DRIFT CARD SIMULATION OF LARVAL DISPERSAL FROM SAN NICOLAS ISLAND, CA, DURING BLACK ABALONE SPAWNING SEASON

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Abstract—The dispersal of pelagic larvae may shape the recovery of marine populations that have been depleted from natural or anthropogenic influences. Black abalones (*Haliotis cracherodii)* underwent mass mortalities throughout their range beginning in 1985 as the result of an exotic bacterial pathogen known to cause Withering Syndrome (WS). San Nicolas Island (SNI) was the last of the California islands to be impacted by the disease, with declines beginning in 1992. Beginning in 2002, a significant black abalone recruitment event was observed at SNI (VanBlaricom unpubl. data), unique in size and persistence among black abalone populations in the southern California Islands since the 1980s. Sea surface circulation surrounding SNI is highly variable and not thoroughly understood, complicating predictions for the dispersal of larvae to and from SNI. In the summers of 2002 and 2003, drift cards were deployed from the shore of SNI to simulate the dispersal of larvae during peaks in black abalone spawning season (August 2002, June 2003). In the 2002 study, drift cards dispersed to Santa Catalina Island and the California mainland, identifying physical linkages among locations, although the majority (40%) of drift cards was found on SNI within 2 km of the release site. In the 2003 study only one drift card was reported beyond SNI and 60% were found on SNI. The results presented here indicate that drift card dispersal varies temporally, and that drift cards are primarily retained locally. As a surrogate for the dispersal of black abalone larvae, this drift card simulation implies that the local retention of larvae may increase successful recruitment and have implications for the conservation and management of the species.

Keywords: abalone, drift cards, larval dispersal, San Nicolas Island, withering syndrome

INTRODUCTION

Marine species with a pelagic larval form have the potential to disperse over large geographic areas (see review by Grantham et al. 2003). Dispersal potential is influenced by the strength and direction of sea surface currents, larval duration and season of spawning (Butman 1987, Reed et al. 2000). Knowledge of the patterns in sea surface currents connecting marine populations may be applied to infer population linkages (Klinger and Ebbesmeyer 2001). Marine populations that are tightly linked through significant larval exchange will likely undergo similar population dynamics, whereas minimal larval exchange may result in spatially independent population dynamics (Reed et al. 2000, Withler 2000). Such an understanding of the connectivity of populations may be used to predict the population recovery dynamics in species that have experienced significant declines due to natural or anthropogenic influences.

Black abalones (*Haliotis cracherodii*) experienced mass mortalities throughout the central California coast and offshore islands as the result of an exotic bacterial pathogen known to cause “Withering Syndrome” (WS) in the species (Haaker et al. 1992, Friedman et al. 2000, Moore et al. 2001). Signs of the disease were first documented in the California Islands (Santa Cruz and Santa Rosa Islands) in 1985 and subsequently spread northward along the central coast of California and southward to other islands off

California. Initial declines were correlated with increases in sea surface temperatures and El Niño events (Raimondi et al. 2002). SNI was the last of the California islands to be impacted by signs of disease, with declines beginning in 1992 (VanBlaricom et al. 1993).

Since the initial declines of black abalones, isolated and failed recruitment events have been observed around the California islands and along the California mainland, with mortalities corresponding to increased sea surface temperatures generally associated with El Niño conditions (Raimondi et al. 2002, D. Richards pers. comm., J. Steinbeck pers. comm). Since 2002, an increasing number of juvenile black abalones have been observed at SNI (VanBlaricom unpubl. data), suggesting the development of a successfully recruiting cohort. The recent emergence of the large juvenile cohort at SNI is temporally correlated with strong La Niña conditions beginning in 1999. The La Niña conditions, characterized by high phytoplankton concentration near the surface, increased zooplankton biomass, low sea surface temperatures and significant upwelling surrounding SNI (Schwing et al. 2000), may have provided ideal conditions for successful recruitment to SNI. During the same time period the inshore countercurrent, characteristic of the Southern California Bight (SCB), increased the sea surface temperatures and salinity around the northern islands (Schwing et al. 2000), possibly creating less favorable conditions for successful recruitment in the northern islands. Such differences in sea surface conditions surrounding SNI in contrast with the other California islands are possible explanations for differing population dynamics of black abalones among the islands.

Patterns of larval dispersal in SCB may be shaped by hydrodynamic forces and biological characteristics. Hydrodynamic conditions in the SCB are influenced by the southward moving California current, the poleward California countercurrent and the southern California Gyre (Dever et al. 1998, Harms and Winant 1998, Winant et al. 1999). During the summer black abalone spawning season, the combination of these three patterns could function to link populations through larval dispersal. However, factors such as hydrodynamic conditions (e.g., Wing et al. 1998), larval behavior (Burton and Feldman 1981), spawning period (Hamm and Burton 2000) and post settlement mortality (Hedgecock 1986) may enhance local recruitment and limit mean dispersal distances. Black abalones spawn only during the summer months, with peaks occurring at the beginning and end of the summer season (Ault 1985). Abalones are dioecious broadcast spawners, with a one to two day post fertilization period prior to hatching into a larval form (Ino 1952). The lecithotrophic larvae (Ino 1952) of abalone species are phototactic (Ino 1952, Mottet 1978), and are thought to migrate to the surface during their swimming phase (Scheltema 1977). Although little is known about larval abalone behavior, they are also thought to move vertically in the water column by cilial beating (Scheltema 1977), potentially allowing the exploitation of tidal currents for local retention (Bilton et al. 2002). Directional lateral movement appears largely dependent on sea surface currents (Scheltema 1988, McShane 1992).

