

Abundance and dispersal of drifting kelp *Macrocystis pyrifera* rafts in the Southern California Bight

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ABSTRACT: Drifting rafts of *Macrocystis pyrifera* are formed when attached plants are separated from the substrate. These kelp rafts have the potential to disperse fauna among isolated kelp forests; however, the success of this dispersal mechanism will be influenced by the abundance and the dispersal paths of the rafts. The abundance of kelp rafts in the Southern California Bight (SCB) was estimated from the loss of attached plants, and by direct observation of rafts at sea. Loss of attached adult plants was highest in winter (23%) and lowest in fall (8%) at 7 sites within 2 coastal kelp beds over the period of 1988 to 1998. Raft density at sea differed among 4 cruises in the period from 1995 to 1997, and ranged from 0.78 to 6.96 km⁻² (average 3.02 km⁻²). In the SCB these densities correspond to an instantaneous abundance of between 39000 and 348000 drifting rafts. The potential raft dispersal paths and the frequency of exchanges among kelp forests were evaluated using satellite-tracked drifters. Southward dispersal away from the coast was observed in all months of the year. Dispersal north, both along the coast and away from the coast, was most likely between July and January (summer–winter), while dispersal south along the coast was likely between January and August (late winter and early spring). A definition of a 'successful connection event' was adopted, based on a drifter starting less than 10 km and ending less than 5 km from the coast. Under this definition, 45% of all drifter releases were successful. Analysis of the temporal pattern and drift trajectories of the mainland-mainland successes revealed that Pt. Conception was always a boundary for north to south connections, but was open to south to north connections between fall and winter (October to January). Drifters released and remaining north or south of Pt. Conception were successful throughout the year. Connections were not made more than 300 km from a release region, under any criteria for success. The results of this study indicate that while rafts may drift long distances, successful connection of kelp forests through kelp rafts is limited to shorter distances.

KEY WORDS: Algal transport · Benthic inputs · Biogeographic boundary · Dispersal · *Macrocystis* rafts · Rafting · Satellite drifters

INTRODUCTION

Dispersal and recruitment are recognized as key processes structuring benthic marine invertebrate populations with complex life cycles (e.g. Roughgarden et al. 1988, Underwood & Fairweather 1989). Larval dispersal and recruitment have been identified as important in maintaining coastal populations (e.g. Rough-

garden et al. 1985, Eckman 1996), but the dispersal of non-planktonic stages has received less attention. Non-planktonic dispersal can involve active movement such as walking or swimming, or passive movement while resident on other moving biotic or abiotic objects. Passive movement, or rafting, on floating objects at the sea surface is an alternative to planktonic larval dispersal for both motile and sessile adults and sub-adult stages (e.g. eggs) and may be particularly important in moving species long distances (Vallentin 1895, Fell 1962, Highsmith 1985, Johannesson 1988). At the ocean surface logs (Hunter & Mitchell 1967),

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pumice (Jokiel 1988, 1990a,b), anthropogenic debris (Venrick et al. 1973, Winston 1982), and algae (Valentin 1895, Bushing 1994) can all provide rafting habitat. Rafting may be the only dispersal mechanism for benthic species with non-planktonic larvae, but can also be important for organisms with limited larval dispersal. Rafting may thus be an important mechanism in connecting isolated marine populations.

Forests of the giant kelp *Macrocystis pyrifera* are found along the west coast of North America between Isla Asuncion (27.5° N, Punta Eugenia, Baja California) and San Francisco (37.5° N, California) (Tegner & Dayton 1987), a latitudinal range of 10° (about 1086 km). These forests, isolated from each other by varying distances of non-kelp forest coast, periodically disappear through the action of both biotic and abiotic factors (Dayton 1985, Ebeling et al. 1985, Tegner & Dayton 1987, Foster & Schiel 1988, North 1994, Tegner et al. 1997). The community associated with forests of *M. pyrifera* includes many species of fish and invertebrates, some of whose abundance is influenced by the presence of the kelp forest (e.g. Dayton 1985, Carr 1989). If a region loses its kelp forest, some of these species may also disappear. Kelp forests can reappear when bare rocky substrate is colonized by kelp spores (Reed et al. 1992, North 1994). Subsequent colonization of the 'new' forest by fauna may be from local animals remaining at the site, or through long-distance immigration. Long-distance planktonic recruitment may be limited because of the short larval lifetime of many invertebrates found within *M. pyrifera* forests. Short larval lifetimes, from minutes to days, coupled with the reduced water flow within kelp forests, may limit the movements of larvae from forest to forest (Jackson & Winant 1983, Tegner 1986, Tegner & Dayton 1987). As an alternative, movements between kelp forests by kelp rafts may both be possible and play a role in kelp fauna population dynamics. Faunal recolonization of new kelp forests as well as genetic exchange and renewal of species between existing forests may all be facilitated by kelp rafts. Long-distance faunal movements are also likely aboard kelp rafts (Fell 1962, Bushing 1994, Hobday 1998).

Macrocystis pyrifera plants are attached to the substrate with a holdfast comprised of haptera. In older plants the strength of the holdfast deteriorates due to death at the center or grazer cavitation (Ghelardi 1971, Tegner et al. 1995), or lack of haptera growth to anchor the large holdfasts (Cribb 1954). When this holdfast attachment is broken, most often due to storm-associated waves (Dayton et al. 1984, Dayton 1985, Ebeling et al. 1985, Seymour et al. 1989), a plant can float to the surface and form a drifting raft. If rafts do not become entangled in the kelp forest or immediately wash to the shore, they may drift at the ocean surface for

up to 100 d (Hobday 1998, A.J.H. unpubl.). Large amounts of kelp may be lost from forests in the form of drifting rafts. Harrold & Lisin (1989) estimated that 130000 t of kelp were exported annually as drift from Monterey, California kelp forests. Harrold & Lisin (1989) also made the only attempt at large-scale tracking of kelp rafts. They radio-tracked 39 *M. pyrifera* rafts in Monterey Bay (a semi-enclosed situation), relocating them several times a day from a small aircraft. Most rafts beached within 5 to 7 d, and the authors thus concluded that most of the rafts originating from Monterey peninsula kelp forests were deposited within the bay and not transported long distances offshore or along the coast. A few rafts were not located, however, suggesting dispersal out of the area had occurred.

Drifting kelp rafts initially carry a subset of the kelp forest fauna, which may persist or be lost. If the kelp rafts return to nearshore kelp forests or other suitable habitats, transfer of the passenger fauna is possible. When the return time of a raft to suitable habitat is longer than the persistence time of a particular species on that raft, dispersal and transfer will not occur (Hobday 1998). Seasonal differences in the abundance of the initial species, coupled with seasonal differences in raft abundance, dispersal paths and times will influence the probability of success at a particular time (Hobday 1998). Behavioral (e.g. faunal fidelity to the rafts) and physiological (e.g. raft floating lifetime) constraints to faunal dispersal exist; these patterns can be overlaid after the raft dispersal patterns are determined.

Information on the seasonal abundance and dispersal paths of kelp rafts is important in establishing the frequency of connections between isolated kelp forests. In this paper, both direct (observation) and indirect methods (loss of attached plants) were used to estimate raft abundance. Dispersal patterns, distances and times for kelp rafts were based on analyses of satellite-tracked surface drifters released in the Southern California Bight (SCB).

METHODS

Raft abundance. Abundance of drifting kelp can be determined from indirect measures such as the amount of beach drift (ZoBell 1971) or loss of attached plants, or by direct observations from boats or planes (Harrold & Lisin 1989, Kingsford 1995). Because of the widely dispersed distribution of kelp rafts (Kingsford 1995), a large survey area is required for direct observations and estimation of kelp raft density.

Abundance via loss of attached plants: Raft abundance was indirectly estimated in Southern California via loss of attached plants from 2 kelp forests. The Dayton/Tegner lab at the Scripps Institution of Oceanogra-

phy monitored individual *Macrocystis pyrifera* plants at the Pt. Loma and the La Jolla kelp forests for the period of 1988 to 1998. At each of 7 sites (6 within the Pt. Loma forest, and 1 at the La Jolla forest) (Fig. 1) located in water depths of between 12 and 18 m, plants were monitored at four 25 × 4 m transects. Each *M. pyrifera* 'recruit' (defined here as a plant having more than 4 stipes at a height 1 m above the substrate) was mapped at these sites. The status of each plant was recorded for each season, summer (June to August), fall (September to November), winter (December to February) and spring (March to May), during the study period.

