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Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel

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Abstract Observational and experimental studies were conducted on the dispersal of fouling organisms on a replica of a 16th-century sailing vessel along an 800 km transect from Yaquina Bay, Oregon to San Francisco Bay, California. The vessel sailed between four bays at slow speeds (3.5 to 4 knots), resided in each bay for approximately 30 d, and spent 1 to 3 d in the open ocean travelling between ports. Natural hull fouling and experimental fouling panels placed on the vessel were sampled upon departure and arrival at each port. All common fouling species survived the open sea voyages between the harbors, with largely no ecologically significant changes in abundance nor significant losses in overall diversity detected. In one port the vessel settled upon the harbor floor periodically; several entrained benthic organisms were then transported 390 km to the next port. Slow-moving, fouled sailing vessels of relatively long port residencies may have significantly altered the distributions of marine and estuarine organisms not only globally (leading to the invasions of non-native species) but also along continental margins (leading to the alteration of aboriginal patterns of distribution). Shipping traffic may further play an important role in gene flow between isolated populations of obligate estuarine organisms, particularly those with non-planktonic larvae.

> "From a zoogeographical point of view it is of no little interest to know what animal forms can be imagined to have been carried to their present range by means of ships ... Particularly in the time of wooden ships certainly no small quantities of animals and plants have been carried about the different seas. If an animal form with a very wide and scattered distribution has only the slightest possibility of this mode of distribution, this possibility should also be taken into consideration."
>
> Bertelsen and Ussing (1936)

Introduction

Ocean-going vessels have long played a role in the dispersal of marine organisms (Chilton 1911; Bertelsen and Ussing 1936; Pyefinch 1950; Allen 1953; Skerman 1960; Zevina and Kuznetsova 1965; Carlton 1987, 1989). Polynesian and other vessels radiated across the South and North Pacific Oceans two thousand and more years ago presumably transporting on (as fouling organisms) and in them (as boring organisms) species previously restricted to the southwestern Pacific Ocean. Seven hundred and more years ago European vessels began to transport around the world species once restricted to northeastern Atlantic waters, not only as fouling and boring assemblages, but in ballast as well (Lindroth 1957; Carlton 1985, 1992). Similar events were repeated many times over the centuries by vessels all over the world (Lloyd 1975; Natkiel and Preston 1986).

While there are clear patterns of ship-associated dispersal events commencing in the 19th-century (Carlton 1979b, 1992), the role of pre-1800 vessels, with rare exception, is lost to antiquity. Dispersal of animals and plants by vessels in earlier centuries went undocumented. An Atlantic species introduced by ships to the Pacific Ocean could subsequently have been distributed both by natural processes and by regional shipping for many centuries before its modern distribution was documented. Species within an ocean basin, and with originally restricted ranges, could have been carried by vessels along continental margins. Most modern distributions of shallow-water marine organisms are interpreted as the result of prehistorical natural processes, such as dispersal on ocean currents or the fragmentation of once broad distributions (Carlton 1987, 1989; Chapman and Carlton 1991).

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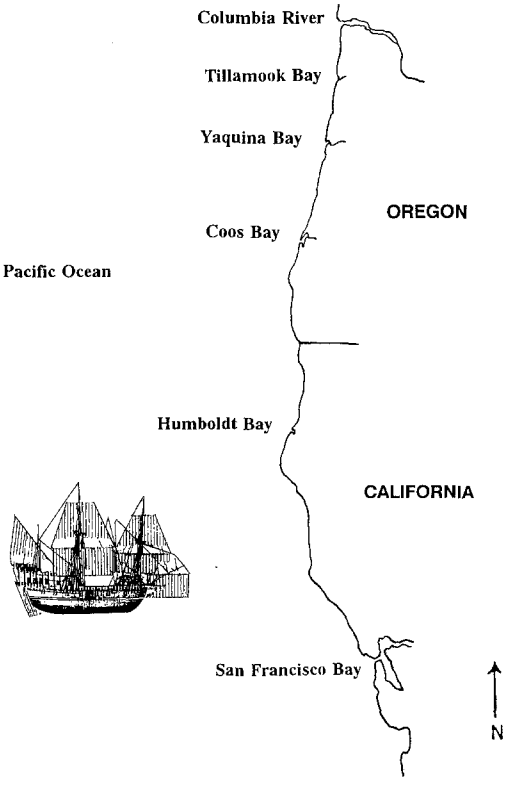

Fig. 1 Ports of call of the voyage of the *Golden Hinde II* in Oregon and California during the present study

Accurate knowledge of human-mediated historical dispersal processes thus would be critical to many disciplines. These include: (1) biogeography, in terms of distinguishing between ancient natural and modern human-mediated dispersal; (2) evolution, in terms of understanding gene flow between otherwise-isolated populations (especially those taxa with non-planktonic life stages); and (3) ecology, in terms of understanding the historical origins of community diversity (the rate and timing of species insertions), knowledge fundamental to interpreting the evolutionary history of species co-occurrences.

Discerning historical ship-dispersal events is difficult since there are no records of fouling or boring communities on ancient ships, other than barnacles and boring organisms [shipworms (teredinid bivalves) and gribbles (limnoriid isopods)] (Clapp and Kenk 1963; Turner 1966). Moll (1928) notes that shipworms were known to Romans and Greeks. Moll (1935) refers to shipworm damage on vessels in the 12th-century in the Mediterranean, and Linschoten (1596) notes that as early as 1590 vessels were forbidden to go to Brazil because of the danger of shipworm damage.

