these variables. It is obvious that for the very largest schools numbers could only be roughly approximated (Table 1). Even with school numbers of 2,000–6,000 and the fact that 2 divers were in reasonable agreement, the results still lack the rigor required. Also we could not obtain measures from schools of intermediate sizes (i.e., from 100–1,500 individuals) because we did not encounter them, except as they migrated from and back to the shallows. This likely would require data during periods of the month(s) when currents tend to be sustained around 5 to 10 cm·sec^{-1}. What we can conclude, however, is that blacksmith densities (ca. 10–15 fish/m^3) do not achieve the densities observed in migrating striped mullet of similar individual size (ca. 100 fish/m^3) where the individuals of each species are similar in size as compared, for example, with anchovies. This makes sense for planktivorous fish that ingest significant numbers of macrozooplankton (for blacksmiths as much as 70–80 % of their primary food, Table 3).

We conclude that the social structure and behaviors of blacksmith schools when foraging represent a complex blend of responses to several variables, the most important of which include current velocity, macrozooplankton concentrations, and the metabolic impact of the school on itself.

Acknowledgements. We thank Drs. William Hamner and Richard Bray for there very useful suggestions during the execution of the field work. This paper is contribution number 168 of the Wrigley Marine Science Center.

Literature Cited

Basu, S. P. 1959. Active respiration of fish in relation to ambient concentrations of oxygen and carbon dioxide. Journal Fisheries Research Board Canada 16:175–212.

Bray, R. N. 1980. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. United States Fisheries Bulletin 78:829–841.

Bray, R. N., L. J. Purcell, and A. C. Miller. 1986. Ammonium excretion in a temperate reef community by a planktivorous fish, *Chromis punctipinnis* (Pomacentridae), and potential uptake by young giant kelp, *Macrocystis pyrifera* (Laminariales). Marine Biology 90:327–334.

Fry, F. E. J. 1957. The aquatic respiration of fish. In: The Physiology of Fishes, Ch. 1, Part 1, Vol. 1 (edited by M. E. Brown), Academic Press, New York.

Fry, F. E. J., and J. S. Hart. 1948. The relation of temperature to oxygen consumption in goldfish. Biological Bulletin 94:66–77.

Hamner, W. M., M. S. Jones, J. H. Hauri, and D. McB. Williams. 1988. Zooplankton, planktivorous fish and water currents on a windward reef face: Great Barrier Reef, Australia. Bulletin Marine Science 42:459–479.

Hobson, E. S. 1968. Predatory behaviour of some shore fishes in the Gulf of California. United States Bureau Sport Fishing and Wildlife Research Report 73:1–92.

Hobson, E. S. 1979. Interactions between piscivorous fishes and their prey. In: Predator-prey Systems in Fisheries Management (edited by H. Clepper), Sport Fishing Institute, Wash. D.C., p. 231–242.

Hobson, E. S., W. N. McFarland, and J. R. Chess. 1981. Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. United States Fisheries Bulletin 79:1–30.

Koslow, J. A. 1981. Feeding selectivity of schools of northern anchovy, *Engraulis mordax*, in the Southern California Bight. United States Fisheries Bulletin 79:131–142.

Liddicoat, M. L., S. Tibbets, and E. I. Butler. 1975. The determination of ammonia in seawater. Limnology and Oceanography 20:131–132.

Magurran, A. E., and T. J. Pitcher. 1987. Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. Proceedings of Royal Society London B 229:439–465.

McFarland, W. N., and S. A. Moss. 1967. Internal behavior in fish schools. Science 156:260–262.

Meyer, J. L., E. T. Schultz, and G. S. Helfman. 1983. Fish schools: an asset to corals. Science 220:1047–1049.

Morgan, M. J., and J-G. J. Godin. 1985. Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). Zeitschrift fur Tierpsychologie 70:236–246.

Moss, S. A., and W. N. McFarland. 1970. The influence of dissolved oxygen and carbon dioxide on fish schooling behavior. Marine Biology 5:100–107.

Oviatt, C. A., A. L. Gall, and S. W. Nixon. 1972. Environmental effects of Atlantic Menhaden on surrounding waters. Cheasapeake Science 13:321–323.

Pitcher, T. J. 1986. Functions of schooling behavior in teleosts. In: The Behavior of Teleost Fishes (edited by T. J. Pitcher), The Johns Hopkins University Press, Baltimore, MD, p. 294–337.

Pitcher, T. J., and C. J. Wyche. 1983. Predator avoidance behaviours of sand-eel schools: why schools seldom split. In: Predators and Prey in Fishes (edited by D. L. G. Noakes, B. G. Lindquist, G. S. Helfman, and J. A. Ward), W. Junk Publ., The Hague, p. 193–204.

Radakov, D. V. 1973. Schooling in the ecology of fishes (Transl. from Russian by H. Mills), John Wesley and Sons, New York.

The Fourth California Islands Symposium: Update on the Status of Resources
Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Biogeographic and Ecological Implications of Kelp Rafting as a Dispersal Vector for Marine Invertebrates

William W. Bushing

Biological Sciences, University of California, Santa Barbara, CA 93106
Tel. (805) 967-3328; Fax (805) 893-8062

Abstract. Islands represent discontinuous habitat for terrestrial taxa, yet it is less obvious that they are also "biological islands" for certain marine species as well. Intertidal and subtidal marine invertebrates, especially those that lack a meroplanktonic larval stage, may face significant difficulty in crossing biogeographic barriers such as the San Pedro Channel. Taxa that are asexual, brood their young, or have "crawl away" juveniles may have significantly lower inherent dispersal ability, yet are often well-represented and exhibit relatively low rates of endemism on islands. Kelp such as *Macrocystis* and *Pelagophycus* provide habitat for numerous marine species. Upon detachment from the substrate, kelp plants drift with the wind and currents, dispersing large numbers of individuals from many taxa over relatively long distances. This mechanism may assist in maintaining these species' geographic ranges as well as increasing genetic exchange between isolated populations. Marine species so dispersed have a high potential for reproductive establishment upon arrival due to the numbers transported, age structure, reproductive status and genetic diversity of the propagules. Of ecological interest is the potential simultaneous introduction of commensals, symbionts, parasites, and predators. Colder ocean temperatures following the last glacial period in addition to historic reductions of kelp due to sea otter hunting, kelp harvesting and other anthropogenic activity suggest kelp may have had an even more significant role in the past.