For analysis the proportion of plants lost since the last survey were arcsine (\sqrt{p}) transformed (Sokal & Rohlf 1981). Data was analyzed to test for differences between seasons and sites, using both 1 and 2-way ANOVAs, with site and season as fixed factors. Posthoc tests of differences were done with Fisher's least-square differences test (Fisher's LSD). Data were back-transformed for graphing and reporting of means and uncertainties. An $\alpha < 0.05$ defined significant differences for these and all subsequent tests.

Abundance via direct observation—line transect surveys: Four transect surveys from ships of opportunity were conducted to provide direct estimates of drifting kelp raft abundance in the SCB (September 1995, February 1996, June 1997, and December 1997).

In addition, information on raft sizes was collected on an earlier cruise (March 1995). Data were collected in an area defined by the coordinates 32.0 to 34.5° N, and 117.0 to 120.5° W, approximately 271 km from north to south and 380 km from east to west (Fig. 1). Transects were random with regard to kelp rafts, and were transit segments between oceanographic stations occupied for other studies. Ship speed was typically 10 knots, and cruises lasted between 6 and 19 d. Transects were approximately 1 h in length, and the start and end positions (latitude and longitude), ship speed (knots), weather (cloud cover, visibility, wind speed and direction) and ocean conditions (swell height and direction, seas) were logged. During each transect the size of each raft >0.5 m diameter and its perpendicular distance from the trackline was estimated, along with any cues that assisted detection (plastics, seabirds). Distances from the trackline were estimated by eye; however, the ship's radar was used to calibrate observers. Prior to sampling, observers would estimate distances to objects that showed up on radar such as boats, moorings and harbor makers, then compare those estimates to those provided by the radar system. On 2 cruises when an additional observer assisted the author, a period of dual observation was carried out at the beginning of the cruise to calibrate observations. Data were not collected when seastate rose above Beaufort

3 and the observations were made from the best side of the trackline in terms of sun glare and wind chop.

Density estimates were calculated using line transect methods described by Buckland et al. (1993) and the program DISTANCE (Laake et al. 1993). Because different ships were used for each cruise, different observation heights and viewing conditions were experienced, and each set of cruise data was modeled separately as the detection function was expected to differ. Data were truncated, with the farthest 5% of observations from the trackline eliminated from analyses, and between 3 and 10 distance bins selected to satisfy the shape criteria (Buckland et al. 1993). Cues played a minor role in the detection of rafts, and were not considered in the analyses. The detection of rafts is likely to vary with raft size: accordingly, density was first estimated without size stratification and then by separately considering rafts larger and smaller than 3 m in diameter. Differences in raft density and size (log [diameter + 0.1] transformed) between cruises were evaluated with the z-test (Buckland et al. 1993).

Dispersal patterns via satellite-tracked drifters. The dispersal paths and distances

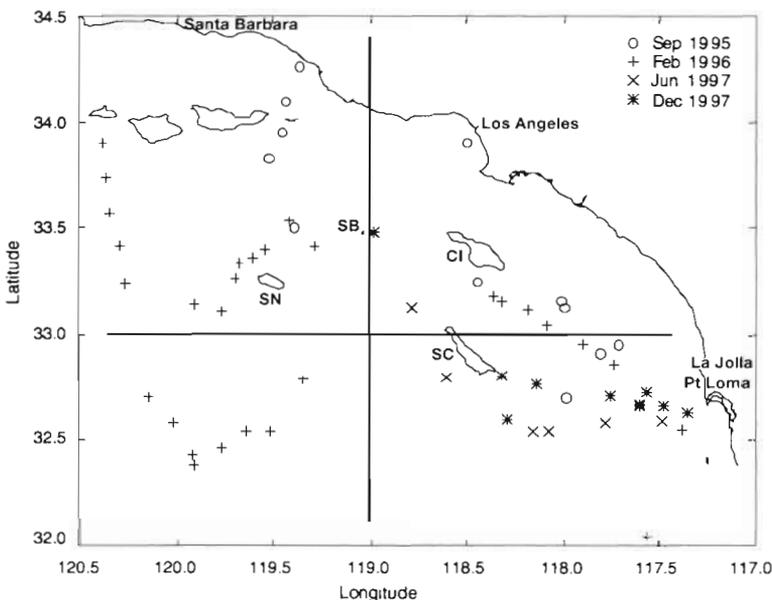


Fig. 1. Location of all ship-based abundance transects from the 4 cruises in the Southern California Bight (SCB). The start location for each transect is shown; at this scale end points would be extremely close to the start points. Transects carried out on each cruise are noted with different symbols. Lines at 119.5° W and 33° N indicate onshore/offshore and north/south divisions of the SCB discussed in the 'Results'. The 4 northern channel islands are, from left to right: San Miguel, Santa Rosa, Santa Cruz and Anacapa. San Clemente (SC), Santa Catalina (SI), San Nicholas (SN) and Santa Barbara (SB) Islands are indicated on the map

traveled by drifting objects such as kelp rafts may be inferred by a variety of methods. These include visual tracking (Kingsford 1995), drift tube studies (Levin 1983, Tegner & Butler 1985, Hlady & Burger 1993), mark-recapture methods (Worcester 1994, Kingsford 1995), genetic markers (Ruckelshaus 1996, Ayre et al. 1997), radio-tracking (Harrold & Lisin 1989), satellite-tracking (Poulain & Niiler 1989, Papi et al. 1997), and oceanographic models. Drift tube, mark-recapture and genetic marker methods provide only the start and end points, and do not always allow the drift time to be determined. Both radio and visual tracking limit the number, time and distance that rafts may be followed. Oceanographic modeling is limited by the spatial and temporal resolution of the available data. Given the space and time scales involved, the best method would be to satellite-track a large number of rafts released from a variety of locations and times. This option was not available; instead a similar data set was used.

Argos satellite-tracked drifters released north and south of Pt. Conception as part of unrelated research by C. Winant et al. (unpubl. data) at the Scripps Institution of Oceanography were used to describe raft dispersal in this study. A total of 441 drifters were released in 29 deployment batches between October 1992 and December 1997. In each deployment, month drifters were released over several days, primarily from 24 permanent sites that coincided with current or historical mooring locations used by Winant et al. (Fig. 2). Of the

total number released, 18 drifters malfunctioned and were eliminated from all analyses.

Each drifter consisted of a submerged, 1 m long vertical tube, an antenna, and 4 cloth vanes supported on rods that extended radially from the top and bottom of the tube (drifter diameter 1.2 m). A small float was attached at the end of each rod. A transmitter inside each tube allowed the drifters to be located by orbiting satellites several times each day, with positional accuracy varying between 150 and 1000 m. If the drifter beached or was removed from the water the data series was truncated to the last free position. The coastline can also be considered as an absorbing boundary for kelp rafts, as beached kelp sinks when returned to the water (ZoBell 1971, Harrold & Lisin 1989, Hobday 1998). The drifters were programmed to transmit for between 40 and 90 d after release. Additional information and pictures of the drifters can be viewed at the following Web site: <http://www-ccs.ucsd.edu/research/sbcsmb/drifters>.

These drifters are suitable mimics of kelp rafts. Like kelp rafts, drifters float at the surface and are passive. While the raft canopy may sometimes protrude slightly above the surface of the water, the influence of winds on rafts, as on the drifters, is minimal (D. Alden pers. comm.). If kelp rafts extend lower in the water column than the 1 m occupied by the drifters, they may be anchored to water masses moving at different velocities than the surface waters. Although the majority of the raft biomass floats at the surface, large kelp rafts and those with holdfasts do occupy space lower in the water column, often down to 5 m. If there is vertical shear in the water column, the kelp raft may not move exactly as a drifter would; however, because at least the upper 10 m or so of the water column typically moves as a slab (Price et al. 1986), kelp rafts and drifters should behave in the same way, and so in this study drifters are assumed to mimic kelp rafts.

The general patterns of ocean surface circulation described by the drifter trajectories in the SCB are first qualitatively described. Drifter trajectories for each release month were classified into 4 ocean zones, radiating out from Pt. Conception (Fig. 2). These zones were 'north along', 'north away', 'south along' and 'south away' from the coast. In addition, months in which drifters remained within the Santa Barbara Channel for a period of time were noted.