Examining modern-day ship fouling communities as windows into these ancient processes is compromised by the attributes of large modern vessels. These attributes include faster speeds, low port residency times, more frequent maintenance, and the use of highly effective antifouling paints. Fishing vessels, while often supporting extensive fouling accumulations due to less maintenance and extended dock time, typically sail in-and-out of the same port and may remain in the open ocean for weeks, patterns that do not mimic long-distance ancient shipping. Smaller recreational vessels (sailing and motorized "pleasure" craft) are often cleaned at frequent intervals (many are simply removed from the water for large parts of the year), travel at relatively fast speeds, and for those on lengthy voyages rarely reside long (>30 d) in any one port.

A unique opportunity to gain insight into ancient ship fouling conditions and dispersal presented itself with the voyage of the replica vessel *Golden Hinde II* (hereafter GHII) along the Pacific coast of North America. The first *Golden Hinde* was a small three-masted English ship built along carrack-galleon lines of 100 tons and 31 m length overall (Golden Hinde 1986). It is best known as the vessel of "the most astonishing voyage of all time" (Cumming 1985) – Sir Francis Drake's circumnavigation of 1577 to 1581.

The GHII was launched in England in 1973; in the spring of 1986 it sailed 22 540 km from England to British Columbia. The vessel then spent 35 d in May 1987 in the freshwater portions of the Columbia River (Fig. 1). We presume that the marine fouling and boring organisms on and in the GHII's hull were eliminated in the Columbia River, with the possible exception of the green alga *Enteromorpha* sp. The GHII left the Columbia River on 15 June and arrived in Tillamook Bay, Oregon (OR) on 17 June, where the ship remained for 14 d prior to leaving on 30 June for 1-d sea voyage to Yaqunia Bay, OR (Fig. 1).

When the GHII arrived in Yaquina Bay the vessel would then have had on it those fouling organisms that had settled: (1) en route from the mouth of the Columbia River to Tillamook Bay; (2) in Tillamook Bay; and (3) en route from Tillamook Bay to Yaquina Bay. For the next 30 d the GHII was docked in Yaquina Bay. While the GHII was treated with copper-based antifouling paints, fouling assemblages were nevertheless present on areas of the hull, keel, and rudder in Yaqunia Bay. Antifouling measures taken by the original *Golden Hinde* are not known. However, Richard Hawkins, who lived between 1562 and 1622, writing of his voyage to the South Seas in 1593 (Hawkins 1622), noted that vessels at that time in England covered their hulls "with tar half a finger thick, then nailing upon it a layer of hair, and finally covering this with thin planks, preferably of elm" (Clapp and Kenk 1963, p. 444). Wilkinson (1841) noted that cast sheet leading was introduced to England for hull coverage by Sebastian Cabot (who lived between 1474? and 1557). Thus, these or other methods may have been used aboard the *Golden Hinde*. However, many vessels of this period likely had little or no hull protection (Clapp and Kenk 1963).

The GHII provided the opportunity to recreate certain aspects of a 16th-century sailing voyage: port residency of up to 1 mo or more, followed by relatively slow (3 to 4 knots) passages to the next coastal port. Our intent was to measure the survival of fouling organisms as the vessel sailed from port to port.

Table 1 Voyage legs and timing. [*ARR* arrival date in port; *DS* d at sea from last port; *DEP* departure date from port; *SPEED* speed of vessel, in knots, average and (maximum); *PR* port residency (d); *ST* sample time after arrival (+) or before departure (–) (h)]

Leg	Location	ARR	DS	DEP	SPEED	PR	ST
I	Yaquina Bay	1 Jul	–	30 Jul	3.5–4 (8)	30	–7
II	Coos Bay	31 Jul	1	26 Aug	3.5–4 (6)	27	+12/–9
III	Humboldt Bay	28 Aug	2	22 Sep	4 (n/a)[a]	25	+1/–6
	San Francisco	25 Sep	3	–	–	–	+2

[a] Maximum speed data not available

Table 2 Port departure, at sea and port arrival temperatures and salinities for voyage legs (see Table 1)

Leg	Temperature (°C)			Salinity (‰)		
	Depart	At sea	Arrival	Depart	At sea	Arrival
I	14.0	13.0–15.9	18.5	28.4	33.5	25.9
II	18.5	10.1–12.0	14.9–18	27.0	34.5	30.2
III	16.1	12.0–14.0	20.0	32.9	34.4	31.4

Materials and methods

Our studies began in Yaquina Bay on the day of the GHII's departure, 30 July 1987, and ended 2 mo later in San Francisco Bay (Fig. 1; Table 1). Arrival, departure, port residence times, voyage speed and duration and time of sampling relative to departure/arrival for all legs are given in Table 1.

Departure and arrival sampling

Yaquina Bay departure

Separate regions of the hull, keel, rudder post and waterline were sampled underwater. On the keel and rudder half of two discrete clusters of mixed species fouling were removed.

Coos Bay arrival, residency and departure

We met the GHII in Coos Bay on 1 August. The ship was adjacent to a new bare wood pier installed for the GHII's arrival. This pier was barren of fouling organisms, and there was no evidence that the vessel was extensively colonized by Coos Bay species during the 12 h preceding our sampling. Samples, including the two remaining halves of the Yaquina Bay fouling clusters, were removed as described above.