Keywords: Macrocystis; Pelagophycus; Nereocystis; Phaeophyta; Channel Islands; Santa Catalina Island; brooding.

Introduction

The Channel Islands off southern California offer an excellent opportunity for the investigation of dispersal phenomena in benthic marine invertebrates. The intertidal and subtidal habitats of these islands offer examples of "biological islands." Although the substrate and medium are continuous with those of similar mainland habitats, the depth of the intervening channels creates significant biogeographic barriers.

Three mechanisms are often posited to account for the present-day distributions of benthic marine taxa: vicariance events linked to continental drift, pelagic larval dispersal, and rafting or "epiplanktonic dispersal" (Edgar 1987). The Channel Islands formed in regional tectonic events initiating in the Miocene when local folding and faulting began. The islands represent exposed portions of topographic highs along submarine ridges and most likely had no mainland connections. Therefore, vicariance events are unlikely mechanisms for explaining the distributions observed. It is assumed the current biota colonized island intertidal and subtidal habitats through cross-channel pelagic dispersal, either by a dispersal stage or rafting.

Dispersal in marine invertebrates is often linked to reproductive mode and life histories (Grant 1990). Most sexually reproducing taxa offer a wide range of dispersal options. Some produce free-swimming meroplanktonic larvae, either planktotrophic or lecithotrophic, that may disperse with ocean currents. Other species brood, either ovoviviparously to a larval stage or viviparously to a benthic subadult. Non-swimming, "crawl away" juveniles are not likely to disperse readily (Highsmith 1985). Taxa that reproduce strictly asexually or through autotomy may possess no free-swimming dispersal stage.

Several authors (Fell 1962; Dell 1972; Highsmith 1985) have suggested the often regionally cosmopolitan distributions of species with limited inherent dispersal capabilities may be explained by rafting on drift material including wood and kelps such as *Macrocystis*. The scarcity of macroalgae in the tropics makes rafting a less likely dispersal mode there than in the temperate zone (Highsmith 1985).

The Southern California Bight, with its historically extensive kelp forests, offers an opportunity to test the hypothesis that "kelp rafting" may help explain the distribution of some marine invertebrates and the low rates of endemism in the region. Our research asked 2 fundamental questions: (1) given local oceanographic conditions, is drift kelp capable of transporting invertebrates over the distances and drift paths required for mainland-to-island or inter-island dispersal; and (2) are marine invertebrates without pelagic larval stages, such as brooders, actually found on drift kelp?

Methods

The author and his students recovered 126 drifting objects (of which 109 were species of brown algae) from 2 December 1969 to 18 February 1973, off Santa Catalina Island and analyzed the invertebrates on them. Sampling was conducted during the academic year only, with peak months of November through March. Drift kelp was sampled by boat, superficially investigated at sea, and interesting rafts were brought into the lab for dissection and analysis. Species observed on the raft were identified, when possible, and recorded along with their numeric frequency. Additional data recorded included the species of kelp, holdfast diameter, overall raft dimensions, geographic location of raft, wind and drift direction, associated rafts and associated species observed at sea.

Rafts were generally sampled along a transect line from the Toyon Bay pier straight out to sea for a distance of 2 mi . However, opportunistic events resulted in sampling from many areas along the leeward side of the island, primarily between Long Point and the East End, from nearshore to distances of about 5 mi . One sample was collected 2 mi off Point Fermin on the mainland. Rafts without holdfasts, or with little obvious informational content, were not sampled and not recorded. Some information loss resulted during the transfer of rafts from the water to the launch and the launch to the lab. Dissection was on a laboratory wet table with the extracted specimens placed in holding tanks for identification.

Because the project spanned a period of more than 4 yr and involved some student help, species identification skills varied. Initially there was no recognition of the different taxa of congeneric kelp and all rafts were assigned to *Macrocystis pyrifera* or *Pelagophycus porra.* Although identification of the invertebrates was largely done in our lab, some specimens were sent to experts at the Museum of Comparative Zoology in Cambridge, Massachusetts, and the Los Angeles County Museum of Natural History for verification.

Results

The findings from our sampling of drift kelp are summarized in Tables 1, 2, and 3. The following section focuses specifically on observations made during this study while a subsequent section discusses these findings relative to the literature.

Kelp species observed adrift

Macrocystis pyrifera was the predominant kelp species recovered during our sampling followed by *Pelagophycus porra* (Table 1), reflecting expectations based on local species composition. The distribution of these 2 species over the entire Southern California Bight

Table 1. Number observed and frequency of kelp rafts by type.

Nature of raft	Number observed	Frequency (%)
Macrocystis	81	64.3
Macrocystis pyrifera	51	40.5
Macrocystis spp. (incl. *pyrifera, integrifolia, angustifolia*)	30	23.8
Pelagophycus	27	21.4
Pelagophycus porra	20	15.9
Pelagophycus giganteus	2	1.6
Nereocystis luetkeana	2	1.6
Egregia sp.	10	7.9
Laminaria sp.	2	1.6
Sargassum sp.	1	0.8
Phyllospadix sp.	1	0.8
Driftwood (logs, man-made objects, etc.)	7	5.6
Miscellaneous (bottles, other organisms, etc.)	11	8.7

Table 2. Frequency of occurrence of major taxonomic groups on rafts (n = 126 rafts).

