desorption of physically adsorbed C_2H_6 are approximately 7.7 kcal/mol and 10^{13} s^{-1}, respectively (*7*), the activation energies, E_r, and preexponential factors, $k_r^{(0)}$, for dissociative chemisorption may be evaluated easily (these values are also listed in Table 1).

From these results, the electronic and geometric effects on C–H bond activation of these four surfaces of Pt and Ir can be discussed quantitatively. The E_r values given in Table 1 provide the magnitudes by which the Ir surfaces of a given geometry are more active than the corresponding Pt surfaces and by which the corrugated (110) surfaces of each metal are more reactive than their atomically flat (111) counterparts. By comparing samples of the same crystallographic orientation, we find that the E_r value on Ir is 5.0 to 6.3 kcal/mol lower than that on Pt. For each metal, the corrugated (110)-(1×2) surfaces have E_r values that are 4.8 to 6.1 kcal/mol lower than those of the close-packed (111) surfaces. Consequently, the Pt(110)-(1×2) and Ir(111) surfaces have approximately equal activity toward C_2H_6 activation, demonstrating that the difference in geometric structure compensates for the intrinsic electronic difference between the two metals. It is known from photoemission and x-ray absorption studies that changes in surface structure induce subtle, and yet significant, changes in the electronic structure of the catalyst surface (*20*). Hence, at the core of the structure sensitivity issue is the profound influence microscopic surface geometry has on surface electronic structure, and the continued study of this important effect is of great interest in the heterogeneous activation of saturated hydrocarbons.

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13. Under these experimental conditions the dissociative chemisorption of C_2H_6 is irreversible, and no gas-phase carbon-containing products of a surface self-hydrogenolysis reaction are formed. The titration conditions and procedure were selected to ensure the complete oxidation of the surface carbon to $^{13}CO_2$.
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Ecological Roulette: The Global Transport of Nonindigenous Marine Organisms

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Ocean-going ships carry, as ballast, seawater that is taken on in port and released at subsequent ports of call. Plankton samples from Japanese ballast water released in Oregon contained 367 taxa. Most taxa with a planktonic phase in their life cycle were found in ballast water, as were all major marine habitat and trophic groups. Transport of entire coastal planktonic assemblages across oceanic barriers to similar habitats renders bays, estuaries, and inland waters among the most threatened ecosystems in the world. Presence of taxonomically difficult or inconspicuous taxa in these samples suggests that ballast water invasions are already pervasive.

Biological invasions are a great threat to the integrity of natural communities of plants and animals and to the preservation of endangered species (*1*). Most invasion studies have focused on terrestrial and freshwater systems in which one or a few successful invaders have had a catastrophic impact on native species (*2*). Island ecosystems, such as New Zealand and the Hawaiian Islands, have in particular been devastated by the invasion of nonindigenous species (*1–3*). Invasions in marine systems have been less studied (*4*), but are of such magnitude that marine invasions may be leading to profound ecological changes in the ocean.

Any mechanism for rapidly transporting large volumes of water containing plankton from shallow, coastal waters across natural oceanic barriers has the potential to facilitate massive invasions of entire assemblages of neritic marine organisms. Such a mechanism exists in the transport of ballast water and plankton by ocean-going ships (*5*), a dispersal mecha-

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nism that has no analog in terrestrial ecosystems. We report here a survey of plankton in ballast water.

Ships have used water as ballast regularly since the 1880s, drawing ambient water into ballast tanks and floodable holds for balance and stability (6). This water is discharged while under way and at subsequent ports-of-call as cargo is loaded (7). Water taken aboard may contain any planktonic organisms in the water column (8). Thus, rich plankton assemblages may be entrained by vessels and then released within days or weeks on a continent or island thousands of kilometers away.

Table 1. Frequency of occurrence and abundance of organisms in ballast water from ships arriving from Japan to the Port of Coos Bay, Oregon, after a transoceanic trip of 11 to 21 days [average 15.1 (SD 1.9) days]. Specificity of identification depended on the phylum or division considered.