While drifters did not travel in straight lines, overall displacement is of interest for the purpose of evaluating the dispersal characteristics of kelp raft mimics. Average drifter displacements for different time periods of drifter transmission were first calculated. If, however, a kelp raft is to connect kelp forests, and the likelihood of this event is to be evaluated from the drifter data, additional conditions should be imposed. Ideally, drifter release positions should match initial

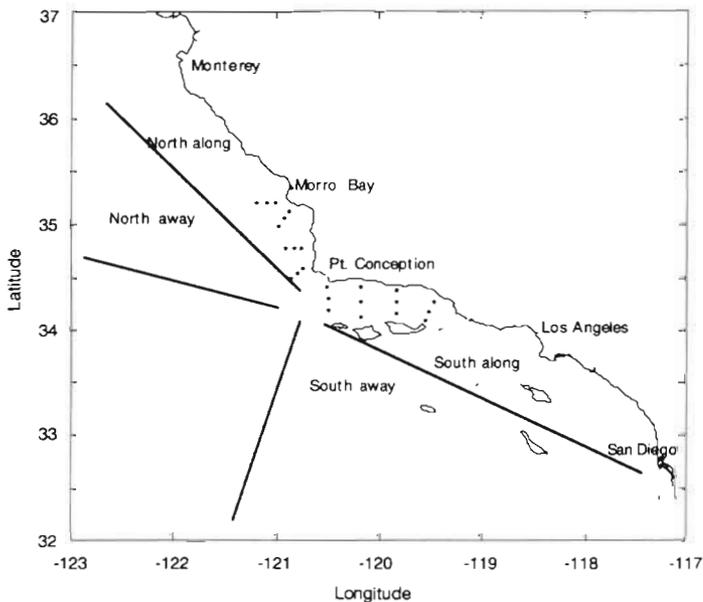


Fig. 2. Drifter trajectory zones. Four ocean zones are defined: 'south along', 'south away', 'north along', and 'north away' from coast. Each set of drifter deployment trajectories was allocated to 1 or more zones, according to the dominant dispersal pattern. *24 permanent drifter deployment sites. Coordinates are in decimal degrees

kelp raft locations, i.e. the outside edge of a kelp forest typically less than 2 km from the coast. For a successful connection, the final position of the drifter should be within a similar distance of the coast. Unfortunately, drifters were not intentionally released close to kelp forests; in fact most were released more than 5 km from the nearest land. These drifter patterns are therefore representative of kelp rafts that have escaped entrapment within the kelp forest. Drifter 'success' was evaluated using scenarios with a variety of start and end distances from the coast. Because of the inaccuracy in the drifter positional fixes and the coastline coordinates, the truncation of drifter files just prior to beaching, and the results from the set of scenarios explored, 'starting less than 10 km and ending less than 5 km from the coast', was defined as the criteria for drifter success in subsequent analyses. The overall and monthly frequency of successful drifters making island-mainland, mainland-island, island-island and mainland-mainland connections was calculated. An investigation of seasonal connections between central and Southern California was also undertaken using the drifters that made successful mainland connections. Pt. Conception is the usual latitudinal feature associated with the biogeographic division of these 2 regions (Newman 1979, Cimberg 1981), and the connectivity across this boundary by drifters (kelp rafts) is of particular interest (Fig. 2).

Finally, to use more of the available drifter data, release locations were divided into those north and south of Pt. Conception. The final latitudinal position was determined for drifters released in each region. The frequency of 'connection success' (final position within 5 km of land) and the average drift time from each release region was found for 0.5° (54 km) latitudinal bins along the Californian coast.

RESULTS

Raft abundance

Abundance via loss of attached plants

There were 177 surveys at the 7 sites, spread over 34 survey months between July 1988 and January 1998. A total of 2516 plants was followed during this period. Plant loss was not significantly related to season, or to site (Table 1). The overall average loss of attached *Macrocystis pyrifera* plants per season was 0.17.

The average age at which plants were lost from the Pt. Loma (6 sites) and La Jolla (1 site) kelp forests was 20.11 mo, and the majority of plants lost were from young cohorts (Fig. 3A). The proportion of plants lost from a cohort was constant and between 0.12 and 0.25

Table 1. ANOVA on the arcsine (\sqrt{p}) transformed percentage of *Macrocystis pyrifera* plant loss data from Pt. Loma and La Jolla kelp beds, 1988–1998. Loss data pooled across all 7 sites

	SS	df	MS	F-ratio	p
2-way ANOVA, all plants					
Season	0.535	3	0.178	2.059	0.108
Site	0.405	6	0.068	0.779	0.587
Season × Site	1.588	18	0.088	1.018	0.443
Error	12.905	143	0.087		
2-way ANOVA, adult plants					
Season	0.644	3	0.215	2.550	0.059
Site	0.944	6	0.157	1.869	0.092
Season × Site	0.918	18	0.051	0.606	0.889
Error	10.188	121	0.084		
1-way ANOVA, adult plants					
Season	0.896	3	0.299	3.612	0.015
Error	11.991	145	0.083		

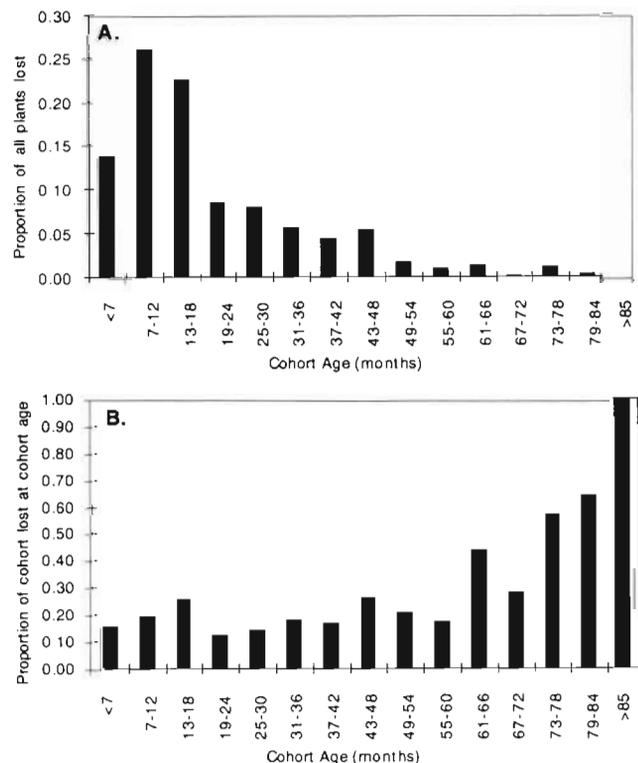


Fig. 3. *Macrocystis pyrifera*. Loss of attached plants from sites at Pt. Loma and La Jolla between 1988 and 1998. (A) Proportion of plants lost as a function of plant cohort age. (B) Proportion of cohort lost as a function of cohort age

per age class. Once plants reached 61 mo of age, loss increased rapidly (Fig. 3B). The oldest plant in this study remained attached for 105 mo (8.75 yr).

Recruitment was not seasonal (average number of recruits per site was compared among 4 seasons,

$p = 0.530$). Many of the lost plants were less than 1 yr of age (Fig. 3), and too small (<10 stipes plant^{-1}) to form visible rafts. When all plants younger than 1 yr were eliminated from the data, 1279 plants remained; these were tracked over 149 surveys over 34 mo at the 7 sites (not all sites were surveyed for the full period of study). The average loss of these adult plants per 3 mo period was 15.4%. Differences in adult plant loss per site per season were marginally non-significant ($p < 0.06$) (Table 1). A Fisher's LSD test (performed even though the ANOVA was non-significant at the 0.05 level), showed that the losses in fall and winter were significantly different ($p < 0.012$), with summer and winter losses marginally non-significant ($p < 0.065$).

When the seasonal losses at the 7 sites were pooled, adult plant loss was found to be significantly different between seasons (Table 1). Loss of adult plants was highest in winter (0.23) (Fig. 4).