The GHII's 27-d residency in Coos Bay provided the opportunity to initiate the first series of experiments. Eight vertical (to mimic settlement on the sides of the ship) and eight horizontal (to mimic settlement on the bottom of the ship) fouling panels held in two racks at a maximum depth of 2.75 m were suspended from the pier, 3 m from the ship. The panels consisted of 15 cm square marine plywood presoaked 24 h before use in 80-μm filtered seawater. We assumed that the same species having access to these panels would have access to the GHII.

On 26 August, the day of departure for Humboldt Bay, the natural fouling community that had settled on the vessel was sampled on the hull, keel, rudder post, and waterline. The vertical and horizontal panels were removed from the racks and half of each were placed on the vessel and half retained for analysis. Because attempts to attach blank panels to the vertical and horizontal surfaces of the hull with underwater cement failed (due perhaps to antifouling paints), we attached all panels vertically to the rudder. We located a 1.25-cm wide, 3-m long metal strip running the length of the rudder with a fortuitous 6.5-mm space between the strip and the rudder itself. The space and the strip provided the opportunity to bolt the eight experimental panels to a 6.5-mm thick plexiglass mounting. Disruption of the fouling was minimized by handling the panels by their edges only.

Humboldt Bay arrival, residency, and departure

On 28 August in Humboldt Bay the panels placed on the GHII's rudder in Coos Bay were removed. We initiated a second series of experiments by placing eight new vertical panels onto the rudder in the previous manner. The natural fouling on the rudder and waterline was sampled. The vessel was too close to the bottom to permit us to take samples from the keel. Two racks with four vertical panels each were suspended from the floating pier 3 m from the vessel at a maximum depth of 2 m. These panels were deployed to compare settlement adjacent to the vessel, on the panels attached to the GHII, and on the GHII itself.

On 21 September we removed for analysis in an alternating fashion four of the eight panels placed on the GHII's hull on August 28. In the spaces provided by the removed panels we inserted four new panels in order to assess in-transit settlement from Humboldt Bay to San Francisco Bay. In addition, we sampled the rudder and waterline of the vessel, the keel still being inaccessible. The dock fouling panels were removed and examined. The GHII anchored for the night inside the bay's mouth and departed on the morning of 22 September for a 3-d voyage to San Francisco Bay.

San Francisco Bay arrival

On 25 September we removed all eight panels immediately upon arrival of the GHII in San Francisco Bay. Samples were also collected from the rudder, waterline and the keel. Panels and samples were returned to the laboratory, placed in a 14 °C cold room overnight, and examined alive the next morning.

Temperatures and salinities

Port water temperatures and salinities were recorded using a YSI salinity-conductivity-temperature (SCT) meter and a field thermometer. At sea temperatures for Legs I and II (Table 2) were determined from NOAA data (NOAA 1987); for Leg III, the GHII crew measured temperature. At sea salinities for Legs I and II were estimated by using peak high tide measurements of inshore coastal water at the Coos Bay entrance taken daily by the University of Oregon Institute of Marine Biology (OIMB). For Leg III, the GHII crew took water samples which were analyzed by an SCT meter.

Sample handling and analyses

All samples were returned to OIMB in Charleston (Coos Bay) and examined alive under a dissecting microscope. Samples were fixed in 10% buffered formalin and later transferred to 70% alcohol. Species were identified with the aide of Smith and Carlton (1975) and Kozloff (1987); additional species were identified by consulting taxonomists. Quantitative analyses were performed on preserved samples. Because of the limited underwater sampling conditions, and because of the presence of fouling clumps in confined spaces, it was not possible to measure the spatial area and the original size of each sample. Samples from the hull were quantified by counts of individual taxa in volumetric samples and converted to number per cubic centimeter. Densities of selected taxa from three matched samples from sites on the rudder and waterline were compared between Coos Bay departure and Humboldt Bay arrival, and Humboldt Bay departure and San Francisco Bay arrival. Fouling on the panels was quan-

tified by 100-point intercept under a binocular dissecting microscope and converted to percent cover. Corners impacted by wingnuts were omitted from the analysis. Mud frequently covered portions of the control departure panels. We analyzed the panels without washing them in order not to disturb amphipod tubes and other fragile organisms and thus to provide an accurate baseline for fouling composition on departure. There was no significant difference between the horizontal and vertical panels removed from the racks adjacent to the vessel in Coos Bay (perhaps due to their short length of exposure), and thus they were combined for analysis. A *t*-test was used to compare the means for each species unless the variances were unequal, in which case a Mann-Whitney *U*-test was performed.

Results

Temperature and salinity variation

Temperatures ranged from 18.5 to 20 °C for the warmer inner bays and from 10.1 to 15.9 °C for the open coast (Table 2), values typical of the coast between Oregon and central California in summer. Salinities ranged from brackish (a low of 26 ‰ at the Coos Bay dock) to marine (34.5 ‰ between Coos Bay and Humboldt Bay) (Table 2). The most extreme temperature changes experienced by the fouling organisms on the GHII were during Legs II and III, when temperatures varied by up to 8.5 °C. The most extreme salinity changes were during Legs I and II, when salinities varied by up to 7.6 ‰.