Taxon	Species (n)	Ships (%) in which taxon was				Adult	
		Abundant (>100/ replicate)	Common (10 to 100/ replicate)	Rare (<10/ replicate)	Present	Habitat*	Trophic group†
Crustacea							
Cirripedia	5	11.0	31.0	41.0	83.0	HE	S
Harpacticoida	5	17.0	29.0	28.0	74.0	HE, SE, PL, EB	SC, H
Calanoida and Cyclopoida	25	61.6	25.7	11.3	98.6	PL, SE	C, H, SC
Decapoda	14	3.1	4.4	40.8	48.3	SE, HE, EB	O, H, C, D, SC, S
Euphausiacea	1	0	0	1.3	1.3	PL	O
Stomatopoda	1	0	0	2.5	2.5	HE, SE	C
Cumacea	3	0.6	1.3	11.3	13.2	SE, I, PL	D
Mysidacea	2	0.6	5.0	28.0	33.6	SE, PL	H, D
Isopoda	4	0	1.3	32.1	33.4	HE, EB	SC, O, D, H, P
Caprellidea	1	0	0	2.5	2.5	EB	C, O
Gammaridea	8	0	1.4	22.0	23.4	SE, HE	H, D, S
Hyperiidea	1	0	0	10.7	10.7	PL	C
Ostracoda	1	0	0	2.5	2.5	HE, SE, PL	H
Cladocera	1	0	0	0.6	0.6	PL	H
Chelicerata							
Acarina	1	0	0	5.0	5.0	HE	D, SC
Echinodermata							
Asteroidea	1	1.2	1.9	11.3	14.4	HE, SE	C, SC
Echinoidea	2	0.6	1.9	15.0	17.5	HE, SE	H, SC
Ophiuroidea	1	0	0	3.1	3.1	HE, SE	D, SC
Holothuroidea	2	0	0	5.7	5.7	I, HE, SE	D, S
Chordata							
Urochordata	10	0.6	0	5.7	6.3	HE, EB	S
Pisces	2	0	0	3.2	3.2	PL	C
Hemichordata							
Enteropneusta	1	0	0	0.7	0.7	I	D
Chaetognatha	3	3.1	14.5	29.5	47.1	PL	C
Phoronida	1	0.6	3.8	24.5	28.9	HE, SE	S
Bryozoa	3	3.1	5.7	20.8	29.6	HE, EB	S
Annelida							
Spionidae	11	23.9	40.3	20.7	84.9	SE, HE	D, H, C, S
Polynoidae	3	1.2	3.1	38.0	42.3	SE, HE	D
Other Polychaeta	28	5.0	18.8	45.3	69.1	I, EB, SE, HE	SC, C, S
Hirudinea	1	0	0	0.7	0.7	PL	P
Platyhelminthes	33	0.6	8.8	55.3	64.7	SE, HE	C, SC, P
Nemertea	1	6.3	0	5.7	12.0	SE, HE, I	C
Mollusca							
Bivalvia	9	22.0	23.9	25.2	71.1	HE, SE, I	D, S
Gastropoda	10	2.5	16.4	42.8	61.7	SE, HE	D, SC, H, C
Sipuncula	1	0	0	2.5	2.5	SE, HE	D
Nematoda	1	0	0	9.4	9.4	SE, HE, EB	D, SC
Rotifera	1	0	0	8.2	8.2	PL	O, H
Cnidaria							
Anthozoa	2	0	0	1.3	1.3	HE	S, C
Scyphozoa	1	0	0	1.9	1.9	PL	S, C
Hydrozoa: *Obelia*	1	0	1.4	21.4	22.8	HE, EB, PL	S, C
Other Hydrozoa	21	0	0.6	19.5	20.1	HE, EB, PL	S, C
Radiolaria	2	0	0	18.9	18.9	PL	C, O
Foraminifera	3	0.6	2.5	6.3	9.4	EB, HE, SE, PL	C, D, SC
Tintinnida	2	15.7	11.3	16.3	43.3	PL	C, SC
Other ciliata	4	‡	‡	‡	‡		
Dinoflagellata	4	6.7	11.4	9.5	27.6	PL	PP
Diatomacea	128	54.7	20.7	17.6	92.4	SE, HE, PL	PP
Chlorophyta	2	0	0	3.8	3.8	SE, HE	PP
Rhodophyta	2	0	0	1.2	1.2	SE, HE	PP
Zosteraceae	1	0	0	0.7	0.7	SE	PP