Abundance via direct observation

Size was estimated for a total of 433 rafts and the distance from the trackline recorded for 358 of these during 737 km of cruise transects. No systematic biases were found between transects covered by different observers so they were not analyzed separately. Uniform, half-normal, hazard rate, and negative exponential estimator models were compared with the frequency distributions of perpendicular distance of kelp

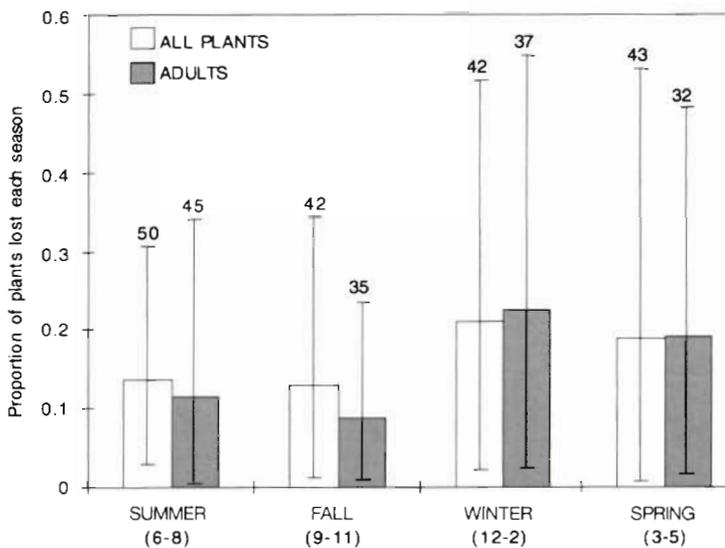


Fig. 4. *Macrocyctis pyrifera*. Proportion of all and adult plants lost by season between 1988 and 1998 at La Jolla and Pt. Loma. Back-transformed data are shown. The months combined for each season are indicated below each season and in the 'Methods'. The number of seasonal replicates (sites \times months surveyed) is shown above each column; bars represent ± 1 SD

Table 2. The best detection function model selected for each drifting raft observation data set by the program DISTANCE. A model may be comprised of a key function plus an adjustment term. Addition of adjustment terms and the number of parameters is carried out in stepwise fashion, and if there is no improvement of the Akaike Information Criterion at the 0.05 level, the extra terms are not retained in the final model (see Buckland et al. 1993 for more details). The chi-squared p-value is a measure of the goodness of fit of the best model to the data for the bin width intervals provided to the DISTANCE program. **Bold** chi-square p-values indicate that the model fit was significantly different from the data

Cruise (size)	Key function	Adjustment term	Chi-squared p-value
9509 (all rafts)	Hazard		0.019
9602 (all rafts)	Hazard	Cosine (2)	0.005
9706 (all rafts)	Half normal		0.305
9712 (all rafts)	Hazard		0.355
9509 (small rafts)	Hazard	Cosine (2, 3)	0.001
9602 (small rafts)	Hazard	Cosine (2)	0.017
9712 (small rafts)	Hazard		0.680
9509 (large rafts)	Hazard		0.300
9602 (large rafts)	Uniform	Polynomial (2)	0.731
9712 (large rafts)	Uniform		0.350

raft to the trackline with the DISTANCE program. Each model can also incorporate adjustment terms that provide a better fit. For each division of the data, the best model was selected according to the lowest Akaike Information Criterion (Buckland et al. 1993). The hazard-rate was the most selected function, and

adjustment terms were not always required to improve the estimator model (Table 2). In only 4 out of 10 cases did the best model fail to provide a significant fit according to the chi-square test. For large rafts, the best model was always a good one (by the chi-square test). The December 1997 large raft data were described best by the uniform model, with no adjustment terms, which means that on this cruise there was no decline in the detection of large rafts over the strip width surveyed.

Total raft density varied from 0.78 to 6.96 km^{-2} (Table 3). Assuming the area sampled is represented a $2^\circ \times 2^\circ$ region (approximately 50000 km^2 , 60 nautical miles per degree latitude; 1 nautical mile = 1.852 km) of the SCB, the range of total raft density estimates corresponds to between 39000 and 348000 rafts. There was no obvious association between raft density and season when cruises were divided into summer (September 1995 and June 1997) and winter (February 1996 and December 1997) cruises. Observations of rafts were size-stratified, into small (<3.0 m diameter), and large (>3.0 m dia-

Table 3. *Macrocystis pyrifera*. Estimated density of rafts from 4 cruises in the Southern California Bight. Densities for all rafts (A), rafts <3 m diameter (S), and rafts >3 m diameter (B) are shown. The number of sightings (before 5% truncation), total distance surveyed, number of transects, estimated density, 95% confidence intervals (CI) for density, and variation in the estimate (CV) are provided. The percentages of the total variation in the estimated density of rafts attributable to uncertainties in detection probabilities and in encounter rate are also shown. Densities that differ significantly in each size group (A, S, B) are indicated by different superscript letters ($p < 0.05$, z-test, Buckland et al. 1993)

Cruise (size)	Rafts (n)	Dist. (km)	Transects (n)	Estimated density (km^{-2})	95% CI	CV (%)	Detection probability (%)	Encounter rate (%)
Sep 95 (A)	177	114	12	6.96 ^a	3.96–12.25	28	42.8	57.2
Feb 96 (A)	66	364	29	2.79 ^{ab}	1.15–6.77	46	45.1	54.9
Jun 97 (A)	18	120	7	0.78 ^b	0.18–3.33	67	9.1	90.9
Dec 97 (A)	79	139	10	1.55 ^b	0.36–6.73	75	12.9	87.1
Sep 95 (S)	118	114	12	5.73 ^a	2.96–11.07	32	33.2	66.8
Feb 96 (S)	49	364	29	2.65 ^b	1.10–6.38	46	48.5	51.5
Dec 97 (S)	55	139	10	1.26 ^b	0.26–6.11	82	8.3	91.7
Sep 95 (B)	59	114	12	0.87 ^a	0.38–1.98	42	57.6	42.4
Feb 96 (B)	17	364	29	0.07 ^b	0.03–0.18	49	13.8	86.2
Dec 97 (B)	24	139	10	0.12 ^b	0.03–0.38	57	0.0	100.0
Average							27.13	72.87

meter) categories for the 3 cruises where sample size was large. Large rafts (range of mean density estimates 0.07 to 0.87 km^{-2}) were less dense than small rafts (1.26 to 5.73 km^{-2}) (Table 3). Some significant differences in densities were found between cruises for both small and large rafts, and were similar to those reported from the analyses of all the rafts. The coefficient of variation (CV) of density estimates ranged from 28 to 80%. The uncertainty of these density estimates is comprised of uncertainty in detection probability and variation in encounter rate. Most of the uncertainty in the density estimates was due to variation in the encounter rate, which averaged 73% of the total (Table 3). This sug-

Table 4. *Macrocystis pyrifera*. Number (n) and average diameter (m) of kelp rafts observed on 5 cruises in the Southern California Bight. Data for all rafts observed, as well as just for those rafts for which distance data were available and used in the density estimates, are provided. (No distance data were taken for the March 1995 cruise). Superscript letters on average sizes are different if the average raft size differed. Differences were evaluated with a z-test on log-transformed data (Buckland et al. 1993). Untransformed means and SE are shown

Cruise	Distance rafts			All rafts		
	n	Average diameter	SE	n	Average size	SE
Mar 1995	–	–	–	18	2.055 ^a	0.300
Sep 1995	177	3.195 ^a	0.163	227	3.330 ^b	0.136
Feb 1996	70	2.770 ^{ac}	0.242	70	2.719 ^b	0.236
Jun 1997	19	1.947 ^{ac}	0.275	21	2.300 ^b	0.294
Dec 1997	82	2.799 ^{bc}	0.287	97	2.750 ^b	0.252

gests that the rafts are patchily distributed.

For cruises where a wide range of the SCB was covered, the area was subdivided to assess north-south or east-west (onshore-offshore) density differences. No north-south density differences were detected about a 33.0° N line for the September 1995 cruise, nor east-west differences about a 119° W line for the February 1996 cruise (Hobday 1998).

Average raft diameter for the cruises was between 1.9 and 3.3 m, and between 75 to 95% of observed rafts were less than 3 m in diameter (Fig. 5). When all size estimates were used, only 1 cruise (March 1995) had a mean diameter of kelp rafts significantly different from the other cruises (Table 4). When only the rafts that were used to provide the density estimates were included, some differences

between cruises were found (Table 4). These differences did not fall into seasonal patterns.

Dispersal patterns via satellite-tracked drifters

Overall drifter patterns

Drifters were released at an average distance of 12.3 km (range 1.7 to 96.7 km) from the nearest coast (island or mainland) and the final position was on average 76.1 km (range 0 to 448 km) from the nearest coast. Drifters transmitted their position for an average of 26 d (range 1 to 89 d). The average drifter displacement was 214 km (range 2.7 to 1092 km). The average displacement speed was 8.5 km d^{-1} (9.84 cm s^{-1}) (range 0.19 to 29.8 km d^{-1}), and displacement was related to the drift time (Table 5).