Frequency	Taxonomic group (occurences)	Frequency	Taxonomic group
78.6	Arthropoda (99)	58.7	Coelenterata (74)
50.8	Amphipoda (64)	51.6	Hydrozoa (65)
41.3	Decapoda (52)	15.9	Anthozoa (20)
38.9	Cirripedia (49)	33.3	Porifera (42)
39.7	Isopoda (14)	16.7	Tunicata (21)
65.9	Mollusca (83)	8.7	Platyhelminthes (11)
58.7	Gastropoda (74)	3.2	Nemertea (4)
32.5	Bivalvia (41)	5.6	Sipunculoidea (7)
1.6	Cephalopoda (2)	1.6	Pycnogonida (2)
69.1	Bryozoa (87)	0.8	Ctenophora (1)
56.4	Annelida (71)	7.9	Vertebrata (10)
52.4	Echinodermata (66)		
50.0	Ophiuroidea (63)		
11.9	Holothuroidea (15)		
11.1	Echinoidea (14)		
5.6	Asteroidea (7)		

made it impossible to state definitely whether long distance dispersal occurred. Some specimens exhibited high degrees of deterioration or encrustation, suggesting longer periods of drift.

The presence of 2 rafts of *Nereocystis luetkeana*, and others assignable to *Macrocystis integrifolia*, confirmed that drift distances of magnitude greater than those in the bight are achievable. Although Abbott and Hollenberg (1976) reported *Nereocystis* as drift from the San Diego area, and there were mistaken reports from Santa Rosa Island (P. Silva 1973, pers. comm.), this species is known only from north of Pt. Conception. Its presence as drift material off Santa Catalina indicates dispersal on drift kelp occurs over distances sufficient to allow mainland-to-island or inter-island dispersal. Drift *M. integrifolia*, noted from British Columbia to central California by Abbott and Hollenberg (1976), adds further confirmation.

Species observed associated with rafting material

Our studies identified 27 species of benthic algae and vascular plants, 179 species of marine invertebrates and at least 25 vertebrates (fish, birds, marine mammals) on or in the vicinity of sampled drift kelp. Table 2 lists the frequency of the major taxonomic groups found in our samples.

Table 3. Marine invertebrate species with limited dispersal capability observed on kelp rafts with frequency of occurrence (N). Reproductive strategy and geographic range based largely on Morris et al. 1980.

Species	Reproductive strategy	Geographic range	N
Porifera	Asexual or short-lived larvae	Various	42
Epiactis prolifera	Broods to crawl-away benthic stage	Alaska to southern California	2
Balanophyllia elegans	Broods to benthic planula	Oregon to southern California	2
Corynactis californica	Asexual	Sonoma County to San Diego	2
Caprella californica	Brooder	Central and southern California	18
Pycnogonum stearnsi	Brooder	British Columbia to central California	2
Phycolimnoria algarum	Brooder	Oregon to Baja California	3
Crepidula spp.	Brooder	Various	6
Octopus bimaculatus	Brooder, short-duration larvae	Santa Barbara to Baja California	2
Haliotis fulgens	Short-duration larvae	Point Conception to Baja California	
Leptasterias hexactis	Brooder	Washington to Santa Catalina Island	1
Henricia leviuscula	Brooder	Alaska to Baja California	1
Linckia columbiae	Autotomizes	Southern and Baja California, Columbia, Galapagos Islands	1
Amphipholis squamata	Brooder	Locally patchy, near world-wide	2
Ophioplocus esmarki	Brooder	Tomales Bay to San Diego	1
Amphiodia occidentalis	May brood	Alaska to San Diego	3
Aplidium californicum	Brooder	British Columbia to La Paz, Mexico	1

The presence on sampled rafts of several invertebrates lacking pelagic larvae (Table 3) validates the hypothesis that drift kelp may be a dispersal vector for them. Many of their distributions suggest patterns expected due to chance dispersal on drift kelp in the California Current system.

The anemone (*Epiactis prolifera*), which broods its young to a crawl-away benthic stage (Highsmith 1985; Fautin and Fu-Shiang 1986), was found on rafts with young in its external brood pits. Another coelenterate (*Balanophyllia elegans*) identified on sampled rafts is the only scleractinian that broods its embryos to a large, strictly benthic, crawling planula (Fadlallah and Pearse 1982).

Morris et al. (1980) listed several other brooding species that were observed on the sampled rafts. The amphipod (*Caprella californica*), a strictly dioecious brooder, occurred on several rafts. Females of *Pycnogonum stearnsi* brood eggs that hatch as non-swimming subadults, and were noted on the rafts. Several species of *Phycolimnoria* are strictly brooding taxa. Among the molluscs found on our rafts, *Crepidula* includes several brooding species, and *Octopus bimaculatus* broods eggs that hatch into larvae of short duration.

Echinoderms observed on our rafts are of interest due to the large numbers encountered. The brooder *Leptasterias hexactis* [= *L. aequalis*] (Morris et al. 1980; Highsmith 1985), was recovered on *Nereocystis luetkeana* indicating long-distance drift. *Henricia leviuscula* is another brooding asteroid observed on one raft. The ophiuroid (*Amphipholis squamata*) broods its eggs to a large juvenile and has no swimming stage (Morris et al. 1980; Highsmith 1985; Walker and Lesser 1989). This species has an often locally patchy but wide distribution and is associated with floating material (Morris et al. 1980). The ophiuroid (*Ophioplocus esmarki*) likewise broods its young to a juvenile stage.

Several tunicates found on our rafts either brood or have short-lived larvae (Morris et al. 1980). *Aplidium californicum* [= *Amaroucium californicum*] retains its eggs internally, brooding them to a short-lived tadpole stage. *Boltenia villosa* releases eggs which develop into short-lived larvae, remaining in the water column only 2–6 days.