*EB, epibiotic (living on other organisms); HE, hard bottom epifaunal; I, infaunal; PL, planktonic; SE, soft bottom epifaunal. †C, carnivore; D, deposit feeder; H, herbivore; O, omnivore; P, parasite; PP, primary producer, S, suspension feeder; SC, scavenger. ‡Ciliate abundance not estimated.

We sampled ballast water from 159 cargo ships in Coos Bay, Oregon. The ships and their ballast water originated from 25 Japanese ports (9). Plankton from these vessels included 16 animal and 3 protist phyla, and 3 plant divisions (Table 1). All major and most minor phyla were represented (*10*), including 47 ordinal or higher taxa and a minimum of 367 distinctly identifiable taxa (*11*). The supraspecific diversity demonstrates the wide taxonomic spectrum represented and emphasizes the broad implications of this phenomenon (*12*).

All major marine trophic groups were represented (Table 1) including carnivores, herbivores, omnivores, deposit feeders, scavengers, suspension feeders, primary producers, and parasites, although the last were rare. Taxa characteristic of most temperate shallow-water marine communities were represented, including those from infaunal, soft and hard bottom epifaunal, epibiotic, and planktonic habitats. The bal-

Table 2. Examples of recent invasions probably mediated by ballast water.

Higher taxon	Taxon	Species	Native distribution	Introduced to	Year introduction first recognized (reference)
Dinoflagellata		*Alexandrium catenella*	Japan	Australia	1986 (*6*)
		Alexandrium minutum	Europe?	Australia	1986 (*6*)
		Gymnodinium catenatum	Japan	Australia	1986 (*6*)
Cnidaria	Scyphozoa	*Phyllorhiza punctata* (*,†)	Indo-Pacific	California	1981 (*28*)
	Hydrozoa	*Cladonema uchidai* (†)	Japan, China	California	1979 (*23*)
Ctenophora		*Mnemiopsis leidyi*	Western Atlantic	Black Sea	1987 (*26*)
Annelida	Oligochaeta	*Teneridrilus mastix* (*)	China	California	1984 (*29*)
	Polychaeta	*Desdemona ornata* (*)	South Africa, Australia	Italy	1986 (*30*)
		Marenzelleria viridis	U.S. Atlantic	Germany	1983 (*31*)
Crustacea	Cladocera	*Bythotrephes cederstroemi*	Europe	Great Lakes	1984 (*32*)
	Mysidacea	*Rhopalophthalmus tattersallae* (*)	Indian Ocean	Kuwait	1981 (*33*)
		Neomysis japonica	Japan	Australia	1977 (*34*)
		Neomysis americana (*)	U.S. Atlantic	Argentina, Uruguay	1979 (*35*)
	Cumacea	*Nippoleucon hinumensis*	Japan	California	1980? (*23*)
				Oregon	1979 (*23*)
	Copepoda	*Pseudodiaptomus inopinus*	Asia	Columbia River	1990 (*36*)
		Pseudodiaptomus marinus	Japan	California	1986 (*37*)
		Pseudodiaptomus forbesi	China	California	1987 (*37*)
		Sinocalanus doerrii	China	California	1978 (*38*)
		Oithona davisae	Asia	California	1979 (*39*)
				Chile	1983 (*40*)
		Limnoithona sinensis	China	California	1979 (*39*)
		Centropages abdominalis	Japan	Chile	1983 (*41*)
		Centropages typicus	U.S. Atlantic	Texas	1985 (*42*)
		Acartia omorii	Japan	Chile	1983 (*40*)