Fouling species survival on the *Golden Hinde II*

Overall patterns of survival

The survival of fouling organisms on the GHII was followed through three transport episodes: Leg I, Yaquina Bay to Coos Bay (135 km), Leg II, Coos Bay to Humboldt Bay (280 km), and Leg III, Humboldt Bay to San Francisco Bay (390 km). A total of 64 taxa were identified as members of the fouling community (both natural fouling on the ship and fouling on experimental panels) in all three legs combined (Table 3). Free-living ciliate protozoans and attached diatoms were present but neither identified nor counted. Shipworm burrows were also noted on the GHII itself, but no attempt was made to sample or count these.

All taxa not identified to species level were scored as "1", although in some instances multiple species were involved (these include two or more species among the acoel turbellarians and the harpacticoid copepods). While three species were identified in the amphipod genus *Corophium* (*C. insidiosum*, *C. acherusicum*, and *C. spinicorne*), we did not attempt to distinguish between them.

In the tabulations in Table 3, certain species were presumed to be present on the GHII at a departure port (although not in vessel departure samples) if the species appeared in our samples of the fouling communities at the arrival port (these taxa are marked with an asterisk; taxa found on the dock, but not on the ship, at the departure port, are marked with two asterisks). We include here only species which we judge were unlikely to colonize the vessel either en route or immediately after arrival in the new port (either because the species does not occur in the open ocean, or because the species did not occur in the new port, or, as noted in "Materials and methods", because the dock in Coos Bay had no fouling organisms on it).

Of the 64 taxa found, 59 (92%) were transported to one or more ports. Those species failing to survive ocean voyages are discussed below.

Leg I: Yaquina Bay to Coos Bay

Twenty taxa were sampled in the natural fouling communities on the bottom of the GHII on the day of departure from Yaquina Bay. Twenty taxa (not all the same as the original 20) were found on the vessel after it arrived in Coos Bay 1 d later. Two gammarid amphipods, *Eogammarus confervicolus* and *Parapleustes pugettensis*, were found on the vessel in Coos Bay but were not sampled on the ship in Yaquina Bay. Both species were present in very small numbers; we interpret these as being from Yaquina Bay for the reasons noted above. Caprellid amphipods and the hydroid-dwelling nudibranch, *Dendronotus frondosus*, were apparently washed off the hydroid (*Obelia* sp.) colonies during the ocean transit and were not present in Coos Bay arrival samples. Twenty-seven d after the vessel's arrival in Coos Bay we found one specimen of *D. frondosus* among hydroids on the GHII. This individual was approximately twice the size of the departure specimens from Yaquina Bay. Since *D. frondosus* was absent from the fouling communities in Coos Bay where the GHII was docked, we believe this specimen was a member of the original Yaquina Bay community. In all, 21 of 22 taxa, or 95%, survived this 1-d voyage.

Leg II: Coos Bay to Humboldt Bay

Twenty-eight taxa were sampled from the GHII on the day of departure from Coos Bay (Table 3). Of these, the boring gribble (isopod), *Limnoria tripunctata*, and sessile ciliate folliculinid protozoans did not occur in samples of the ship's hull, but were on the panels we placed on the vessel at departure. Of the 28 taxa, the nudibranch *Dendronotus frondosus* (as discussed above) and the limpet *Collisella* sp. (also not occurring at the dock in Coos Bay where the GHII was located) probably originated from Yaquina Bay.

Twenty-six taxa were found on the vessel after it arrived in Humboldt Bay 2 d later. The snail *Alvinia* sp. was present (one specimen found) on the vessel upon arrival; while absent from Coos Bay samples, we interpret this as a Coos Bay species for the reasons noted earlier. Three species were absent in arrival samples: the nudibranchs, *Dendronotus frondosus* and *Cuthona albocrusta*, and the limpet, *Collisella* sp. All three species were uncommon upon departure from Coos Bay (only a few *C. albocrusta* were seen on Coos Bay departure panels, and only one each of the

Table 3 Fouling taxa on the *Golden Hinde II*. [* not sampled on ship, but presumed present; ** present on dockside panels, not sampled on ship but presumed present; + introduced species, status as introductions established by Carlton (1979a, b) and Conlan (1990)]