Drifter trajectories

A constant feature in all months of the year was retention of some drifters in the cyclonic (anticlockwise) circulation within the Santa Barbara Channel. Dispersal to the south away from the coast occurred in all months, usually drifters released at and north of Pt. Conception were carried into this zone (Table 6). Trajectories revealed that along-coast connections to the south were most likely in winter and early spring (January to April), and occasionally occurred in the

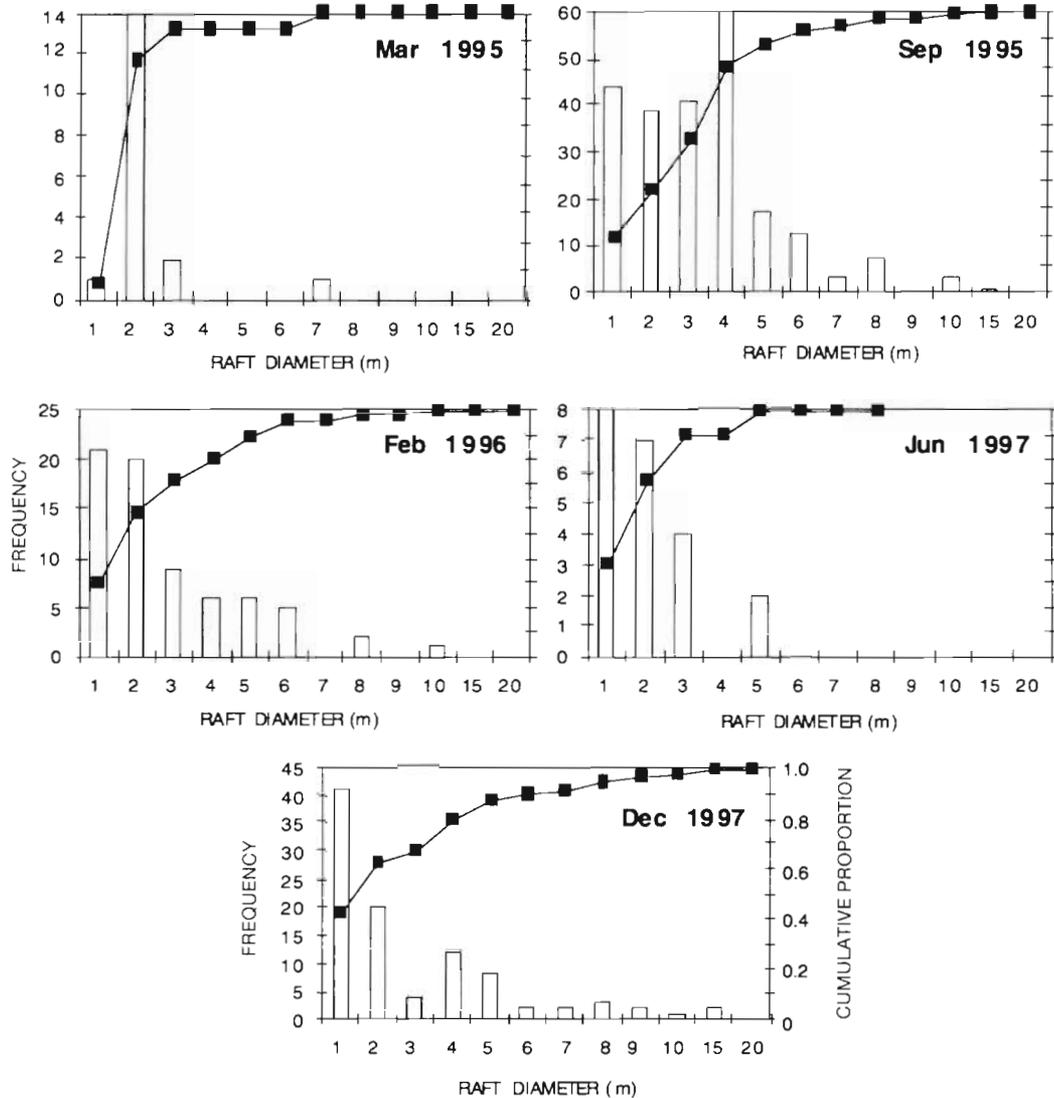


Fig. 5. *Macrocytis pyrifera*. Size distribution of rafts observed on 5 cruises. Cumulative size distribution is shown on the second y-axis. Sample description is given in Table 4. Note the change in scale of the first y-axes between panels

summer (July and August). Northward trajectories, both along the coast and away from the coast, occurred at similar times in late summer, fall and winter (August to January). In late spring (May to June) the drifters revealed a lack of along-coast dispersal in either direction from the Channel release region.

Dispersal scenarios

The success of drifters as 'kelp rafts' was evaluated using various starting and end distances from the coast (Table 7). As the criteria for successful connections were relaxed (i.e. as initial and final distance from the coast increased), the maximum displacement of successful journeys increased. The success for each set of

final distances decreased with increasing initial release distance from the coast. Between 17 and 58% of releases resulted in successful connections for all scenarios. With connection success defined as 'drifters beginning within 10 km and ending within 5 km of the coast', 45% (92/204) of the drifters were successful, drifting for an average of 10 d (range 1 to 38 d) and a displacement of 56 km (range 3 to 220 km).

Specific connection events

Using the above definition of success, the 92 successful drifter connections were divided into combinations of island and mainland connections. During the period of study, mainland-mainland connection events were

Table 5. Average displacements for drifters by time drifting. Drifters were released in the study between October 1992 and December 1997. Sample size for each time bin is shown, total $n = 423$. Average displacement is distance between the first and last position transmitted for each drifter. The maximum and minimum displacements for each time bin are also provided. The number of drifters that floated for more than some time can be calculated by summing the number in each appropriate bin

Drift time (d)	n	Average displacement (km)	Range (km)
1-5	87	26.75	3.87-133.15
6-10	40	39.16	2.71-110.30
11-20	53	114.93	14.10-114.93
21-30	43	186.99	31.2-661.72
31-40	165	326.75	7.56-979.45
41-50	13	508.45	332.07-734.31
51-60	7	336.88	198.56-503.34
61-70	0		
71-80	14	646.12	205-1092
80-90	1	591.30	

the most common ($n = 47$), followed by mainland-island ($n = 26$, 13 in each direction), and island-island ($n = 19$, 9 between different islands) (Table 8). The success of drifters beginning within 10 km of islands (46%) was similar to the success of drifters beginning within 10 km of the mainland (44%). There was no difference in time required for island-mainland and mainland-island successful connection events (t -test, $p < 0.30$, $df = 24$), but there was a difference in the displacement (t -test, $p < 0.005$, $df = 24$), with island-mainland drifters covering almost twice the distance (Table 8). No other differences in time or distance were found for the possible connection events. All but 1 of the 9 inter-island connection events were between the 4 northern islands (San Miguel, Santa Rosa, Santa Cruz and Anacapa).

One drifter connected Santa Barbara and Anacapa islands. Similarly, 11 out of 13 successful mainland-island trajectories were to the northern islands. Santa Barbara Island and the Coronado Island group were the end points for 1 drifter each. Successful island-mainland connection events ($n = 13$) were to the mainland both north and south of Pt. Conception. There were no obvious differences in the frequency of successful events that occurred during the year.

Mainland arrival events

Temporal patterns in the direction of the successful mainland connections were examined further by dividing mainland-mainland and island-mainland events into those that started to the south of Pt. Conception, those that started to the north, and within each of these 2 groups those that ended to the north, and those that ended south (Table 9). Of the 204 drifters that started within 10 km of the coast, 29% arrived at the mainland. South-to-south and north-to-north events occurred throughout the year. Of the 163 drifters that began south of Pt. Conception, only 14 traveled to the north. These south-to-north connections occurred mainly between October and January (Table 9). Of the 41 drifters released north of Pt. Conception, none successfully dispersed from north to south. Displacements and drift times were lower for successes within each region than for between the 2 regions (Table 9).