	Decapoda: Brachyura	*Hemigrapsus sanguineus*	Asia	New Jersey	1988 (*43*)
		Charybdis helleri	Indo-Pacific, Israel	Colombia (Caribbean)	1987 (*44*)
	Decapoda: Caridea	*Salmoneus gracilipes* (*)	Japan, Micronesia	California	1986 (*45*)
		Hippolyte zostericola (*)	Western Atlantic	Colombia (Atlantic)	1984 (*46*)
		Exopalaemon styliferus (*)	Indonesia, India	Iraq, Kuwait	1983 (*47*)
Mollusca	Gastropoda	*Tritonia plebeia*	Europe	Massachusetts	1983 (*4*)
	Bivalvia	*Potamocorbula amurensis*	Asia	California	1986 (*23*)
		Dreissena polymorpha	Eurasia	Great Lakes	1988 (*24*)
		Dreissena sp.	Eurasia	Great Lakes	1990 (*25*)
		Rangia cuneata (*)	Southern U.S.	New York	1991 (*48*)
		Theora fragilis	Asia	California	1982 (*23*)
		Musculista senhousia (†)	Japan	New Zealand	1980 (*49*)
				Australia	1982 (*49*)
		Ensis americanus	U.S. Atlantic	Germany	1979 (*50*)
Ectoprocta		*Membranipora membranacea* (*)	Europe	New Hampshire, Maine	1987 (*51*)
Pisces		*Gymnocephalus cernuus*	Europe	Great Lakes	1987 (*52*)
		Proterorhinus marmoratus	Black Sea	Great Lakes	1990 (*53*)
		Neogobious melanostomus	Mediterranean	Great Lakes	1990 (*53*)
		Butis koilomatodon	Indo-west Pacific	Nigeria, Cameroon	1983 (*54*)
				Panama Canal	1972 (*54*)
		Rhinogobius brunneus	Japan	Arabian Gulf	1987 (*55*)
		Mugiligobius sp.	Taiwan, Philippines	Hawaii	1987 (*56*)
		Sparidentex hasta	Arabian Sea	Australia	1985 (*57*)
		Parablennius thysanius	Philippines, Indian Ocean	Hawaii	1971 (*58*)

*Suggested herein as a ballast-mediated invasion. †An alternative means of dispersal includes transport as external fouling on ships' hulls. Here we suggest that transport as ephyrae (for Scyphozoa) and hydromedusae (for Hydrozoa) are as probable as transport as fouling polyps.

last biota included meroplankton (organisms spending part of their life cycle in the water column), holoplankton (spending all of their lives in the water column), demersal plankton (benthic species that vertically migrate into the water), and tychoplankton (suspended benthic organisms). Ballast water therefore acts as a phyletically and ecologically nonselective transport vector. Certain taxa occurred in high densities: we estimated copepod densities were greater than 1.5×10^3 per cubic meter and spionid polychaete larvae, barnacle nauplii, and bivalve veligers greater than 2×10^2 per cubic meter (*13*).

Despite the lack of selectivity, certain taxa predominate. Five phyla accounted for more than 80% of taxa recorded: crustaceans (31% of all taxa present), polychaete annelids (18%), turbellarian flatworms (14%), cnidarians (11%), and mollusks (8%). Taxa found in many or most vessels included copepods (present in 99% of ships), polychaetes (89%), barnacles (83%), bivalve mollusks (71%), flatworms (65%), diatoms (93%), gastropod mollusks (62%), decapod crustaceans (48%), and chaetognaths (47%).