Species	Leg I		Leg II		Leg III	
	Depart Yaquina	Arrive Coos	Depart Coos	Arrive Humboldt	Depart Humboldt	Arrive San Francisco
Protozoa (Ciliata)						
Vorticella sp.	–	–	–	–	X	X
Zoothamnium sp.	X	X	X	X	X	X
Folliculinidae	–	–	X	X	X	X
Coelenterata (Hydrozoa)						
+*Obelia* sp.	X	X	X	X	X	X
+*Tubularia crocea*	–	–	X	X	X	X
Nematoda						
Unidentified	X	X	X	X	X	X
Platyhelminthes (Turbellaria)						
Acoela	X	X	X	X	X	X
Polycladida	X	X	–	–	X	X
Annelida (Polychaeta)						
Spionidae	X	X	X	X	–	–
Nereidae	–	–	X	X	X	X
Polynoidae	–	–	–	–	X	X
Phyllodocidae	–	–	–	–	X	X
Syllidae	–	–	–	–	X	X
Capitellidae	–	–	–	–	*	X
Serpulidae	–	–	–	–	X	X
Mollusca						
Bivalvia						
Mytilus trossulus	X	X	X	X	X	X
Gastropoda						
Opisthobranchia						
Flabellina trilineata	–	–	–	–	X	–
Dendronotus frondosus	X	*	X	–	–	–
Cuthona albocrusta	–	–	X	–	–	–
Onchidoris bilamellata	X	X	X	X	–	–
+*Tenellia adspersa* (+eggs)	–	–	X	X	–	–
Archidoris montereyensis	–	–	–	–	**	X
Prosobranchia						
Alvinia sp.	–	–	*	X	–	–
Mitrella sp.	–	–	–	–	**	X
Collisella sp.	–	–	X	–	–	–
Lacuna marmorata	X	X	–	–	–	–
Crustacea						
Ostracoda						
Unidentified	–	–	–	–	X	X
Cirripedia						
Balanus crenatus	X	X	X	X	X	X
Copepoda						
Harpacticoida	X	X	X	X	X	X
Tanaidacea						
+*Leptochelia savignyi*	X	X	X	X	X	X
Isopoda						
Gnorimosphaeroma oregonense	X	X	X	X	X	X
Munna ubiquita	–	–	–	–	X	X
+*Limnoria tripunctata*	X	X	X	X	X	X
Amphipoda						
Gammaridea						
Corophium spp.	X	X	X	X	X	X
Eogammarus confervicolus	*	X	–	–	–	–
+*Jassa marmorata*	X	X	X	X	X	X
+*Ampithoe valida*	–	–	X	X	X	–
Parapleustes pugettensis	*	X	–	–	–	–
Photis sp.	–	–	–	–	*	X
+*Stenothoe valida*	–	–	–	–	X	X
Caprellidea	X	–	X	X	X	X
Decapoda						
Brachyura						
Cancer sp.	–	–	–	–	X	X

Table 3 (continued)

Species	Leg I		Leg II		Leg III	
	Depart Yaquina	Arrive Coos	Depart Coos	Arrive Humboldt	Depart Humboldt	Arrive San Francisco
Caridea						
Heptacarpus sp.	–	–	–	–	X	–
Insecta (Diptera)						
Chironomidae, larvae	–	–	X	X	X	X
Uniramia (Acarina)						
mite, unidentified	–	–	–	–	X	X
Ectoprocta						
Cheilostomata						
+*Conopeum tenuissimum*	–	–	X	X	X	X
+*Bugula neritina*	–	–	–	–	X	X
Bugula sp.	–	–	–	–	X	X
+*Bowerbankia gracilis*	–	–	–	–	X	X
+*Schizoporella unicornis*	–	–	–	–	X	X
Caulibugula ciliata	–	–	–	–	X	X
Ctenostomata						
Alcyonidium sp.	–	–	–	–	X	X
Chordata						
Urochordata (Ascidiacea)						
+*Molgula manhattensis*	–	–	X	X	X	X
+*Botrylloides violaceus*	–	–	–	–	X	X
+*Botryllus schlosseri*	–	–	–	–	X	–
Unidentified sp.	–	–	–	–	X	X
Algae						
Rhodophyta						
Polysiphonia sp.	X	X	X	X	X	X
Unidentified sp. A	–	–	–	–	*	X
Unidentified sp. B	–	–	–	–	*	X
Chlorophyta						
Enteromorpha sp.	X	X	X	X	X	X
Total taxa sampled:	20	20	28	26	44	46
Total taxa presumed present (see "Results"):	22	21	29	26	50	46
Percent survival of taxa:	95%		90%		92%	

other two species were found). Twenty-six of 29 taxa, or 90%, survived this 2-d voyage.

Taxa transported from Coos Bay to Humboldt Bay, as determined by comparative analysis of matched samples of the natural fouling (Table 4) and of the experimental panels (Table 5), showed no significant declines in abundance. The only significant change was noted in the bryozoan, *Conopeum tenuissimum*, on the experimental panels which appeared to increase in abundance. We believe this is due to the presence of mud that obscured some of the colonies on the panels during plate analysis. To test this hypothesis, we gently washed the thin layer of mud off the control Coos Bay panels (after we had quantified the fouling community present). The only changes noted were the loss of loosely attached *Corophium* sp. tubes and an increase in the number of *C. tenuissimum* colonies. On three unwashed panels the percent cover of *C. tenuissimum* was 2, 2, and 5%; on the same panels after washing it "increased" to 9, 3, and 13%.

It is of interest to note that the hydroid, *Tubularia crocea*, underwent extensive hydranth autotomy during the ocean voyage from Coos Bay to Humboldt Bay. We counted 50 hydroids to determine the number with and without hydranths on the eight control departure Coos Bay panels and on the eight arrival Humboldt Bay panels. There were 32.9 ± 7.3 (mean ± SD) *T. crocea* with hydranths on departure, and 4.4 ± 4.5 (mean ± SD) with hydranths on arrival.

Leg III: Humboldt Bay to San Francisco Bay

Forty-four taxa were sampled from the GHII on the day of departure from Humboldt Bay (Table 3). Of these, four species were found only on the experimental panels that had been placed on the vessel 25 d earlier. These were two bryozoans, *Schizoporella unicornis* and *Caulibugula ciliata*, and two algae, *Enteromorpha* sp. and *Polysiphonia* sp. Some of these species may have been on the vessel's keel that we were unable to sample on the day of departure. Of the taxa on the hull of the GHII, the bryozoan, *Conopeum tenuissimum*, and the solitary seasquirt, *Molgula manhattensis*, were Coos Bay species; neither occurred at the site in Humboldt Bay where the GHII was located.