The present study delineates the results of a drift card study conducted to increase the understanding of sea surface circulation at SNI and its potential influence on larval recruitment and dispersal during the peak of black abalone spawning season. Drift card studies have been used to evaluate the potential for broad scale larval dispersal and to estimate the significance of larval exchange between isolated populations (e.g., Schwartzlose 1962). Such studies can also be used on a smaller scale, to identify patterns of local retention and localized recolonization of populations. Our primary goal was assessment of the potential for SNI to function as a broodstock for the recovery of black abalone populations throughout the original range of the species.

MATERIALS AND METHODS

Drift Card Construction

Drift cards were constructed based on a protocol developed by Klinger and Ebbesmeyer (2001) with alterations suggested by Carl Schoch (pers comm). Sheets of plywood were coated with bright yellow paint and cut into 7.6- x 10.2-cm cards. The word “HELP” was stamped onto one side of each card with bright red paint. On the other side, a message written on plain white paper was affixed to each card using three coats of marine polyeurethane varnish. Each card contained a unique identifying letter and number along with contact information and instructions for returning the card.

For the June 2003 deployment, drift cards were constructed in two batches. Batch one cards were identical to those deployed in August 2002. Batch two cards were altered slightly to minimize the direct effects of wind by affixing a bolt to one end of each card causing the card to float vertically in the water column so that only the upper edges of batch two cards were in contact with the sea-air interface (Fig. 1).

Notices were sent to staff at the Channel Islands National Park and researchers throughout the region announcing the study and drawing attention to the possibility of stranded cards. Residents and visitors of SNI were informed of the drift card study during both years of the study. Fliers were posted in highly trafficked areas on SNI. Island biologists documented the locations of stranded drift cards on a publicly displayed island map of SNI.

Drift Card Deployment

The first drift card deployment occurred at SNI 9–11 August 2002. A total of 1,170 cards was deployed from 9 study sites. The deployment sites were consistent with black abalone population census sites monitored annually by VanBlaricom (1993; Fig. 2). Equal numbers (130) of cards were deployed from each of the nine study sites at the peak high tide of the release day. Coordinates of release sites were recorded using a GPS unit (Garmin, GPSMAP, Olathe, KS). All cards were deployed from shore at high tide by tossing cards individually beyond the surf zone. During the first three days after drift card deployment, observers walked readily accessible portions of the shoreline and recorded the GPS coordinates of recovered cards. Observers returned to SNI 21–24 in September 2002 (approx. 40 days after deployment) to search for additional stranded cards. During the September search period, approximately 80% of the island coastline was surveyed, with an effort to avoid areas where human presence would disturb pinnipeds or seabirds.

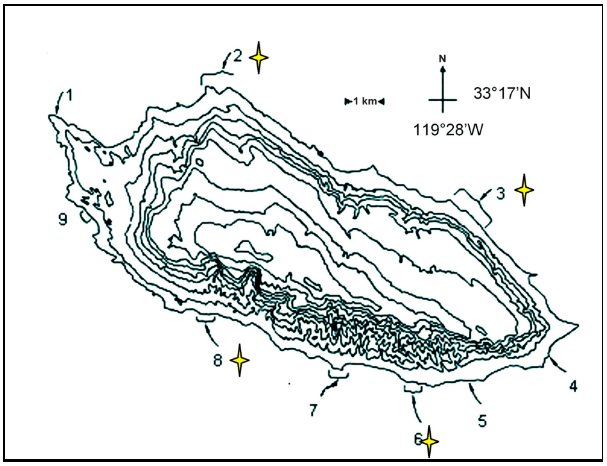

Figure 2. Drift card release sites. In August 2002, releases occurred at all sites (1–9). Starred sites indicate points for both the August 2002 and June 2003 releases. The map is adapted from VanBlaricom (1993).

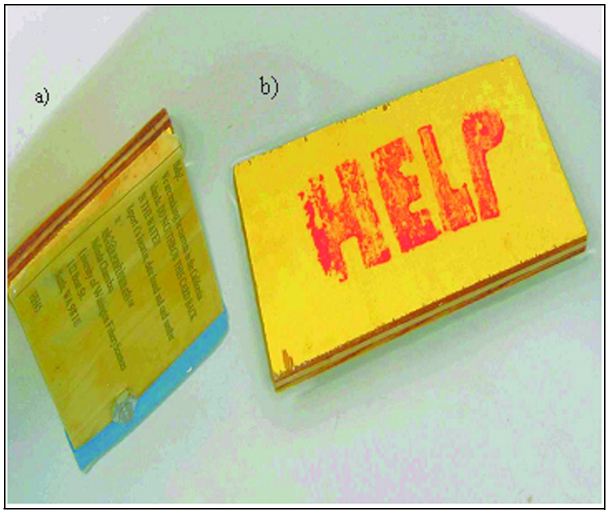

Figure 1. Photograph of drift card with “HELP” on one side and message on the opposite site. a) Card suspended vertically in the water column with a bolt affixed to one end (batch two; see text); b) card floating horizontally on the surface (batch one).

The second drift card deployment occurred 31 May – 1 June 2003 using methods similar to the June 2002 deployment except as described below. A total of 2,480 cards were deployed, 1,050 with bolts and the remainder without bolts. Equal numbers of cards (63 with bolts, 358 without bolts) were deployed from sites 2, 3, 6, and 8 (VanBlaricom 1993; Fig. 2), coinciding with four geographic quadrants of the island (NW, NE, SW, SE). Three of the four releases occurred at the high but ebbing tide (NW, NE and SW). The other (SE) occurred during a nearly high flooding tide. No effort was made to collect stranded cards 1–7 days after deployment. Extensive surveys for stranded cards were conducted at SNI 7–9 days and 15–17 days after deployment. Surveys for stranded cards on the other islands and the mainland were beyond the scope of this study. Information on cards found beyond SNI is based entirely on sightings reported voluntarily following chance encounters.