Based on life history information (Morris et al. 1980), some invertebrates on the sampled rafts reproduce asexually. Several sponges, which may reproduce through fragmentation, were observed. The coelenterate (*Corynactis californica*) reproduces strictly by asexual fission. *Linckia columbiae* may autotomize readily (McAlary 1987).

Some species found on rafts such as abalone (*Haliotis fulgens*) possess pelagic larvae which settle out too quickly for adequate planktonic dispersal (Tegner and Butler 1985). The presence of *Lepas* spp. and juvenile *Pachygrapsus crassipes* suggests species possessing larvae capable of long-distance dispersal may still benefit from kelp rafting if their larvae metamorphose and settle on a drifting kelp raft, facilitating dispersal. Species that postpone metamorphosis until suitable substrate is encountered may especially benefit. Many nudibranchs (*Melibe leonina*, *Triopha* spp., *Hermissenda crassicornis*) transported as adults were observed laying eggs on the kelp raft that could later hatch, releasing pelagic stages into the open water.

Discussion

Kelps as dispersal agents

Several kelps (Laminariales, Lessoniaceae) from central and southern California may play a role in dispersal. This research focused on *Macrocystis pyrifera*, *M. integrifolia*, *Pelagophycus porra* and *Nereocystis luetkeana* as recognized by Abbott and Hollenberg (1976). Morphologies similar to species proposed, including *Macrocystis angustifolia* (Neushul 1971) and *Pelagophycus giganteus* (Dawson 1962), were observed.

Each of the major kelps offers a unique combination of geographic range, depth and substrate preferences, and holdfast morphology that affect their suitability as rafting vehicles and the species that might be transported by them. These differences are summarized in Table 4 compiled largely from Abbott and Hollenberg (1976).

Geographic range and depth distribution determine the raft's origin and the associated invertebrate species complex that might be rafted. The 5 kelps range geographically from Alaska to Baja California in depths from the lower intertidal to 90 m. Differentiation between species found only north (*M. integrifolia* and *N. luetkeana*) or only south (*P. porra*) of Point Conception reflect its recognition as a biogeographic transition zone (Seapy and Littler 1980). Local subspecific morphological variation such as the "island" *Macrocystis pyrifera* on Santa Catalina (Harger 1983) or local "endemics" like *Pelagophycus giganteus* (Dawson 1962) may allow more precise identification of raft origin. Substrate preferences for the different kelp species may determine the susceptibility to detachment and the associated invertebrate complex.

Holdfast morphology helps establish the "carrying capacity" of the raft as well as the degree of protection from predation, or other loss, it offers to rafted invertebrates. The massive, complex holdfasts of *Macrocystis pyrifera* have a higher transport capacity than the smaller, less complex holdfasts of *Pelagophycus* and *Nereocystis* or the rhizomatous, spreading holdfast of *Macrocystis integrifolia*.

Pelagophycus porra and *Nereocystis luetkeana* morphologies involve single stipes that are more likely to break under storm duress leaving the holdfast attached to the substrate. *Macrocystis* with its multiple fronds emanating from the holdfast is more likely to detach intact. The structural simplicity of *P. porra* and *N. leutkeana* blades makes them less suitable for long distance transport of invertebrates than the more complex fronds of *Macrocystis*.

The role of kelp as an agent for the colonization of the Channel Islands cannot be adequately evaluated based on current patterns of distribution. Changes in kelp cover over geologic and historic time suggest the role of kelp may have been more significant in the past.

Modern kelp (*Julescrania* and possibly *Pelagophycus*) first appeared in the California fossil record during the Miocene (Parker and Dawson 1965; Clayton 1984), when the southern California Channel Islands began forming. As the islands emerged and their subtidal habitats formed, kelp was available as a potential dispersal mechanism for their colonization by invertebrates. Cooler temperatures in the North Pacific during the Pleistocene would enhance the distribution of kelp in the bight (Lüning 1990). Concurrent sea level lowering likely increased the areal extent of intertidal and subtidal habitats around the emerging islands, and reduced mainland-to-island and inter-island distances, enhancing the probability of transport by kelp.

Table 4. Comparison of potential kelp raft vehicles including geographic distribution, depth distribution, substrate preference and holdfast morphology (based largely on Abbott and Hollenberg 1976).

Characteristic	*Macrocystis pyrifera*	*Macrocystis integrifolia*	*Pelagophycus porra*	*"Pelagophycus giganteus"*	*Nereocystis leutkeana*
Geographic distribution	Central California to Bahia Magdalena, Baja California; South America; New Zealand; Tasmania; Subantarctic islands	Alaska to Central California; South America	Point Conception to Isla San Benito, Baja California	Santa Catalina Island (endemic species?)	Aleutian Islands to San Luis Obispo County
Depth distribution	6–20 m or more	Lower intertidal to shallow subtidal	30–90 m		10–17 m
Substrate preference	Rocky substrate over most of range; coarse sandy bottom off Santa Barbara	Rocky substrate	Primarily rocky bottom, extending into unconsolidated substrate (sand or shell)	Sand, gravel and other unconsolidated substrate	Rocky substrate
Holdfast size	To 1 m or more	10–20 cm	10–40 cm	To 1 m or more	To 40 cm
Morphology	Conical in shape	Flattened, rhizome-like with lateral hapterae	Compact	Spreading	Compact, hemispherical

Aboriginal occupants of Santa Catalina Island harvested marine resources from kelp beds over several thousand years, impacting local kelp (Meighan 1959). Other historic and recent anthropogenic factors including sea otter hunting, commercial and sport abalone and sea urchin harvesting, sewage pollution, kelp harvesting also affected kelp bed distribution (Harger 1983).