Table 4 Common fouling taxa (no. cm^{-3}) from matched samples of the natural fouling on the *Golden Hinde II*. (* no significant difference; ** $p<0.05$; *CB* Coos Bay; *HB* Humboldt Bay; SF San Francisco Bay)

Leg	Taxon	Sample 1*		Sample 2*		Sample 3*	
		CB	HB	CB	HB	CB	HB
II	*Corophium* spp.	36.4	30.0	11.0	10.0	17.2	13.7
	Gnorimosphaeroma oregonense	2.1	5.3	1.0	0	0.1	0.1
	Leptochelia savignyi	1.2	1.2	0.5	0	3.1	0.4
	Mytilus trossulus	4.4	3.5	0.5	0.6	0.1	0.5
		Sample 1*		Sample 2*		Sample 3*	
		HB	SF	HB	SF	HB	SF
III	*Corophium* spp.	13.5	16.5	4.6	2.3	4.6	16.7
	Jassa marmorata	3.8	10.0	8.6	3.3	0.5	1.3
	Stenothoe valida	0	0	5.1	0.1	0	0
	Gnorimosphaeroma oregonense	0.8	0.5	0.1	0	0.5	0.3
	Leptochelia savignyi	0.7	0.6	0.6	0.1	0.5	0.3
	Mytilus trossulus	0	0	0	0	0.1	0

Table 5 Selected fouling taxa (% cover, mean ± SD) on panels transported by the *Golden Hinde II*

	Coos Bay departure ($n=8$ panels)	Humboldt Bay arrival ($n=8$ panels)	
Bare panel	36.3±11.8	48.3±14.5	
Tubularia crocea	43.8±14.0	32.3±15.7	
Obelia sp.	0.5±0.8	0.1±0.4	
Corophium spp.	2.1±2.1	1.1±1.4	
Limnoria tripunctata	0.1±0.4	0.4±0.5	
Balanus crenatus	4.4±2.6	4.1±0.8	
Conopeum tenuissimum	2.8±2.0	7.9±2.6	$p<0.05$
Molgula manhattensis	10.8±11.9	6.1±7.8	
	Humboldt Bay departure ($n=4$ panels)	San Francisco Bay arrival ($n=4$ panels)	
Bare panel	79.5±6.6	81.0±3.8	
Tubularia crocea	1.5±2.4	1.0±0	
Obelia sp.	2.3±4.5	2.8±2.8	
Corophium tenuissimum	1.8±1.7	0.8±1.5	
Limnoria tripunctata	0.5±1.0	0.8±1.5	
Balanus crenatus	7.0±1.8	10.3±5.4	
Bugula spp.	1.5±1.9	0.2±0.5	

Forty-six taxa were found on the vessel after it arrived in San Francisco Bay 3 d later. Four species found only in small numbers (one to several individuals) on the GHII in Humboldt Bay were absent in arrival samples: the nudibranch *Flabellina trilineata*, the amphipod *Ampithoe valida*, the shrimp *Heptacarpus* sp., and the compound seasquirt *Botryllus schlosseri*. Six species, not sampled in Humboldt Bay but found on the vessel in San Francisco Bay, are interpreted nevertheless as Humboldt Bay taxa. These were the capitellid worms, the amphipod, *Photis* sp., two species of red algae, the nudibranch, *Archidoris montereyensis*, and the snail, *Mitrella* sp. (the latter two were, however, found in pier samples from Humboldt Bay taken adjacent to the GHII). All six of these taxa were uncommon. In all, 46 of 50 taxa, or 92%, survived this 3-d voyage.

Taxa transported from Humboldt Bay to San Francisco Bay generally showed no significant declines in abundance. One set of matched samples from the vessel (sample 2) was significantly different ($p<0.05$). In these samples there were significantly fewer gammarid amphipods, which may be due to either: (1) the patchiness of populations on the ship; or (2) large numbers of amphipods being washed away. We believe that the first possibility is more likely, given the lack of significant differences in samples 1 and 3 (Table 4).

After the four in-transit panels were placed on the GHII, the vessel spent 6 h at the marina in Humboldt Bay, and then approximately another 8 h anchored near the entrance to Humboldt Bay. The vessel then was at sea for 3 d. Ample time was thus available for larval settlement on the blank panels, with possible larval sources being Humboldt Bay, the open ocean, and San Francisco Bay (although the vessel was in San Francisco Bay for only about 6 h prior to being sampled). On the in-transit panels were newly settled barnacles (*Balanus* sp.), including metamorphosing cyprids, compound seasquirts, harpaticoid copepods, an empty tube of the amphipod, *Corophium* sp., and loosely attached chains of diatoms and pieces of the green alga, *Enteromorpha* sp. It is probable that the copepods and *Corophium* sp. moved onto the plates from other sites on the vessel. The compound ascidians consisted of three colonies on two of the panels; all colonies were at the 4-zooid stage, suggesting settlement at an earlier phase of the 3-d voyage. Ascidian tadpoles could have been encountered by the vessel in transit or could have been derived from resident tunicates on the vessel.