Data Analysis

The GPS coordinates of release and recovery locations of individual drift cards were plotted using ArcView (ESRI 1999). The distances between release and recovery sites were measured as the shortest straight-line distance (km) between respective GPS coordinates. Straight line distance was used in order to maintain consistency among travel and distance rates. Statistical analysis was conducted using SPSS for Windows (SPSS Inc. 2001). For the 2002 survey, the average distance traveled was also analyzed for dependence on release site (nine total release sites) and survey effort with a two-way analysis of variance (ANOVA) statistical test. Two-way ANOVA statistical tests were used to evaluate the dependent variable of the distance cards traveled with respect to independent variables including the year and site of release and time until recovery (Zar 1999). Comparisons in distance traveled by drift cards between the 2002 and 2003 releases were evaluated with respect to year and site of release (comparisons were made between the four sites where releases occurred both years), as well as year of release and time until recovery. An analysis of covariance (ANCOVA) was used to evaluate the distance cards traveled with respect to the tidal condition (ebbing or flooding), with site as the covariate. A one-way ANOVA statistical test was used to evaluate significant differences between cards with and without bolts. Tukey's post hoc test was used for all ANOVAs in order to identify specific patterns of differences among means (Zar 1999).

Wind Simulation

To account for the influence of wind on the dispersal of drift cards, wind data were downloaded from the NOAA weather buoy at Tanner Banks (http://www.ndbc.noaa.gov/station_page.phtml). The weather buoy nearest SNI does not archive wind data and the Tanner Banks weather buoy, located 60 km south of SNI, was the closest alternative. Wind speed and direction were averaged over the three-day release period and subsequent month for each deployment. A one-way ANOVA was used to compare the speed and direction of wind between the two release periods.

General NOAA Oil Modeling Environment (GNOME) software (NOAA/HAZMAT 2002) was developed to model passively floating sea surface particles for simulating oil dispersal following large spills. The GNOME model is supported by location files that include wind, current and tidal data as inputs for developing trajectory results. A GNOME location file has not yet been developed for the region surrounding SNI. However, a wind only drifter model was developed especially for this project (CJ Beegle-Krause) providing a mechanism for comparing exclusively wind-driven dispersal with the drift card trajectories from the present study. The model was started with a hypothetical mass spawning around the entire perimeter of SNI. Archived wind data from the Tanner Bank buoy were imported into the GNOME model in ten-minute intervals, for the 15 days following the initial release of drift cards, for both the 2002 and 2003 simulations.

RESULTS

Over the course of the two-year study 1,989 (54%) of the deployed cards were recovered. Following the August 2002 release, 51% of cards were recovered; of these, 74% (572 cards) were found within 2 km of the release site, 25% (159 cards) were found between 2–10 km of the release site (Table 1), and fewer than one percent (nine cards) were returned from beyond SNI from either Santa Catalina Island or the mainland coast (Table 2). Following the June 2003 release 65% of deployed cards (802 cards without bolts and 810 with bolts) were recovered with more than 99% recovered within 2 km of the release site (Table 1). Drift cards with bolts traveled significantly farther (avg. = 185 m) than those without bolts (avg. = 114 m; P = 0032; Table 3). Consequently, inter-annual comparisons were made based only on cards without bolts.

Recoveries on SNI showed that drift cards traveled in an eastward direction on the north and

Table 1. Characteristics of drift card travel for cards recovered on San Nicolas Island according to the site of deployment, for both the August 2002 and June 2003 releases. The mean time to recovery, maximum travel rate, mean rate and mean distance traveled are included for all cards that were recovered beyond 2 km of the release site. Summary data include the total number of cards recovered and the mean time, rate and distance for cards that traveled beyond 2 km. For the June 2003 release, results include only cards without bolts (details in text).

	No. Cards recovered by deployment location				Cards recovered > 2km from deployment location			
	No. released	Within 2 km	Beyond 2 km	% recovered	Mean time (#days)	Max.rate (km/day)	Mean rate (km/day)	Mean distance (km)
AUGUST 2002								
Location								
Northeast	270	151	8	59%	8.63	9.59	5.32	16.24
Northwest	270	57	6	23%	24.33	4.42	1.62	6.57
Southeast	360	277	13	81%	16.62	0.98	0.63	2.30
Southwest	270	87	132	81%	15.60	2.14	1.76	5.30
SUM	1170	572	159		16.29	4.28	2.33	7.60
JUNE 2003[a]								
Location								
Northeast	358	252	0	70%	-	-	-	-
Northwest	358	145	2	41%	10.00	1.32	0.92	7.26
Southeast[b]	356	199	0	56%	-	-	-	-
Southwest	358	159	0	44%	-	-	-	-
SUM	1430	755	2		10.00	1.32	0.92	7.26

[a] Results here include only cards without bolts.

[b] Tidal condition: high, flooding. All other releases occurred at a high but ebbing tide.

Table 2. Travel of cards beyond San Nicolas Island following the August 2002 and June 2003 release period.

