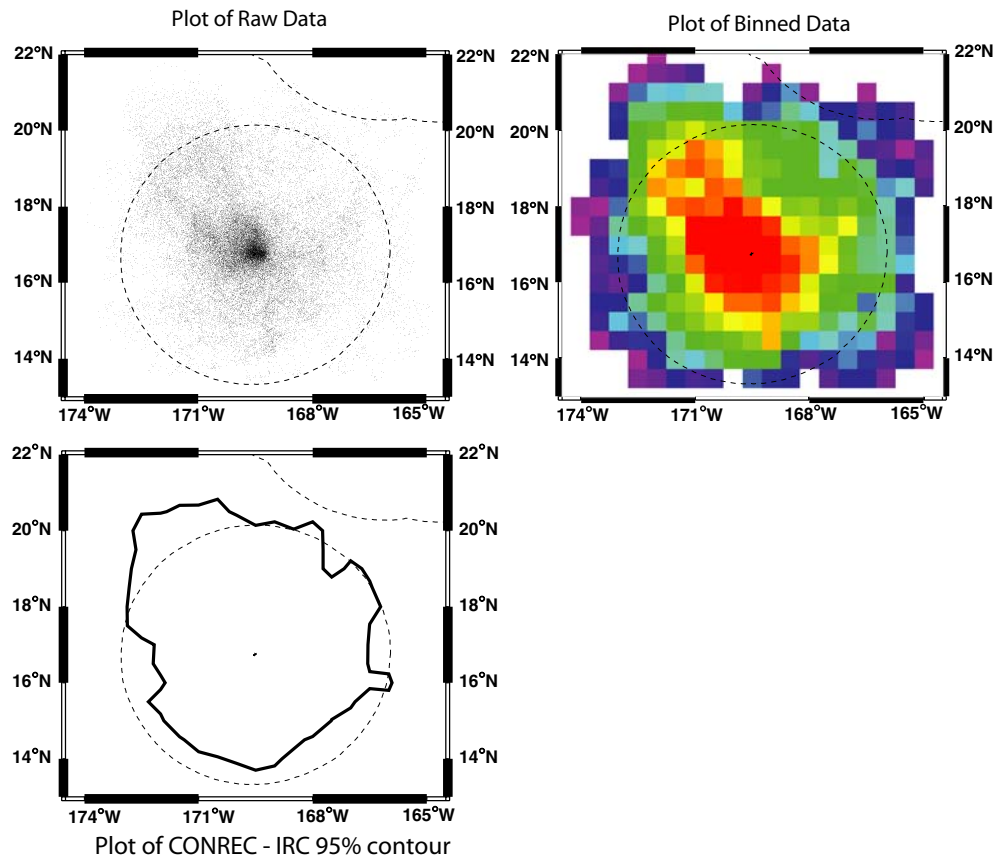
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