Discussion

Overall patterns of survival and individual transport episodes

The GHII travelled at slow speeds (average 3.5 to 4 knots, maximum 6 to 8 knots) in a voyage of over 800 km divided into three transport episodes each of short duration (1, 2 and 3 d). Under these conditions all common fouling spe-

cies survived during open sea voyages between protected harbors, and there were no ecologically significant changes in abundance (with the possible exception of the loss of amphipods on Leg III). Similarly, there was little loss in overall number of taxa, with 95, 90, and 92% surviving voyages of 1, 2, and 3 d, respectively.

Two additional phenomena of (1) differential survival and (2) biological consequences of the open ocean voyages are of note. When the GHII departed Yaquina Bay, small hydroid-eating nudibranchs (*Dendronotus frondosus*) were present on the hydroid fouling on the ship's hull. Also present were the barnacle-eating nudibranchs *Onchidoris bilamellata*. Dendronotid nudibranchs have elongate, branched respiratory cerata projecting above their backs, and these highly mobile seaslugs wander freely among hydroid colonies. In contrast, *O. bilamellata* is a low-profile, limpet-like nudibranch (with only slightly projecting gills) moving slowly among barnacles. When the GHII arrived in Coos Bay, *D. frondosus* was not found on the vessel while *O. bilamellata* was still present. This suggests that higher profile, more mobile species may be more susceptible to being washed off small or exposed hydroid colonies during an ocean passage. The successful transport of hydroid-associated seaslugs [such as *Tenellia adspersa* (Roginskaya 1970; Carlton 1979 b, 1987)] may thus have historically been dependent upon more massive fouling communities. Conversely, seaslug transport today may more effectively take place in ships' ballast water rather than on ships' hulls.

The hydroid, *Tubularia crocea*, suffered extensive loss of hydranths during the passage between Coos Bay (where they settled on the vessel) and Humboldt Bay. While hydranth autotomy in *T. crocea* has been related to changing seasonal (e.g. temperature) conditions (Rungger 1969), autotomy in this instance may have been triggered by the increased water motion after the GHII set out sea. However, under suitable conditions, *T. crocea* can regenerate a hydranth within 24 h (Rungger 1969). It is of further interest to note that the loss of hydranths by *T. crocea* at sea may, in fact, increase the dispersal of this hydroid, as autotomized hydranths continue to live for as long as 30 d and continue to mature and release gametes and larvae (Rungger 1969). Such autotomized hydranths could drift into small, isolated coastal lagoons and bays – where shipping traffic may be absent or minimal – thus obscuring the role of shipping for species such as *T. crocea*.

In the cruise track between the four bays neither temperature nor salinity variations appear to have been large enough to influence the abundance or survival of the generally euryhaline and eurythermal organisms that dominated the fouling biota.

Implications for biogeography and evolution

The recognition of biological invasions and long-distance dispersal has important implications for biogeographical and evolutionary work (Kornberg and Williamson 1986; Mooney and Drake 1986; Drake et al. 1989). Here we explore the implications of vessel-mediated dispersal for coastal marine and estuarine organisms.

There are no studies of the aboriginal distributions of coastal organisms prior to the onset of coastal shipping, nor do the present data clarify the aboriginal distribution of any of the species treated here. A working assumption in biogeography is that the distribution of most organisms along continental margins is natural, unless specific historical evidence of changes in distribution is available. The slow transport of organisms from one bay to another by vessels over the centuries would suggest that the assumption that modern day distributions of many organisms along a given coastline are the same as aboriginal distributions should be re-examined. The role of shipping may have been important historically, and may continue to be important (due to coastal craft such as pleasure boats and barges, under low-speed and relatively lengthy port residency conditions), in extending the distributions of species along continental margins across local barriers (capes, ponts, and coastal or ocean currents). Of interest in this regard is the transportation by the GHII of a suite of native Pacific coast species which lack planktonic larvae. These include brooding peracarid crustaceans such as the isopods *Gnorimosphaeroma oregonense* and *Munna ubiquita* and the amphipods *Parapleustes pugettensis* and *Corophium spinicorne*.

The GHII also transported along the coast a number of introduced species (marked with a + sign in Table 3). Many non-indigenous species were first introduced by transoceanic shipping into larger ports. Little is known about the role of coastal shipping in the subsequent secondary dispersal of such species to smaller bays, harbors, and lagoon systems. In the present study, the GHII transported the Atlantic seasquirt *Molgula manhattensis* from Coos Bay (where large populations occur) to Humboldt Bay (where the species is absent). *M. manhattensis* persisted on the vessel hull throughout the Humboldt Bay residency. Historically, transportation events such as these could have lead to the widespread dispersal of species well outside major shipping lanes.

As noted earlier the GHII was so close to the bottom in Humboldt Bay that we could not sample the keel. The crew reported that on a number of occasions the GHII fully rested on the mud bottom of the harbor. Evidence for this was the discovery in San Francisco Bay of a relatively large (35 mm) seaslug, *Archidoris montereyensis*, which apparently crawled up the rudder of the ship (perhaps from an immediately adjacent, touching hard substrate on the harbor bottom) and became wedged in between one of the experimental panels and the mounting plate holding the panel to rudder. Large *A. montereyensis* were common on the pier next to the GHII. Upon sampling the keel in San Francisco Bay, a single specimen of a capitellid polychaete was found in the keel fouling as well; typically a mud bottom infaunal organism, this worm may similarly have been picked up by the GHII when it settled onto the bottom. The presence of *A. montereyensis* (and perhaps of the capitellid) suggests that historical shipping may have played an important role in the distribution of species not normally as-

sociated with ship fouling. The phenomenon of vessels settling onto harbor floors – and thus the potential for the entrainment of benthic organisms – may have been far more common in prior centuries, before bays and ports were dredged and adequate shipping channels created.