Release site	Distance (km)[a]	Recovery time (days)	Transport rate (km/day)
August 2002			
4	178.5	14	12.8
4	181.3	20	9.1
4	186.5	20	9.3
4	118.3	22	5.4
4	183.3	26	7.1
4	118.3	11	10.8
4	117.9	20	5.9
4	110.1	60	1.8
4	129.2	30	4.3
Mean	147.1	25	5.9
SD	33.96	14.37	3.42
June 2003			
2	181.3	192	0.9

[a] Distance is measured as the shortest straight line distance between the release and recovery points (km).

south sides of the island, without exception. The majority of cards were recovered within 2 km of the release site, during intensive survey efforts by researchers, following both releases (Table 1, Figs. 3 and 4). Comparisons between the two releases (August 2002, June 2003) show that drift cards traveled further following the August 2002 release, and that the distance traveled by drift cards varied significantly among site of release, and time to drift card recovery (ANOVA, $P < 0.001$; Table 3). Tukey's post hoc tests comparing distance traveled by cards with respect to collection date, showed that cards recovered between intensive surveys traveled significantly further than cards collected by researchers during intensive surveys on SNI. Following the August 2002 release, data from surveys by researchers immediately following the release and data from surveys by researchers 40 days post release indicated similar distances (Fig. 3).

Distance traveled by drift cards varied among release sites following both releases. More

Table 3. Results of statistical tests for factors influencing distance traveled by drift cards.

Statistical test factor	df	F	P
Two-Way ANOVA: release year and site			
Site of release	3	27.57	0.000
Year of release[a]	1	139.12	0.000
Site × Year	1	27.58	0.000
Two-Way ANOVA: release year and collection date			
Collection date	3	510.10	0.000
Year of release	1	141.73	0.000
Collection date × year	1	15.15	0.000
Two-Way ANOVA: year one site and time comparisons			
Time after release	3	82.78	0.000
Site of release	8	11.54	0.000
Time after release × Site	6	15.26	0.000
ANCOVA: site and tidal elevation			
Intercept	1	2.12	0.145
Tide	1	0.83	0.364
Site of release	3	1.88	0.132
One-Way ANOVA: with and without bolt			
Bolts	1	7.16	0.032

[a] August 2002 release or June 2003 release

specifically, post hoc tests showed that cards released from the northwest side of the island traveled significantly further than cards released from the other three sites (Table 3, Figs. 5 and 6). Following the August 2002 release, the average distance traveled by cards from the northwest sites (sites 1 and 2) and northeast sites (3 and 4) were 16.24 and 6.57 km, respectively. Following the June 2003 release, only the northwest site (site 2) contributed to long distance dispersal (avg. distance traveled by cards = 7.26 km; Fig. 6). A significant interaction was detected between the release site and time to recovery (two-way ANOVA; $P < 0.001$). Tidal elevation at the time of release showed little influence on the distance cards traveled. Analysis of covariance between site

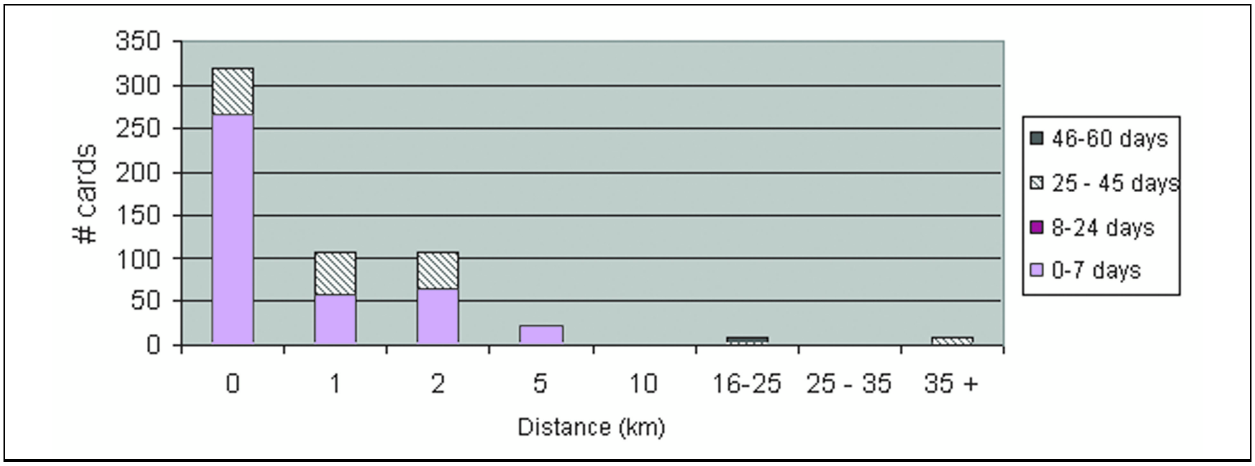

Figure 3. Distance traveled and the number of cards recovered by time after release for the August 2002 deployment. Intensive surveys by researchers occurred 0–7 and 25–45 days after deployment.

and tidal elevation at the time of release were not significant ($P > 0.05$; Table 3).

Drift cards recovered from beyond SNI were dependent on returns by beachgoers. Following the August 2002 release, drift cards were recovered from Santa Catalina Island and the California mainland, with two of three cards recovered from Santa Catalina Island found within the 5–15 day black abalone larval period. Nine drift cards deployed from SNI in August 2002, and one card from the June 2003 release, were later recovered on the southern California mainland (Table 2). Likely trajectories for cards recovered on the mainland were inferred from known sea surface circulation patterns in the SCB (Fig. 7).

Wind Dispersal Simulations

During the three day release period of the June 2003 study, the average wind speed was nearly half that of the August 2002 release (Table 4). As the study period progressed the difference in wind speed between the two releases diminished, but overall, winds were stronger during the June release than during the August release ($P < 0.001$). During both the August 2002 and June 2003 release periods, northwesterly winds were consistently recorded. Over the full span of the drift card recovery period, the mean wind directions varied significantly between the two studies, with the wind shifting more northerly toward the end of the August 2002 study ($P < 0.001$).