For some taxa the number of released individuals may vary greatly among ships, whereas the frequency of release may be high (Table 1). Gastropods were abundant in only 2.5% of ships but present in 62% of ships sampled, decapods were abundant in only 3.1% and present in 48% of ships, spionids were abundant in 24% of ships and present in 85% of ships, and nonharpacticoid copepods were abundant in 61% of ships and present in 98% of ships.

Behavioral and life history traits make some taxa less prone to being transported by ballast water. Taxa with both a strictly benthic life-style and with brooded or crawl-away young [for example, brooding gastropods, bivalves, and anthozoans (*14*)] would rarely be in the water column when ballast is pumped on board. Similarly, organisms with an extremely short planktonic life (sponges, direct-developing bryozoans, and ascidians) would rarely be caught. Nektonic organisms (such as fish) may be able to resist either the water intake pressures of the ballast pump or may be able to avoid the plankton net. However, any taxa likely to attach to algae (*15*) could be taken up along with the drift algae (*16, 17*).

In the past 20 years, numerous aquatic invasions have occurred (Table 2). Many of these now appear to be related to ballast water transport (*18*). The taxa of these documented invasions (Table 2) are all represented (except comb jellies) in our samples of ballast water (Table 1). However, some higher taxa frequently found in ballast water have not been often reported as invasive species. Conversely, some higher taxa that are reported relatively frequently as invaders were not found frequently in our samples. Although we recognize that high frequency of release does not necessarily lead to successful invasions, we suggest that there have been far more introductions of polychaetes, flatworms, and diatoms than have been reported. Invasions of intensely studied larger-size animals (such as fish, mollusks, and decapods) are more apparent and thus more noticeable. We predict that more invasions of both large and small organisms will be recognized as susceptible regions are investigated and that new invasions will be discovered in well-studied regions (*19*).

Knowledge of species' natural geographic distributions is of paramount importance for interpreting patterns in ecology, evolution, and biogeography. Unfortunately, the systematics of most marine taxa are far from complete, and the discovery of previously unrecognized species in regions impacted by ballast water release (almost all coastal zones of the world) must now be viewed critically as potential invasions (*20*). Conversely, for easily identified species, unrecognized historical transport may have led to false conclusions of natural cosmopolitanism. Thus, many introduced species may be cryptic, having invaded and gone unrecognized or been mistaken as native species. Both these situations confound our understanding of historical patterns of dispersal, gene flow, and speciation: geographic barriers to dispersal and gene flow are readily breached by ballast water transport. Similarly, we must now recognize that the composition of aquatic communities may be influenced by both recognized and cryptic invasions.

Ships take up and release ballast water in bays, estuaries, and inland waters and then release this water into similar environments around the world. Many of these bodies of water are disturbed by the effects of extensive urbanization (*21*), rendering them especially susceptible to invasions (*22*) that further alter community structure and function. The invasion of the Asian clam *Potamocorbula amurensis* in San Francisco Bay (*23*), the zebra mussels *Dreissena polymorpha* and *Dreissena* sp. in the Laurentian Great Lakes (*24, 25*), and the comb jelly *Mnemiopsis leidyi* in the Black Sea (*26*) are dramatic examples of the catastrophic impact of ballast water introductions. The ecological roles and impacts of invading species can only be partially predicted from knowledge of their biology and ecology in donor regions (*2*). For these reasons, bays, estuaries, and inland waters with deep water ports—marine analogs of despoiled, highly invaded oceanic islands—may be among the most threatened ecosystems on the planet (*27*).