Origin regions and latitudinal connection success

Although the probability of arrival at the coast was related to the initial release distance from the coast

Table 6. Dispersal zones occupied by month for drifters released between October 1992 and December 1997. Each month of releases is classed according to the dominant zone, or zones, in which drift trajectories were observed. The total number of months in the time period with releases is given, and the year in which the month's releases dispersed into a zone is listed. More than 1 zone may receive drifters. Months with drifters circulating within the channel are noted by year. A description of each zone is given in the 'Methods'

Month	n	Within channel	Dispersal zone			
			South along	South away	North away	North along
Jan	3	1995, 1996	1996	1995, 1996	1996	1993, 1995
Feb	1	1994	1994	1994		
Mar	3	1997	1993, 1995	1997		
Apr	1	1994	1994	1994		
May	5	1993, 1995, 1996		1993, 1994, 1995, 1996		
Jun	1	1994		1994		
Jul	3	1993, 1995, 1997	1993, 1995	1993, 1995	1993, 1997	1997
Aug	2	1995, 1996	1995	1995, 1996	1996	
Sep	2	1994		1994, 1996	1996	1996
Oct	3	1992, 1993, 1995		1993, 1995	1995	1993
Nov	3	1992, 1994, 1997		1994	1994	1997
Dec	2	1993, 1996		1993		1993, 1996

Table 7. Connection scenarios for the drifters released between 1992 and 1997. The average drift time and displacement (mean and range) for drifters satisfying each set of start and end conditions are shown. Success is the proportion of drifters that started within some distance and returned to within a particular end distance from the coast. The definition used in most analyses here is in **bold**. Categories are not exclusive and so success does not sum to 1 within any category

If start distance (km)	n	and end distance (km)	n	Time (d)	Displacement (km)	Success
<1	0	<1	0			
<2	1	<1	0			
<5	48	<1	16	6 (1–18)	33 (3–208)	0.36
<10	204	<1	46	10 (1–36)	50 (3–208)	0.23
>10	219	<1	38	12 (1–26)	60 (11–246)	0.17
<2	1	<2	0			
<5	48	<2	25	7 (1–25)	38 (3–208)	0.52
<10	204	<2	79	10 (1–36)	54 (3–220)	0.39
>10	219	<2	61	10 (1–35)	73 (10–209)	0.28
<2	1	<5	0			
<5	48	<5	26	6 (1–25)	38 (3–208)	0.54
<10	204	<5	92	10 (1–38)	56 (3–220)	0.45
>10	219	<5	70	12 (1–39)	69 (10–290)	0.32
<2	1	<10	0			
<5	48	<10	28	6 (1–25)	38 (3–208)	0.58
<10	204	<10	102	10 (1–39)	58 (3–478)	0.50
>10	219	<10	75	14 (1–75)	76 (10–342)	0.34
<2	1	>10	1	31	274	1.00
<5	48	>10	17	40 (1–75)	352 (30–825)	0.35
<10	204	>10	102	34 (6–89)	299 (32–877)	0.50
>10	219	>10	144	37 (1–79)	336 (7–1092)	0.66

(Table 7), preliminary analysis showed that within a latitudinal group the distance offshore for each release did not affect the connection success, perhaps due to small sample size. Thus, all drifters released north and south of Pt. Conception, regardless of the distance released offshore, were included in an analysis of drifter success as a function of latitude ($n = 423$).

The overall chance of successful arrival at the coast for drifters released north of Pt. Conception was 34.8%. A total of 40 of the 89 drifters released north of Pt. Conception did drift south, but none approached 5 km of the coast south of Pt. Conception (Fig. 6). Of those drifters that remained north of Pt. Conception ($n = 49$), 63% arrived within 5 km of the coast. In any 1 latitudinal band the likelihood of success after release ranged from 0 to 18% (Fig. 7). The greatest chance of arrival occurred in the band in which the drifters were released. No drifter arrived at the coast north of 37° N. The maximum northward displacement for a successful drifter released north of Pt. Conception was 207.5 km (latitudinal displacement 176.2 km) and

took 14 d. The average displacement speed was 14.8 km d⁻¹, and ended at the mainland at 36.97° N. The time for successful drifters increased from an average of 5 d for the latitudinal band in which the drifters were released (34.5 to 35.5° N), to 17 d at the northernmost latitudinal band reached (36.5 to 37° N) (Fig. 6).

Drifters released south of Pt. Conception beached or last transmitted at locations to the south and to the north of Pt. Conception (Fig. 6). Overall, 40% of the drifters beached or were closer than 5 km to the coast when transmission ceased. The chance of beaching in any 1 latitudinal band was between 0 and 26%, with the greatest chance of beaching occurring in the band in which most drifters were released (Fig. 6). A total of 36 of 334 drifters (10.8%) released south of Pt. Conception drifted north of Pt. Conception, with 18 (50%) successfully drifting to the mainland. Of the 298 that drifted south, 114 (38.3%) came within 5 km of the coast. The farthest northern lati-

tudinal band reached was the same as for drifters released north of Pt. Conception (Fig. 7). The farthest northern latitude reached by a successful southern drifter was 36.68° N, a displacement of 289.6 km (latitudinal displacement 262.2 km), and took 17 d at a speed of 17.04 km d⁻¹. The furthest southern latitude reached by a drifter released south of Pt. Conception was 32.42° N, a displacement of 124.64 km (latitudinal displacement 112.7 km), which took 21 d at a speed of

Table 8. Results for drifter connection scenarios for island-mainland, mainland-island, mainland-mainland, and island-island connections. The number of drifters for each condition, the average connection time and range, and average displacement and range are provided

	n	Time in days (range)	Displacement in km (range)
Starting <10 km from an island	69	20.54 (1–76)	138.38 (7.56–769.79)
Ending <5 km from an island	19	9.11 (1–36)	34.53 (9.56–94.90)
Ending <5 km from the mainland	13	18.77 (5–34)	123.11 (36.61–220.27)
Overall success (%)	46.4		
Starting <10 km from the mainland	135	23.02 (1–89)	198.96 (2.71–876.71)
Ending <5 km from the mainland	47	6.49 (1–25)	45.22 (2.71–219.18)
Ending <5 km from an island	13	14.08 (2–38)	60.53 (31.61–124.64)
Overall success (%)	44.4		
Ending (after any start position, total releases = 423)			
All <10 km from an island	64	10.97 (1–39)	47.36 (9.56–341.82)
All <10 km from the mainland	114	12.69 (1–75)	78.29 (2.71–477.75)

Table 9. Successful drifters that arrived at the mainland after release within 10 km of the coast (island or mainland). The successes are divided into those beginning north or south of Pt. Conception (34.5° N), and within this division, those ending north or south of the same latitude. No drifters released north of 34.5° N were successful south of 34.5° N in any month, and so these data are not shown. The total number released in each region (n_i), and the number of successful drifters in each region is shown for each month (n), along with the average (and range) time and displacement

Month	Start < 34.5° N (South of Pt. Conception)						Start > 34.5° N (North of Pt. Conception)				
	End < 34.5° N		End > 34.5° N		End > 34.5° N		End > 34.5° N				
	n _i	n	Time in days (range)	Displacement in km (range)	n	Time in days (range)	Displacement in km (range)	n _i	n	Time in days (range)	Displacement in km (range)
Jan	14	3	22 (14-34)	72 (37-119)	2	24.5 (16-33)	180 (164-198)	1	1	3	21
Feb	6	2	3.5 (2-5)	23 (7-40)	0			2	0		
Mar	14	4	13.8 (8-16)	130 (5-220)	0			6	3	6.3 (1-9)	17 (3-26)
Apr	5	3	6.3 (2-11)	52 (8-135)	0			0	0		
May	20	4	9.0 (1-31)	29 (9-52)	1	1	28	6	1	2	20
Jun	5	1	7	15	0			0	0		
Jul	17	3	1.3 (1-2)	19 (9-32)	3	5 (1-10)	36 (4-77)	6	3	5.0 (1-11)	51 (4-148)
Aug	14	4	13.8 (1-30)	94 (7-169)	0			6	2	3.5 (3-4)	14 (11-17)
Sep	11	3	3.0 (1-5)	26 (9-40)	0			2	0		
Oct	33	1	9	42	2	7.5 (5-10)	89 (67-110)	0	0		
Nov	14	3	6.3 (1-11)	47 (21-95)	3	3.7 (3-5)	42 (8-60)	6	2	11.5 (5-18)	17 (15-19)
Dec	10	1	16	87	3	19 (15-25)	124 (57-219)	6	2	15.5 (14-17)	200 (192-208)
Total	163	32			14			41	14		

5.94 km d⁻¹. Successful drifters drifted for an average of 9 d before beaching in the release latitudinal band (34.0 to 34.5° N). This time spent drifting for successful events also increased to an average of 25 d for drifters that went south (32.5 to 33.5° N), and 31 d for those that

went north of Pt. Conception (36.5 to 37° N). Drifters from both release regions were recorded as far south as 24.6° N (with maximum displacement and latitudinal displacements of about 1000 km), but were far from the coast (>300 km) when transmission ceased.