Kelp surveys, aerial photographs and satellite imagery dating back to 1911 (Crandall 1912; Jensen et al. 1987) allow quantitative evaluations of historic changes in kelp canopy. Two such studies indicate Santa Catalina Island kelp beds declined in area from a maximum in 1911 to a low in the mid-1950s (Hodder and Mel 1978; Neushul Mariculture Inc. 1981). These same studies found similar trends in the beds around San Clemente, Santa Cruz, and Santa Rosa islands during the same period.

Factors influencing detachment and drift

Important causes of detachment for large kelp sporophytes include actual removal by storm waves (North 1991), weakening of holdfasts and increased potential for detachment in storm-damaged plants (McPeak et al. 1988), and grazing on the holdfast by gribbles (*Phycolimnoria algarum*). Santa Catalina Island is impacted by NW or WNW winter storms on the windward side, Santa Ana storms on the leeward side, or southern swell during the summer months. The seasonal timing of storms and detachment peaks also affects the taxonomic composition, age structure and biomass of rafted invertebrates in the bight.

The rate of export of detached plants from beds on open coasts is significant. Harrold and Lisin (1989) estimated export rates of *Macrocystis pyrifera* from Monterey Peninsula forests at 130,000 t/yr. Given such rates, there is a high potential for detachment and drift in the bight.

Sightings of drift kelp at sea, and speculation on its potential role as a dispersal agent, date back many years. Documented evidence of actual transport is rarer. Two authors (Fell 1962; Arnaud et al. 1976) offer evidence of dispersal by invertebrates on drift kelp over distances of several thousand kilometers. While no comparable distances were observed in our study, duration of drift in local waters is sufficient to effect transport over distances comparable to those in the Bight.

The complex ocean circulation pattern in the Southern California Bight, with its seasonally reversing gyre, significant inter-annual variation, and mesoscale eddies has been described previously (Owen 1980; Seapy and Littler 1980; Lynn and Simpson 1987; Poulain and Niiler 1989; Pares-Siera and O'Brien 1989). Velocities for the California Current are variously reported as 4–50 cm/sec but typically less than 25 cm/sec (Jennings and Schwartzlose 1960; Reid and Schwartzlose 1962; Owen 1980; Lynn and Simpson 1987; Poulain and Niiler 1989).

This complex current pattern makes it difficult to measure "dispersal distances." Linear distances between islands and mainland sources have less value in predicting dispersal potential than for motile forms such as large marine fishes. The seasonally reversing circulation pattern in the bight allows transport from both northern and southern origins.

Macrocystis canopy may protrude 1–2 cm above the water surface (Jensen et al. 1980), suggesting wind patterns may affect drift direction and velocity at sea, as borne out by observations during this research. Harrold and Lisin (1989) also found drifting kelp off Monterey was influenced by seasonally variable winds that dominated current directions.

Once detached, kelp must persist in the open ocean long enough to effect transport over the required distances. Factors such as water temperature, nitrate levels, and population densities of grazing organisms may play as significant a role as the local current and wind patterns in determining drift kelp dispersal (Edgar 1987). Laboratory experiments on *Macrocystis pyrifera* found pneumatocysts lost their buoyancy after about 7 dy (Yaninek 1980). Edgar (1987) noted holdfasts disintegrated in less than 6 mo due to grazing by boring isopods (*Phycolimnoria*), placing a potential upper limit on drift dispersal for infested rafts. *Phycolimnoria* were also observed on rafts in our study with evidence of significant damage to the holdfasts.

Rafted invertebrates must remain alive until the raft reaches a new habitat suitable for colonization. Physical factors for organisms on drift kelp differ from those in attached forests, and may alter mortality rates. Increased IR, UV and visible light levels, and temperature changes result from the buoying up of the holdfast and the reduction in canopy shading from neighboring plants. Holdfasts entangle in the floating fronds and become desiccated. Salinity, O_2 and CO_2 levels, dissolved nutrients, and water turbulence may also exhibit departures from those normally experienced at the bottom.

Trophic interactions that may sustain or deplete the rafted organisms include grazing on the kelp or attached algae by herbivores, utilization of organic matter in holdfast sediments, or predation on other rafting invertebrates. Reduced plankton densities in pelagic waters compared to the richer nearshore environment may affect filter feeders. Aquatic birds including gulls, cormorants and great blue herons, as well as fish, were observed feeding on the invertebrates on drifting rafts.

Beaching may involve high mortality. M. Lovenburg (1970, pers. comm.) found 27 of 46 mussels on 31 tagged algae were lost during drift and beaching. Rocky subtidal species rafted on kelp are often deposited in sandy subtidal areas where they become easy prey for predators or become desiccated and die before locating suitable habitat.

Marine invertebrates associated with kelp

Kelp forests offer a vertically and horizontally structured habitat for many marine taxa. More than 300 algae and almost 800 animals are associated with *M. pyrifera* in southern California and northern Baja California (Earle 1980; Foster and Schiel 1985). This species complex includes a wide range of candidates for kelp raft dispersal.

Observations of motile invertebrates associated with *Macrocystis* off Santa Catalina Island by Coyer (1984) noted 114 species with the mean number of species and biomass both increasing from canopy to holdfast. Although species composition did not vary appreciably, biomass showed marked seasonal increases during winter months when most of our sampling was undertaken.

The kelp holdfast provides protection for many species of sponges, worms, crabs and other arthropods, bryozoans, brittle stars, sea cucumbers, and other invertebrates (McConaughey and McConaughey 1985). Species inventories on attached holdfasts identified 128 to 175 taxa (Ghelardi 1971; Jones 1971; Foster and Schiel 1985; McPeak et al. 1988). These numbers are comparable to the 179 species identified on drifting kelp in this research.