GNOME model runs (Fig. 8) suggested that wind-driven current patterns could result in different dispersal patterns following the August 2002 and June 2003 releases. Following the August 2002 release, surface particles were predicted to travel further offshore than predictions following the June 2003 release. Both simulations predicted that wind driven particles would not be discovered on the CA mainland, north of the U.S./ Mexico border.

Table 4. Means of wind speed and direction (wind source) during release period (days 1–3) and the subsequent drift period and release period combined (days 1–15). Data from NOAA weather buoy at Tanner Banks, 60 km south of San Nicolas Island.

Release period	Days after release	Mean Speed (knots)	Mean Direction
June 2003	1–3	4.71	289°
	1–15	6.2	296°
August 2002	1–3	7.63	293°
	1–15	6.6	309°

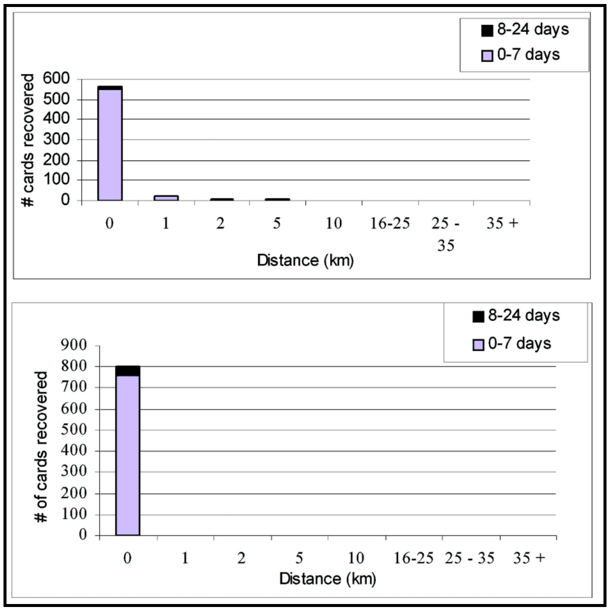

Figure 4. Distance traveled and the number of cards recovered by time after release for the June 2003 deployment. a) Cards with bolts; b) cards without bolts. Intensive surveys by researchers occurred 5–7 and 13–15 days after deployment.

DISCUSSION

Drift card simulations provide a snapshot of what might occur to passively floating particles on the ocean surface and may be useful for studying patterns of marine larval dispersal. Results of the two drift card simulations described herein suggest that if abalone larval dispersal is largely influenced by surface currents, then larvae released from SNI would have traveled exclusively an eastward direction along SNI, possibly as far as Santa Catalina Island or the California mainland, as the drift cards did. Drift cards tended to travel further following the 2002 release than the 2003 release, with only one card recovered beyond SNI after the 2003 release. The data indicate probable temporal variation in sea surface circulation and imply primarily local retention of surface floating particles at SNI, with some potential for broad-scale dispersal.

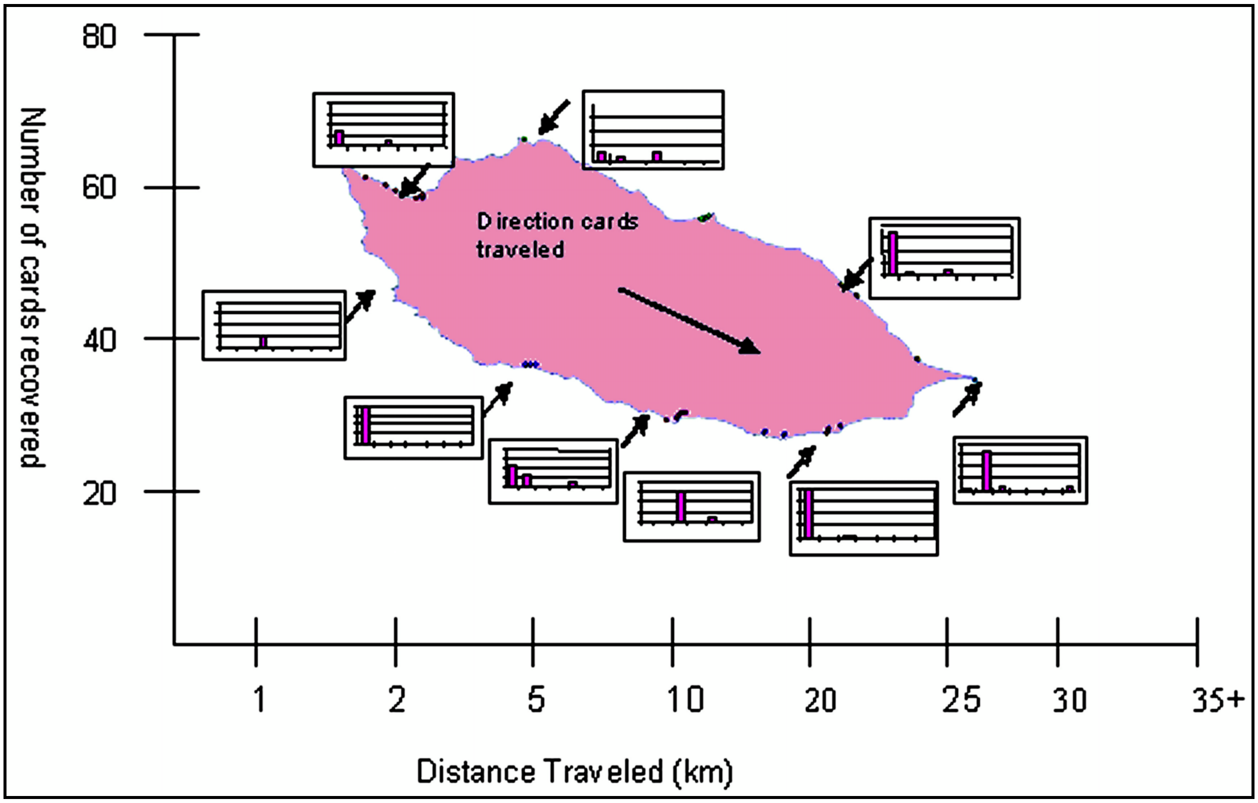

Figure 5. Histograms of distance traveled and number of cards recovered for each release site following the August 2002 release. The large arrow indicates that drift cards traveled eastward from the site of release, without exception. The small arrows point to the release sites. Dots along the shoreline map indicate points of drift card recovery. The axes of each small graph are identical to the larger axes labeled traveled (x) and number of cards recovered (y).