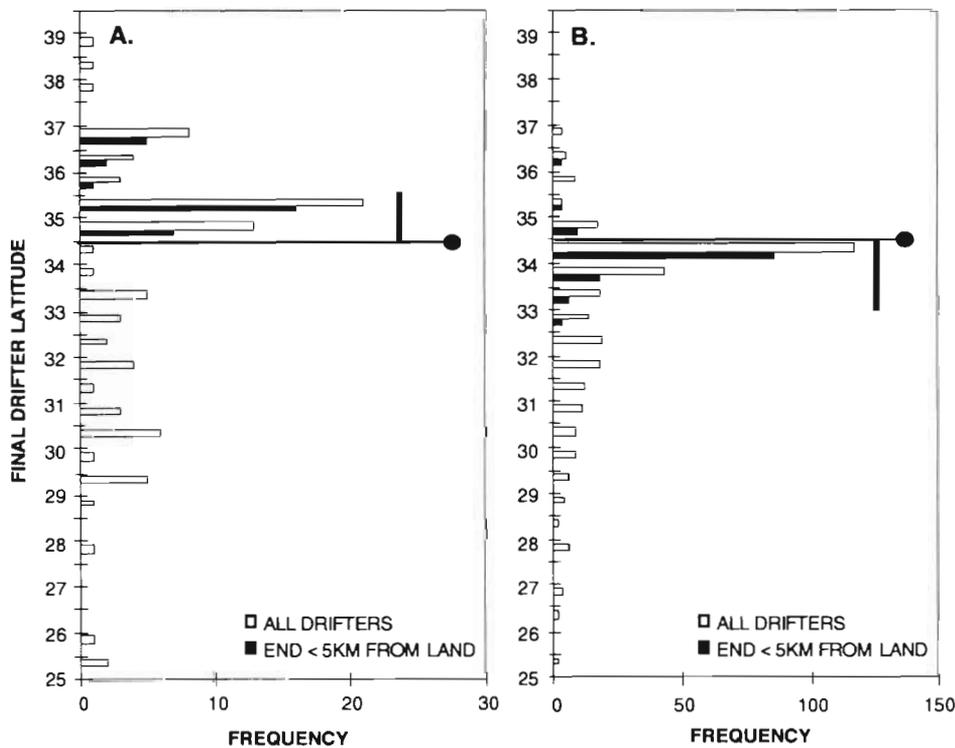


Fig. 6. Final drifter latitudes for releases from locations (A) north and (B) south of Pt. Conception. Solid bars represent drifters with a final location less than 5 km from the coast in the particular latitudinal bin; open bars represent the frequency of the final latitude bin recorded for drifters, regardless of the distance to the nearest coast. The line with a circle represents the latitude of Pt. Conception. Vertical bars on the right of each panel represent the latitudinal extent of each release region

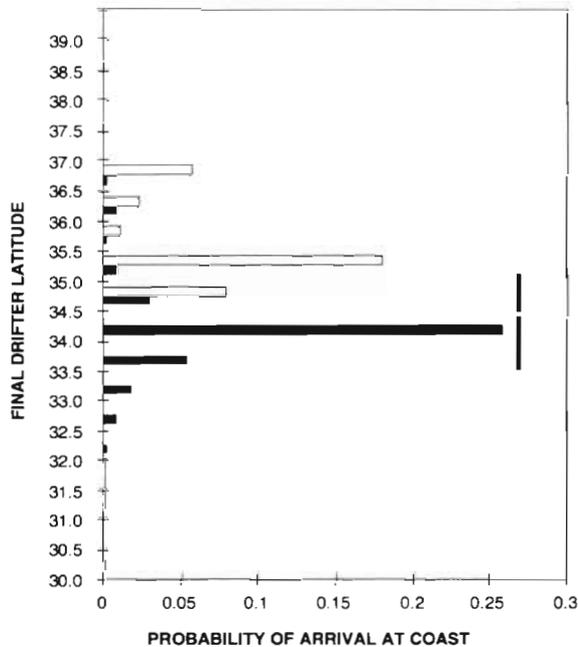


Fig. 7. Probability of successful drifters arriving at the California coast for 0.5° latitudinal bands. Probability is calculated as the number arriving at the coast in each bin, divided by the total number released in each region. A total of 89 drifters were released north of Pt. Conception, while 334 drifters were released south of Pt. Conception. Solid bars represent northern releases; open bars represent drifters released south of Pt. Conception. Vertical bars on the right of the graph represent the latitudinal extent of the north and south release regions. Gap between the bars represents the latitude of Pt. Conception. Coordinates are in decimal degrees

DISCUSSION

Raft abundance

To determine if *Macrocystis pyrifera* rafts can successfully connect isolated kelp forests and transport fauna, information about raft abundance and dispersal paths is required. Abundance of kelp rafts in the SCB was estimated indirectly based on loss of attached plants from kelp forests, and was highest in the winter with much interannual variation in seasonal mortality. Winter mortality of adult *M. pyrifera* at Pt. Loma during the period from 1982 to 1988 was also extremely variable (2 to 94%) (Seymour et al. 1989). If those data are averaged over all sites and all winters, an average of 41% plants was lost each winter. If the winter of 1988, when the largest recorded storm in Southern Californian history removed most of the kelp forests, is eliminated, the average winter loss in the remaining 4 yr was 30%, close to the average winter loss of 23% observed in this study. Interaction between plant age and the timing of large storm events may be responsible for

much of the interannual variation in plant loss (Dayton et al. 1984, 1992, Ebeling et al. 1985, Tegner et al. 1997), and hence production of kelp rafts. Substantial plant losses seem to follow recruitment events, and likely represent density-dependent self-thinning (Dayton et al. 1984, 1992). This means that a kelp forest dominated by young plants may not be affected by a large winter storm as much as a forest with many old plants.

Most kelp plants are lost when wave action is highest (Dayton & Tegner 1984, Dayton et al. 1984, Seymour et al. 1989, Utter & Denny 1996); however, coastal kelp forests such as the 2 considered in this study may differ in wave exposure and hence plant loss and raft production compared to island kelp forests. The area of island forests is, however, much smaller than the coastal forests, and the bias in raft production estimates may not be severe. Overall, the pattern of highest plant loss in winter should still be preserved. The accumulation of beached drift is also highest in the winter months (ZoBell 1971). All evidence suggests that the production of rafts is highest in winter, and so the abundance of drifting rafts should also be highest at this time.

Direct observations also provided estimates of raft abundance in this study, with differences in raft abundance found between cruises; however, these differences could not be divided into seasonal patterns. Intraseasonal variation in abundance and raft size has been shown elsewhere to be as extreme as the interseasonal variation (Kingsford 1995). This may be due to several factors, including inadequate temporal sampling, seasonal differences in number of plants forming a raft, and seasonal differences in residence time in the study region due to current speeds.

As mentioned, one possibility for lack of a seasonal pattern in raft abundance, despite the difference in loss of attached plants, is that the number of plants per raft may differ seasonally. Plants may become entangled following detachment and 'snowball' to form large rafts (Dayton et al. 1984). Snowballing may be more common during stronger winter storms, meaning that even if more plants are lost, there may not be more individual rafts produced. Neither the size nor number of individual plants in a raft was established in the abundance surveys carried out here, due to the amount of ship time available and the difficulty of sampling and untangling the rafts to determine plant numbers. The number of holdfasts in a raft provides a minimum estimate of the number of plants forming a raft, as plants may detach above the holdfasts, or holdfasts may be lost during drifting (Hobday 1998).

Finally, the abundance of drifting rafts is dependent on the status of the attached kelp populations which can change markedly due to oceanic conditions. For example, in the 1982–1983 El Niño, the area of

attached kelp canopy between Pt. Conception and San Diego declined from 63 to 6 km² (Gerard 1984). This would have dramatically reduced the number of rafts in the SCB during this time. Much greater effort in surveying the abundance of drifting rafts (comparable to the 10 yr of data used in the attached plant loss section) may be required before seasonal raft abundance patterns become apparent.

In this study, an estimate of total drifting biomass may be made using the average density and weight of rafts observed. Using the maximum and minimum average total densities observed (0.78 to 6.96 km⁻²), and the range of average size of rafts observed on each cruise (diameter 2.3 to 3.3 m, which corresponds to an estimated raft weight range of 50 to 150 kg; Hobday 1998), the estimated standing crop of drifting kelp rafts in the SCB is between 39 and 1044 kg km⁻². The only other estimate of drifting kelp biomass was made by Kingsford (1995), who estimated biomass to be in excess of 150 kg km⁻² in the Santa Barbara Channel.