Ecological significance of kelp rafting

Kelp rafting enhances the reproductive and ecological establishment of a taxon due to the potential numbers rafted in a single dispersal event. One sampled raft had 1,500–2,000 ophiuroids on it, while another had 400–600 of 3 different species. Transport of taxa in such high numbers also has consequences for their genetic diversity.

Dispersal on drift kelp may effect a shift in the age structure of propagules towards the adult or subadult stages. Dispersed individuals in reproductive condition on sampled rafts included gravid decapods, brooding *Epiactis prolifera*, and egg laying and synchronously copulating nudibranchs (*Melibe leonina*, *Triopha* spp., *Hermissenda*). Relatively high numbers of mature organisms offer higher probability of establishment than a flux of non-reproductive pelagic larvae. Dell (1972) states brooding females may be better colonists than larvae. Highsmith (1985) suggests the small adult sizes of most brooding invertebrates is advantageous for dispersal by rafting.

The simultaneous transport and introduction of predator/prey, parasite/host, commensal and symbiont species pairs is more likely on drift kelp. Predator/prey introductions observed in our studies included caprellid amphipods and hydroids, nudibranchs (*Corambe pacifica*) and bryozoa (*Membranipora* spp.), gastropods (*Tylodina fungina*) on sponges (*Aplysina fistularis*), and a pelagic nudibranch (*Fiona pinnata*) and barnacle (*Lepas* sp.). Parasite/host pairs included the isopod (*Phycolimnoria algarum*) and *Macrocystis*. Recognized commensals include the pea crab (*Pinnixa*) transported within annelid (*Chaetopterus*) tubes, and zooxanthellae within anthozoan coelenterates (*Anthopleura* spp.), although zooxanthellae are also known from coelenterate planula larvae (Trench 1987).

Biogeographic significance of rafting

Kelp distribution is important in understanding the biogeography of the Channel Islands region (Neushul et al. 1967) and dispersal via drift kelp expands this role. Both today and in the past, kelp has probably played a role in the maintenance and expansion of species' geographic ranges, enhanced the genetic diversity of the propagules, helped maintain gene flow with source populations, and promoted relatively low rates of speciation and endemism.

Seapy and Littler (1980) found strong biogeographic affinities in marine invertebrates between Santa Catalina, San Clemente and Anacapa islands. Regional ocean current patterns may be helpful in explaining this, assuming dispersal by pelagic larvae or drift kelp. A similar study on the marine algae in the bight revealed a similar pattern (Murray et al. 1980). Kelp rafting may play a role in the distribution of the kelp themselves, and attached understory algae with limited spore or gamete dispersal.

The transport of *Pugettia producta* (= *Epialtus productus*) and *Leptasterias hexactis* on *Nereocystis luetkeana* from the cold-temperate Oregonian Province north of Point Conception to the warm-temperate California Province indicates mixing of marine invertebrates from different biogeographic regions may result. The recovery of *Eupenctata quinquesemita* on drift *Macrocystis* off Santa Catalina Island, south of its normal geographic limit at Morro Bay is another example.

There are also paleobiogeographic, paleoecological and paleontological ramifications to kelp rafting. Valentine and Lipps (1963) noted late Pleistocene fossil assemblages from mixed habitats on Anacapa Island which M. Lovenburg (1970 pers. comm.) suggested may have resulted from kelp transport of material from one habitat type into another.

Summary

This research verified the hypothesis that drift kelp may be partially responsible for the colonization of marine habitats on the southern California Channel Islands from local mainland populations. Kelp rafts from source areas outside the bight were found to enter our region with living marine invertebrates attached, some not normally found in our waters. Benthic invertebrate taxa lacking pelagic dispersal stages were observed on rafts, verifying the potential role of kelp rafting in their distribution. The transport of large numbers of mature individuals enhances the role of drift kelp in ensuring reproductive and ecological establishment even in taxa which possess dispersal stages. The co-introduction of ecologically linked species (commensals, etc.) may be an important consequence of kelp rafting. The probable higher density of kelp forests in past geologic and historic periods suggests an enhanced role in affecting local biogeography during the critical stages when island marine habitats were evolving.

Acknowledgements. This research was supported in part by National Science Foundation grant GB-3532 to H. Barraclough Fell, Museum of Comparative Zoology, Harvard University. I am grateful to H. B. Fell and E. O. Wilson for initiating my interest in kelp rafting and the biogeography of islands. This project would not have been possible without the support of the Catalina Island School, its staff and students, especially John S. Iversen and Barry Aires. Assistance with species identification was provided by Ruth Turner of the Museum of Comparative Zoology, James Morin of University of California Los Angeles, and Camm Swift of the Los Angeles County Museum of Natural History. Merv Lovenburg, formerly of the University of California at Davis, also provided access to his data and comments through the early stages of our work.

Literature Cited

Abbott, I., and G. Hollenberg. 1976. Marine Algae of California. Stanford University Press. Stanford, California. 827 pp.

Arnaud, F., P. M. Arnaud, A. Intes, and P. LeLoeuff. 1976. Transport d'invertébrés benthiques entre l'Afrique du Sud et Sainte Helene par les laminaires (Phaeophyceae). Bulletin of the Museum of Natural History, Paris 3(384):49–55.

Clayton, M. N. 1984. Evolution of the Phaeophyta with particular reference to the Fucales. Progress in Phycological Research 3:11–46.

Coyer, J. A. 1984. The invertebrate assemblage associated with the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California: a general description with emphasis on amphipods, copepods, mysids, and shrimps. Fishery Bulletin 82(1):55–66.

Crandall, W. C. 1912. The kelps of the southern California coast. Fertilizer Resources, United States 62nd Congress, 2nd Senate Session, Document 190, Appendix N:209–213.