Variation in Recovery Rates

Most recovered cards were found on sandy beaches where cards were readily visible on the southern California coast and Santa Catalina Island. While many of the drift cards were not recovered immediately upon stranding, recovered cards provided useful knowledge of general dispersal patterns. Other factors contributing to biases in drift card recovery included coastal topography, human population density, release methodology, survey effort, and natural temporal fluctuations in sea surface circulation (Tegner and Butler 1985). High cliffs limit pedestrian access to beaches along portions of the offshore islands as well as portions of the southern California mainland coast. This limitation could have limited drift card recovery, and subsequently resulted in an underestimate of drift card dispersal potential. The amount of human foot traffic and potential encounters with drift cards varied by season. June is characterized by cool foggy days, whereas August is typically the sunniest and warmest month of the year, bringing more people out to the coast and to visit beaches, with a greater potential for drift card encounter. Finally, the northern California Islands and San Clemente Island are not densely populated. It is highly probable that drift cards reached San Clemente Island during either or both of the releases, but were not recovered because access to the shoreline is restricted by Naval operations. Santa Barbara, Anacapa, Santa Cruz, Santa Rosa and San Miguel Islands are located north of SNI with limited pedestrian access. These five northern islands comprise Channel Islands National Park. Employees of the park responsible for monitoring isolated stretches of island shorelines would have recovered cards if they were encountered; however the chance of recovery was likely to be low.

Variation in Dispersal Distance

The distance traveled and recovery rate of drift cards in the present study may have been influenced by factors including deployment

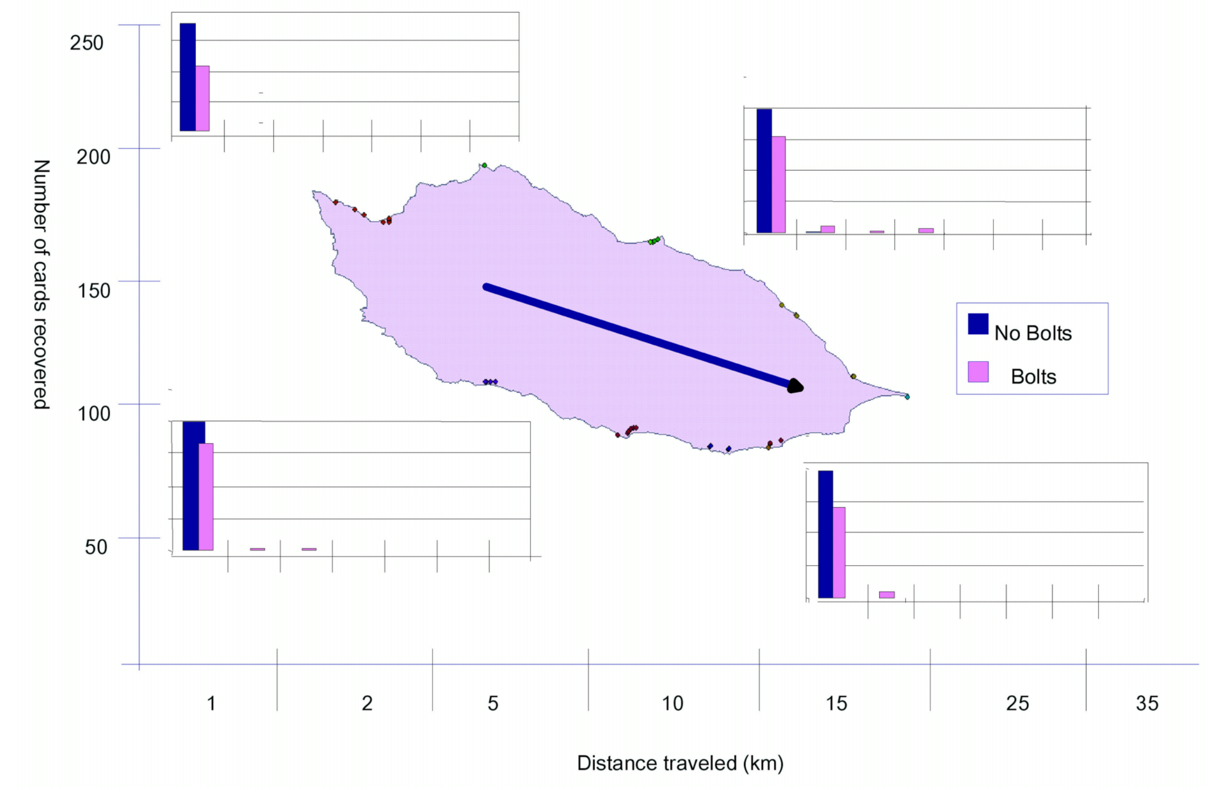

Figure 6. Histograms of distance traveled and number of cards recovered for each release site following the June 2003 release periods. The small arrows point to the release site. The large arrow indicates that drift cards traveled eastward from the site of release, without exception. Dots along the shoreline map indicate points of drift card recovery. The axes of each small graph are identical to the larger axes labeled distance traveled (x) and number of cards recovered (y).