The range of drifting biomass estimates, coupled with the residence time (half of the maximum lifetime of 100 d; Hobday 1998), the number of 'raft generations' per year (360 d/50 d floating = 7.2 generations), and area considered (50 000 km²), can be used to calculate an annual drifting kelp biomass range of between 14 000 and 376 000 t of kelp in the SCB. This range compares favorably with export estimates of 130 000 t yr⁻¹ from a Monterey kelp forest (Harrold & Lisin 1989), and the total SCB annual commercial *Macrocystis pyrifera* harvest of between 100 000 and 190 000 t (North 1994). The maximum biomass estimate from the highest raft density (376 000 t) is certainly an underestimate, as only rafts larger than 0.5 m diameter were considered in this study.

Similarly, the raft density estimate of 3.02 km⁻² combined with the average raft weight (55.5 kg; Hobday 1998), can be used to calculate the amount of carbon in surface waters contained in kelp rafts. These average density and average weight estimates provide a total kelp biomass estimate of 0.16 g C m⁻². Given that the dry weight of kelp averages 12% of the wet weight (North 1994), and the carbon content is approximately 30% of the dry weight (Gerard 1984), the standing crop of carbon in the surface waters in drifting kelp is about 0.006 g C m⁻². This amount is much less than the estimates of integrated carbon biomass of phytoplankton in the same region (4.27 g C m⁻², Eppley 1972). Smith (1983) calculated from sea floor surveys that the standing crop of *Macrocystis pyrifera* on the floor of the Santa Catalina Basin was 0.0062 g C m⁻², a number very similar to the kelp surface carbon estimated here. The export of concentrated carbon to the sea floor in sinking rafts might also be locally important (Smith 1983, 1994). A single raft, weighing 50 kg and approx-

imately 2 m in diameter, settling onto the sea floor would provide a local pulsed input of 573 g C m⁻², over 100 times higher than the background carbon flux to the SCB sea floor of 4.05 g C m⁻² yr⁻¹ (Smith et al. 1987). In summary, drifting rafts of *M. pyrifera* represent a large amount of drifting habitat and pulsed carbon input to the sea floor in the SCB.

Drifter dispersal

Drifters did move long distances; however, more than half the successful drifter events were restricted to regions within 1 degree of latitude (approximately 100 km) of the release site. Rarely (<5% of the time), drifters traveled greater distances and arrived back at the coast. If drifters that were not at the coast after they ceased transmitting reached the coast in the remaining period of time that a raft would float, then the estimates here would underestimate the probabilities of successful kelp raft connections.

In spring and early summer, when conditions associated with upwelling (equator-ward winds) exist, drifters moved south into the SCB through the passes that separate the Channel Islands from each other and the mainland, and remained close to shore. In late summer to early winter, when equator-ward winds relax, a pole-ward current concentrated over the shelf moves north along the coast (Hickey 1979, Owen 1980, Jackson 1986, Harms & Winant 1998). This current carried drifters from north of Pt. Conception and the northeastern part of the Channel to the north. Lack of north-south connections during May and June may be due to intense cyclonic circulation with only weak flow out of the Channel (Harms & Winant 1998). Thus, the likelihood of north-south connections along the Californian coast depends on the time of year.

The average displacement velocity of all drifters in this study (9.84 cm s⁻¹) was comparable to the speeds noted for drifting kelp rafts in the only 2 other studies. Harrold & Lisin (1989) found that raft displacement speeds in Monterey Bay ranged from 5 to 65 cm s⁻¹, and averaged 20 cm s⁻¹. They found that drift directions were influenced by seasonal winds that also determined the direction of surface currents; however, in the SCB wind-influenced surface flow is not strong compared to current speeds which average 25 cm s⁻¹ (Bushing 1994, Hobday unpubl. data). Kingsford (1995) observed rafts moving distances of 10 to 12 km in a 24 h period (13 cm s⁻¹). The lower displacements in the SCB found in this study are consistent with the reduced surface current velocities in this region (Jackson 1986), with drifters following the large-scale circulation patterns.

Mark-recapture studies using drift tubes can provide estimates of distances traveled for comparison with this

study; however, results are based on returns from beached tubes and lags in tube recovery prevent accurate determination of drift time. Levin (1983) released drift-tubes in Mission Bay, the mouth of which is close to the Pt. Loma kelp forest. The open coast recovery rate of tubes released at the bay mouth was 30.5%; this measure of 'connection success' is comparable to the success rates reported here.

Of particular interest in evaluating the role of kelp rafts in linking kelp forest faunal populations is the connectivity between the offshore islands and the mainland. Drifters were successful in traveling in either direction between islands and the mainland. The connection times for these 2 events were not significantly different (14 vs 18 d), but the island-mainland displacements were significantly different from, and twice as large as, the successful mainland-island displacements. This is partly because most drifters were released in the Santa Barbara Channel and were already close to the northern channel islands; if they did not collide in a short distance, there were fewer chances of success farther to the south or north, where there are fewer islands. Drifters released close to the islands could still collide with the mainland far to the north and south of the release site, allowing a larger region for successes to occur. Tegner & Butler (1985) released drift tubes at a number of the Channel Islands, but only 0.24% ($n = 3$) of tubes drifted between islands, compared to 13% (9 of 69) in this study. Tegner & Butler (1985) reported a similar recovery rate of mainland releases at mainland locations (36%) to this study (34%), and similar average recovery times (4 to 12 d) to this study (6.5 d). The similarity between the 2 mainland-mainland success estimates suggests that the drift tube island connection estimates were low due to the difficulty of successful tube recovery, while 'recovery' of satellite-tracked drifters was 100%.

The drifter results presented here demonstrate that Pt. Conception is a leaky, 1-way boundary for drifters. Successful transport from south of Pt. Conception to the northern coast is possible, but southward travel around this boundary was not successful. Both the overall dispersal path analysis (all drifters) and the mainland-mainland analyses (successful drifters only) showed that connections from south of Pt. Conception to the north occurred mainly from October to January. Similar patterns are expected for kelp rafts.

Allocating all drifters to a release region, regardless of their starting distance from the coast was a less conservative way of estimating connection success. This type of analysis assumed that drifters did originate at the coast at some time in the past; however the drift record began only when they were some distance offshore. If it is accepted that a drifter can move from the coast to these 'starting positions', the success given

that location can be evaluated. The overall chance of arrival at the coast was similar for the 2 release regions (35 and 40%). Arrivals followed average drift lifetimes of between 5 and 25 d, depending on the latitudinal bands. These lifetimes are less than the estimated maximum lifetimes for rafts (Hobday 1998).

None of the 423 drifters released in this study successfully beached more than 300 km from a release site. Thus the probability of release in the SCB, and arrival at the coast further than 300 km distant is less than 1/423 (0.24%). Longer journeys appear to carry rafts too far from shore for them to be returned. The barrier to raft dispersal in this study appears to be patterns of surface circulation; however, other barriers to raft dispersal may also exist. Edgar (1987) suggested that kelp rafts cannot drift across the Tasman Sea from Tasmania to New Zealand because the waters separating the 2 land masses are depleted in dissolved nitrate, which leads to loss of buoyancy and subsequent sinking. However, dispersal of echinoderms on kelp rafts in the southern hemisphere has been implicated in their circumpolar distribution (Fell 1962). Distances far in excess of 300 km must have been covered by these kelp rafts.

While the longest drifter journey (1092 km) is equivalent to the entire latitudinal range of *Macrocystis pyrifera*, and hence all forests could be linked by rafts, this drifter journey was not successful. Based on the results of this research, kelp forests separated by more than 300 km have less than a 0.24% chance of being linked by drifting kelp rafts in a 5 yr period. In this study, the coast was not divided into regions of kelp habitat and non-kelp habitat, which would certainly affect the success of raft connections. Because of unknown temporal variation in the presence of kelp forests along the coast over the period examined, such an analysis was not attempted. Such fine-scale dispersal patterns deserve greater attention. In managing the coastline of the SCB, kelp forests should be considered a chain of stepping stones, and losing the forests over a band of coast may prevent faunal exchange through drifting rafts. Natural or anthropogenic losses may thus lead to subdivision of the kelp forest populations and the failure of full faunal communities to return to individual kelp forests following recovery.

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