Dawson, E. Y. 1962. On the recognition of a second species of the genus *Pelagophycus*. Bulletin of the Southern California Academy of Science 61:153–160.

Dell, R. K. 1972. Antarctic benthos. In: Advances in Marine Biology, Vol. 10 (edited by F. S. Russell and M. Yonge), Academic Press, New York, pp. 1–216.

Earle, S. 1980. Undersea World of a Kelp Forest. National Geographic, September, 1980, pp. 411–426.

Edgar, G. J. 1987. Dispersal of faunal and floral propagules associated with drifting *Macrocystis pyrifera* plants. Marine Biology 95:599–610.

Fadlallah, Y. H., and J. S. Pearse. 1982. Sexual reproduction in solitary corals: overlapping oogenic and brooding cycles, and benthic planulas in *Balanophyllia elegans*. Marine Biology 71(3):223–231.

Fautin, D. G., and Chia Fu-Shiang. 1986. Revision of sea anemone genus *Epiactus* (Coelenterata: Actinaria) on the Pacific coast of North America, with descriptions of two new brooding species. Canadian Journal of Zoology 64(8):1665–1674.

Fell, H. B. 1962. West-wind drift dispersal of echinoderms in the southern hemisphere. Nature 193(4817): 759–761.

Foster, M., and D. Schiel. 1985. The ecology of giant kelp forests in California: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.2). 152 pp.

Ghelardi, R. J. 1971. Species structure of the animal community that lives in *Macrocystis pyrifera* holdfasts. In: The Biology of Giant Kelp Beds (*Macrocystis*) in California (edited by W. J. North), Beihefte Zur Nova Hedwigia 32:381–420.

Grant, A. 1990. Mode of development and reproductive effort in marine invertebrates: should there be any relationship? Functional Ecology 4(1):128–130.

Harger, B. W. 1983. A historical overview of kelp in southern California. In: The Effects of Waste Disposal on Kelp Communities, California Sea Grant Symposium (edited by W. Bascom), pp. 70–83.

Harrold, C., and S. Lisin. 1989. Radio-tracking rafts of giant kelp: local production and regional transport. Journal of Experimental Marine Biology and Ecology 130:237–251.

Highsmith, R. C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Marine Ecology (Progress Series) 25(2):169–179.

Hodder, D., and M. Mel. 1978. Kelp survey of the Southern California Bight. Esca-Tech Corp. and Science Applications, Inc. Technical Report Volume III - Report 1.4 to the Bureau of Land Management (Year II SCOCS Program), Contract No. AA550-CT6-40, La Jolla.

Jennings, F. D., and R. A. Schwartzlose. 1960. Measurements of the California Current in March 1958. Deep Sea Research 7:42–47.

Jensen, J., J. E. Estes, and Larry Tinney. 1980. Remote sensing techniques for kelp surveys. Photogrammetric Engineering and Remote Sensing 46(6):743–755.

Jensen, J., J. E. Estes, and J. Scepan 1987. Monitoring changes in giant kelp distribution using digital remote sensor data. Photo Interpretation 1987-1(4):25–26.

Jones, L. G. 1971. Studies on selected small herbivorous invertebrates inhabiting Macrocystis canopies and holdfasts in southern California kelp beds. In: The Biology of Giant Kelp Beds (*Macrocystis*) in California (edited by W. J. North), Beihefte Zur Nova Hedwigia 32:343–367.

Lüning, K. 1990. Seaweeds: their environment, biogeography and ecophysiology. C. Yarish, H. Kirkman (ed.). John Wiley & Sons, Inc. New York.

Lynn, R. J., and J. J. Simpson 1987. The California Current system: the seasonal variability of its physical characteristics. Journal of Geophysical Research 92(C12):12,947–12,966.

McAlary, F. 1987. Ray autonomy as a mode of asexual reproduction in the Sea Star Linckia Columbiae. Oral presentation, 5 March 1987, at the Third California Islands Symposium, Santa Barbara Museum of Natural History.

McConaughey, B., and E. McConaughey. 1985. Pacific Coast. The Audubon Society Nature Guides. Chanticleer Press, New York. 633 pp.

McPeak, R., D. Glantz, and C. Shaw 1988. The amber forest. Watersport Publishing, Inc. San Diego, California. 144 pp.

Meighan, C. W. 1959. The Little Harbor site, Catalina Island: an example of ecological interpretation in archaeology. American Antiquity 24:383–405.

Morris, R. H., D. P. Abbott, and E. C. Haderlie 1980. Intertidal Invertebrates of California. Stanford University Press. Stanford, California. 690 pp.

Murray, S. N., M. M. Littler, and I. A. Abbott. 1980. Biogeography of the California marine algae with emphasis on the southern California islands. In: The Channel Islands: Proceedings of a Multidisciplinary Symposium (edited by D. Power), Santa Barbara Museum of Natural History, pp. 325–339.

Neushul, M., et al. 1967. Subtidal plant and animal communities of the southern California islands. In: Proceedings of the Symposium on the Biology of the California Islands, Santa Barbara Botanic Garden, pp. 37–55.

Neushul, M. 1971. The species of *Macrocystis* with particular reference to those of North and South America. In: The Biology of Giant Kelp Beds (*Macrocystis*) in California (edited by W. J. North), Beihefte Zur Nova Hedwigia 32:211–222.

Neushul Mariculture, Inc. 1981. Historical review of kelp beds in the Southern California Bight. Southern California Edison Company Research Report Series Number 81-RD-98. 74 pp.

North, W. J. 1991. The Kelp Beds of San Diego and Orange Counties. Published by Wheeler J. North, 15 March 1991. 270 pp.

Owen, R. W. 1980. Eddies of the California Current system: physical and ecological characteristics. In: The Channel Islands: Proceedings of a Multidisciplinary Symposium (edited by D. Power), Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 237–263.