As vessels travelled along coastlines, resided for a period of time in a harbor, and then resumed their voyage, there was a potential for the sequential accumulation or loss of species. Vessels on long voyages may well have been virtual "zoos" and "gardens" of animals and plants. Because few coastal estuarine species are now unique to any given bay, or indeed unique even to relatively limited regions, measuring this phenomenon is difficult. There were six possible transport combinations within the three transit episodes in the present study: (1) Yaquina Bay (YB) to Coos Bay (CB); (2) CB to Humboldt Bay (HB); (3) HB to San Francisco Bay (SFB); (4) YB to HB; (5) YB to SFB; and (6) CB to SFB. Species survived transport in scenarios (1), (2), and (3). Evidence for transport in scenarios (4) and (5) is circumstantial and equivocal. Arriving in Humboldt Bay and San Francisco Bay on the GHII were a number of species present in prior bays (Table 3). These included the hydroid, *Obelia* sp., the mussel, *Mytilus trossulus*, the barnacle, *Balanus crenatus*, the isopods, *Leptochelia savignyi*, *Gnorimosphaeroma oregonense*, and *Limnoria tripunctata*, and the amphipods, *Corophium* spp. and *Jassa marmorata*. *G. oregonense* was not found, for example, in dockside fouling in Coos Bay during the vessel's 27-d residency there. The isopod was still present on the GHII when it departed for Humboldt Bay, and was found again in Humboldt Bay (where it does occur in dockside fouling) and again in San Francisco Bay. The possibility remains that at least part of the *G. oregonense* population on the GHII when it arrived in San Francisco Bay was derived from the first port, Yaquina Bay. Evidence for scenario (6) has been noted above; Coos Bay species (the seasquirt *Molgula manhattensis* and the bryozoan *Conopeum tenuissimum*), transported through Humboldt Bay, arrived alive in San Francisco Bay.

The probabilities of gene flow between populations of the same species of estuarine organisms, often occurring in estuaries isolated from each other by hundreds of kilometers, depend upon a number of factors. These include the tolerance of dispersal stages to open ocean salinities and temperatures, the likelihood of dispersal stages being transported out of the estuary, and the subsequent likelihood of being transported back into another, suitable estuarine environment. Furman et al. (1989) have characterized the latter prohability as "very small indeed". For obligate estuarine taxa with larval retention mechanisms (Carriker 1967; de Wolf 1974; Cronin 1982), no intermediate open coast populations (Furman et al. 1989), or nonplanktonic dispersal stages, gene flow between populations must be rare.

Shipping activity provides much more likely, continuous, and regular transportation possibilities between isolated estuaries. Coastal shipping could thus be critical in both establishing new populations and in influencing gene flow between estuarine populations, as Furman and Yule (1991) have noted for the barnacle, *Balanus improvisus*.

Increased commercial vessel speeds (and thus decreased retention of fouling organisms), decreased port residency times (and thus decreased fouling accumulations), increased use and efficacy of toxic antifouling paints, and increased vessel maintenance in the late 20th century may have all led to a decline in the role of modern vessels in transporting marine organisms on their hulls, keels, and rudders (Carlton and Scanlon 1985; Carlton 1992). Indeed, the historical role of fouling may have been replaced in large part by the transportation of ballast water (Carlton 1985; Carlton et al. 1990; Carlton and Geller 1993). A specific parallel may be modern container ships which pick up and release ballast water in port after port as they move along coastlines.

Nevertheless, modern vessels continue to carry fouling organisms along coastlines, although we have not located studies similar to ours which indicate the magnitude or ubiquity of this phenomenon. Two phenomena may, in fact, have modestly sustained the importance of the ship as an agent of dispersal for fouling organisms into the 21st-century. First, as Roos (1979) has noted, the greater ocean-going speeds of vessels may have effectively decreased the length of time oligohaline-euryhaline species may be submerged during open ocean transits in full-strength seawater. Roos (1979) invoked this argument to explain the relatively recent global expansion of the Eurasian brackish water hydroid, *Cordylophora caspia*. Second, certain organisms have evolved populations that are now resistant to copper-based antifouling paints. The fouling brown alga, *Ectocarpus siliculosus*, is the best known example of this phenomenon (Hall 1981) – an adaptation that Russell and Morris (1973) have referred to as "ship fouling as an evolutionary process".

Allen (1953) has noted that "No doubt, in the days of sail, translocations were more easily made than at the present time, for voyages were long and slow and antifouling protection was poor. As a result organisms would have had little difficulty in settling on the wooden hulls which present a more favorable surface for settlement than does steel, and the sedate speeds to 5 to 6 knots would offer no great barrier to the survival of the organisms". The voyage of the *Golden Hinde II* is an effective demonstration of the potential that vessels, travelling along coastlines, and across and between oceans, must have had for the dispersal of marine plants and animals around the world, centuries before the first systematic biological investigations commenced.

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