method, wave action, entrapment in local embayments, and temporal variation in sea surface circulation patterns. In an effort to accurately simulate the broadcast spawning of intertidal species, we deployed cards by tossing them from shore. It is likely that many of the cards failed to leave the surf zone and were heavily influenced by local wave action, ultimately preventing broad scale dispersal. Similarly, Schwartzlose (1962) indicated that cards released near shore showed a higher, local, recovery rate than cards released offshore. Cards that did become entrained in currents and traveled beyond the release site varied in the distance traveled between years of deployment. Temporal variation in sea surface circulation patterns may also explain the variation in distance traveled between the two release periods. The August 2002 release occurred at the very beginning of the 2002–2003 El Niño, and the June 2003 release occurred near the transition from the El Niño event to the subsequent La Niña. El Niño events are strongly correlated with reduced spawning and recruitment of larvae in many marine species (McFarlane et al. 2000). The effect of sea surface temperature differences combined with differences in upwelling patterns could potentially alter circulation patterns (Winant et al. 1999), perhaps explaining the differences in sea surface current patterns observed between the August and June release dates.

Survey effort at SNI significantly influenced recovery rates. Following both releases, the majority of cards were recovered during intensive survey periods. Our results indicate that most of the drift cards recovered at SNI were beached within one day of release. For beaches surveyed both 1–2 days and 25 days after release, all card recoveries were made during the survey done 1–2 days post-release. Likewise, the entire perimeter of the island was surveyed twice following the June 2003 release. Almost all cards recovered after that release were retrieved during the first intensive survey effort. The fact that recovered cards were not found farther from the release site as time after

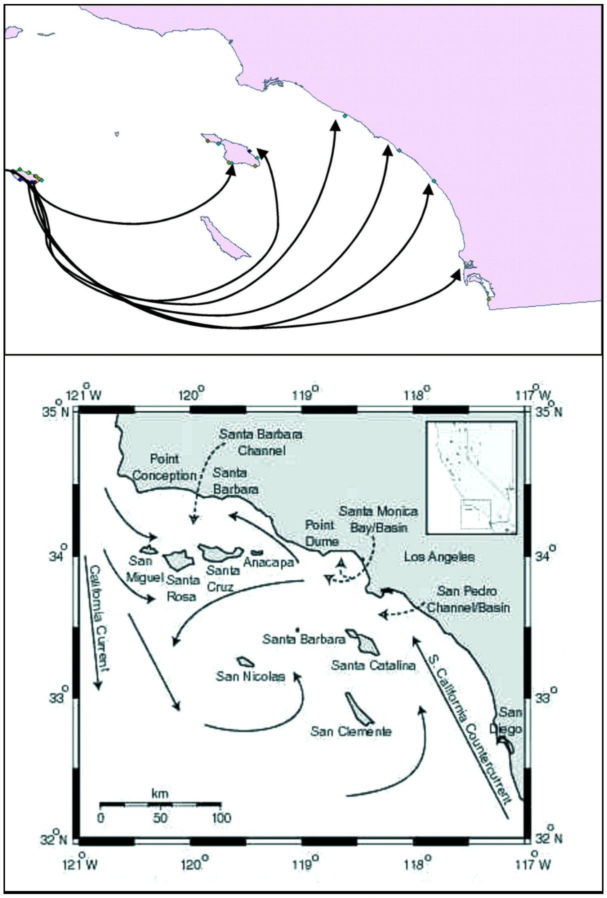

Figure 7. Likely drift card trajectories (upper map) based on published sea surface circulation patterns (lower map; after Hickey 1992).

the initial deployment elapsed suggests that in general, the drift cards were stranded rapidly and locally after release, and that subsequent re-flotation of stranded cards was rare. Additionally, it may be assumed that un-recovered cards dispersed longer distances than cards recovered in the immediate vicinity of the deployment site. This limitation may have led to the under-sampling of cards traveling longer distances.

No cards were returned from north of Point Conception or south of the U.S./Mexico border. It is possible that drift cards traveled to the Baja California coast. Historically, the return rates from Baja California have been low (Schwartzlose 1962), and drift card dispersal south of the U.S./Mexico border is poorly understood. Travel north of Point Conception would require drift cards to become entrained in the California countercurrent. Previous studies imply that Point Conception limits the travel of drift cards from southern California northward (Schwartzlose 1962), because of variations in current patterns.

One criticism of drift card studies is that drift cards are more affected by wind-driven currents than geostrophic currents. The data resulting from the wind simulation imply surface particle movement patterns different from the drift card data. The drift card data corresponded with known patterns of sea surface circulation in the SCB, whereas results from the wind simulation did not. These results suggest that the observed drift card trajectories resulted from geostrophic currents, as well as from wind forcing.