Pares-Sierra, A., and J. J. O'Brien. 1989. The seasonal and interannual variability of the California Current System: an numerical model. Journal of Geophysical Research 94(C3):3159–3180.

Parker, B. C., and E. Y. Dawson. 1965. Non-calcareous marine algae from California Miocene deposits. Nova Hedwigia 10:273–295.

Poulain, P., and P. P. Niiler. 1989. Statistical analysis of the surface circulation in the California Current system using satellite-tracked drifters. Journal of Physical Oceanography 19:1588–1603.

Reid, J. L., and R. A. Schwartzlose. 1962. Direct measurements of the Davidson Current off central California. Journal of Geophysical Research 67:2491–2497.

Seapy, R., and M. Littler, 1980. Biogeography of rocky intertidal macroinvertebrates of the southern California Islands. In: The Channel Islands: Proceedings of a Multidisciplinary Symposium (edited by D. Power), Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 307–323.

Tegner, M. J., and R. A. Butler. 1985. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the Southern California Bight: implications for recovery of depleted populations. Marine Ecology (Progress Series) 26(1-2):73–84.

Trench, R. 1987. Dinoflagellates in non-parasitic symbiosis. In: The Biology of Dinoflagellates (edited by F. J. R. Taylor), Blackwell Scientific, Oxford, England, pp. 530–570.

Valentine, J. W., and J. H. Lipps. 1963. Late Cenozoic rocky-shore assemblages from Anacapa Island, California. Journal of Paleontology 37(6):1293–1302

Walker, C. W., and M. P. Lesser. 1989. Nutrition and development of brooded embryos in the brittlestar *Amphipholis squamata*: do endosymbiotic bacteria play a role? Marine Biology 103(4):519–530.

Yaninek, S. 1980. Beach wrack: phenology of an imported resource and utilization by macroinvertebrates of sandy beaches. Master's thesis, University of California at Berkeley, Berkeley, California. 159 pp.

The Fourth California Islands Symposium: Update on the Status of Resources
Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Entanglement of Marine Mammals in Synthetic Debris

Peter C. Howorth

Marine Mammal Center of Santa Barbara, 3930 Harrold Avenue, Santa Barbara, CA 93110-1524
Tel. (805) 687-3255; Fax. (805) 687-2368

Abstract. In the last decade, fisheries observers, pinniped census takers, and marine mammal rehabilitation clinics began reporting growing numbers of pinnipeds and cetaceans entangled in synthetic debris. During a 3-yr period, 100 samples of such debris were collected, including many from the southern California Channel Islands, by the Marine Mammal Center of Santa Barbara. Most entanglements came from live specimens, although a few dead, beach-cast specimens were also recorded. Entanglements were analyzed by type, size, color, and material of debris. Data thus obtained were then compared with the numbers, species, sex, and age of each marine mammal involved. Subadult California sea lions *(Zalophus c. californianus)* entangled in plastic monofilament gillnet fragments comprised the vast majority of specimens analyzed.

Keywords: Southern California Bight; Channel Islands; California sea lion *(Zalophus c. californianus)*; cetacean; pinniped; gillnet; drift net; set net; ghost net; Marine Mammal Stranding Network; plastic; pollution; fisheries.

Introduction

Entanglement of marine animals in synthetic debris has become a rather well-known global pollution problem. In some areas, this problem has escalated so rapidly that it apparently has significantly contributed to the decline of certain species, particularly the northern fur seal (*Callorhinus ursinus*) in the Pribilof Islands of the Bering Sea (Fowler 1982, 1984, 1985, 1987, 1989; Fowler et al. 1985; Bengston et al. 1988; Fowler and Baba 1991). Entangled marine mammals, perhaps because of their conspicuous size and popularity with the public, gather considerable attention, particularly in areas like Southern California, which has a dense human population. Nonetheless, in the mid 1970s, relatively few such entanglements were reported anywhere in California. Within the past decade, however, reports of such entanglements, especially involving commercial fishing nets, began increasing in California (K. Lee, D. Zumwalt, and G. Hoffman 1990–1993, pers. comms.). Participants in the Marine Mammal Stranding Network, organized by the National Marine Fisheries Service, rescued a number of these entangled animals. Meanwhile, data from fisheries observers obtained over the same period suggested a general corresponding trend toward significantly higher mortality of marine mammals entangled in commercial fishing gear, especially in nets. Finally, pinniped census takers at the southern California Channel Islands began to notice more live entangled specimens (M. Lowry and R. L. DeLong 1990–1993, pers. comms.).

This paper outlines the apparent correlation between increased marine mammal mortality rates (estimated from fisheries observer data and other sources), the increased occurrence of entangled specimens reported by census takers, and the greater numbers of strandings involving entangled specimens. Evidence to support the most significant cause of this increased entanglement is given.

Methods

A literature review was conducted on subjects including fisheries observer data and reports, assessments of marine mammal-fisheries interactions, entanglement of marine animals in synthetic debris, and marine mammal censuses in the Southern California Bight. Certain researchers involved in such studies were interviewed on specific aspects of the entanglement issue. Live sighting records and stranding reports of entangled marine mammals were examined from the Marine Mammal Center of Santa Barbara's files.

Samples of entanglement debris were obtained from all living, stranded, or dead, beach-cast specimens recovered over a 3-yr period from January 1990 through October 1993. Photographs and videotapes were taken of many of these specimens. The number of samples was stopped when the 100 mark was reached to allow time for the preparation of this paper, but samples continue to be taken. The sampling area included the mainland coast of California from parts of Los Angeles County through all of Ventura and Santa Barbara counties, as well as parts of the southern California Channel Islands. One stranding was also recorded from Cambria, California, because of its similarity to another stranding in Santa Barbara County. Reports of entangled animals were channeled to the Marine Mammal Center of Santa Barbara's hotline,