Population Linkages and Implications for Abalone Larval Dispersal

The data presented here demonstrate significant retention of drift cards at SNI with intermittent dispersal to neighboring islands and the California mainland. Genetic data corroborate the results of the present drift card study; abalone

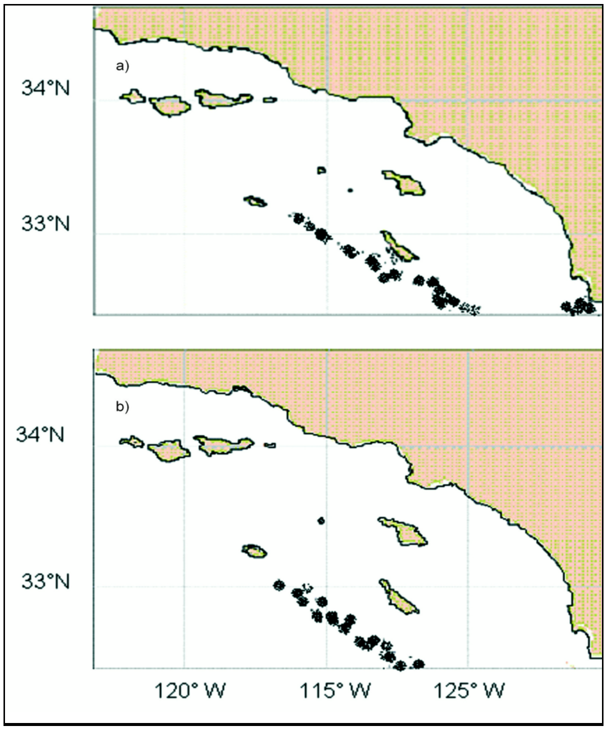

Figure 8. Results of GNOME simulation model of wind driven particle dispersal after 15 days. The simulation began with particles distributed around the perimeter of SNI, and then dispersed according to wind speed and direction during the 15 days following release. Size and color of particles are uniform. The darker and larger appearing particles are actually clusters of particles. Map a) depicts results from August 2002, and map b) depicts the results from June 2003.

populations separated by approximately 2 km on SNI are as genetically differentiated as individual island populations (Chambers 2004), suggesting local larval retention. Similarly, along the central California coast, neighboring black abalone populations were significantly differentiated genetically (Hamm and Burton 2000). Both the genetic data (Hamm and Burton 2000, Chambers 2004) and the drift card data presented here suggest the potential for the persistence of a metapopulation structure in the system, in which occasional migrants prevent inbreeding within subpopulations (Frankham et al. 2002), while localized recruitment contributes to metapopulation persistence (Armsworth 2001). Armsworth (2001) conducted simulations to evaluate population persistence and recovery of systems with high local retention of larvae in comparison to populations connected by significant larval flow and concluded that persistence of a meta-population depends on a combination of local retention and long-distance migration. Metapopulation persistence of black abalones may be limited by the low population densities of black abalones at Santa Catalina Island and the southern California mainland. Black abalone population densities lower than a critical threshold approach functional extinction due to the decreasing probability of successful union of gametes (Tegner 1992). Our results suggest that it is un-likely, albeit uncertain, that the occasional migrants from SNI will succeed in replenishing those depleted populations.

One of the flaws of using a passively drifting surrogate for determining the migrating distance of fish and invertebrate larvae is the inability to incorporate larval behavior into the simulation. Studies of abalone larval behavior indicate that the larvae of the genus initially swim upward in the water column, settling to the bottom as their shells develop (Crisp 1974, Forward et al. 1989). During the surface stage of larval development, drift cards function as good surrogates for studying larval dispersal. It is also possible for larvae to form clusters and travel as swarms (Highsmith 1985) or by attachment to drift kelp or other surface floating objects. Abalone larvae attached to surface floating objects may actually travel more like drift cards than individual larvae. Other larval behavior, such as migration through the water column, could play a substantial role in larval dispersal (Young 1995). For example, Young (1995) determined that the vertical migration of crab zoea larvae maximized offshore transport. Additional studies indicated that vertical migration was necessary for invertebrate larvae to exit a low inflow estuary (DiBacco et al. 2001). The position and behavior of abalone larvae in the water column is not well understood, but likely influences the dispersal potential of the species.

The significant retention of drift cards in the present study indicates great potential for future self-generated recruitment by abalone into the remnant population, particularly on the south side of SNI where black abalone densities have consistently been highest (VanBlaricom 1993). If larval retention is consistent with the high retention of drift cards implied by the present study, then it is probable that larvae will settle in highly suitable habitat. While abalone larvae cannot settle within the 1–2 day drift card recovery period reported here, they may remain near their source site by becoming entrained by local wave action or becoming trapped in local embayments (e.g., Butman 1987, Dibaccio et al. 2001, Gramtham et al. 2003).

Implications for Management and Recovery of Black Abalone Populations

The natural recovery of severely reduced abalone populations can be a very slow process (e.g., Tegner 1992). Management options to expedite the process of recovery and increase population densities to historic levels include translocation and supplementation efforts. Population enhancement efforts have been made in other abalone species by translocations (Tegner and Butler 1985), seeding (Gaffney et al. 1996, Burton and Tegner 2000), and transplantation of local broodstock (Tegner 1992). Previous enhancement projects have been plagued by problems including high mortality rates (from 91% to 68%; Tegner and Butler 1989, Schiel 1992), failed reproduction and poaching (Tegner et al. 1992). The most successful and cost effective method may be the transplantation of local broodstock. According to Tegner and Butler (1989), the density of recruiting green abalone (*Haliotis fulgens*) increased in abundance following transplantation. The availability of long term population data sets (VanBlaricom unpubl. data), population genetics data and larval dispersal information may make broodstock transplantation an effective management tool for black abalones in the California Islands. However, before such a management effort is made, it must be confirmed that WS resistance has emerged in black abalone populations. Lacking resistance on a population scale, a purposeful increase in abalone density may increase transmission rates of WS.

The drift card data presented in this study imply that black abalone larvae may be locally retained with occasional migrants from SNI to Santa Catalina Island and the California mainland. The population at SNI may recover from disease-induced catastrophic mortality if recruitment to the population continues. If similar recruitment begins to occur at the other islands and the California mainland coast, there is potential for the species to recover throughout its original range.

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