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7. Ballast water may also be taken aboard and discharged in many other patterns. For example, offshore water may be ballasted in one ocean and deballasted in another ocean, which would result in the movement of oceanic taxa in addition to neritic taxa.
8. Larger (>2 cm) organisms (such as fish) may fail to pass through the intake grates or may be destroyed by the impeller pump blades.
9. Ships were sampled from 1986 to 1991. Five to six vertical quantitative hauls were made in each vessel using an 80-μm mesh, 0.5-m-diameter plankton net towed at 0.5 m s^{-1} in 10 to 20 meters of ballast water of floodable cargo holds. Samples were examined alive under a stereomicroscope to ensure the inclusion of fragile specimens. All samples were preserved and retained. Specimens of many taxa were cultured until they grew to a size that permitted identification. Information on the volume, source, and age of ballast water was obtained. Cargo holds sampled contained an average of 1.09×10^4 (SD = 2.7×10^3) metric tons (=1.09×10^7 liters, SD = 2.7×10^6) of water; total ballast water on board averaged 2.01×10^4 (SD = 6.4×10^3) metric tons (=2.01×10^7 liters, SD = 6.4×10^6) of water.
10. Two relatively common marine phyla not found in our samples are the Porifera (sponges) and Ctenophora (comb jellies). The absence of ctenophores may reflect a bias against extremely fragile taxa. Alternatively, ctenophore distribution is often temporally and spatially uneven [K. Mountford, *Estuarine Coastal Mar. Sci.* **10**, 393 (1980); E. Deason, *Estuarine Coastal Shelf Sci.* **15**, 121

(1982)] and their absence may reflect chance. The planktonic larvae of sponges are short-lived and may survive only short voyages.
11. True species diversity in these samples is underestimated because larval and postlarval forms of many species are morphologically indistinguishable. Also, animal, plant, and protist taxa smaller than 80 μm (the size of the plankton net mesh) were not efficiently retained.
12. We estimate (assuming 20 to 30 taxa per vessel, and several thousand ships out of a world fleet of 35,000 with ballast water at sea at any given time) that, on any one day, several thousand species may be in motion in ballast water "conveyor belts" around the world. Therefore, comparing known invasions (Table 2) with any particular ballast sample may rarely reveal the same taxa, underscoring the importance of recognizing this phenomenon at a supraspecific level.
13. Densities of plankton were estimated by mixing and splitting each replicate, counting the organisms, and multiplying by the volume of water sampled per replicate (*9*).
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16. Organisms with a short larval phase can be entrained in ballast water and then settle. We found metamorphosed ascidians (1 to 2 mm) settled on floating wood chips, and, in five ships that had completed voyages of 13 to 16 days, we found unattached ascidian tadpoles but no adults. Although we found few fish in our samples, more than 20 ship's captains in the Great Lakes, and on the U.S. Atlantic, Gulf, and Pacific coasts, have reported to us live fish in ballast water tanks.
17. Freshwater ballast transferred to other freshwater endpoints (such as from Europe to the Laurentian Great Lakes, or vice versa) may transfer encysted stages of many taxa (such as sponge gemmules and bryozoan statoblasts). Such stages remaining in ship's ballast sediments after open ocean exchange may resist saltwater immersion.
18. The recent increase in invasions caused by ballast water may be due to a variety of factors, including increases in the size, number, and speed of ships (*4, 5*).
19. We expect that several of the six species of Asian copepods now recognized on the Pacific coast of North America will also be found in eastern Australia, a region that receives large volumes of ballast water from the same sources in Japan and China as does the North American Pacific coast.
20. Over 50 examples are now known where introduced species were mistakenly described as "new" species, some several times from different places around the world (J. T. Carlton, in *San Francisco Bay: The Urbanized Estuary*, T. J. Conomos, Ed. (American Association for the Advancement of Science, Washington, DC, 1979), pp. 427–444; J. W. Chapman and J. T. Carlton, *J. Crustacean Biol.* **11**, 386 (1991); J. T. Carlton, unpublished results.
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27. Recent changes in policy have reflected a recognition of the damage caused by introductions mediated through ballast water. Federal regulations to control the discharge of ballast water into the Great Lakes, Australia, and New Zealand are in effect and national studies are under way in Australia, Canada, and the United States on control mechanisms to reduce the number of living specimens arriving in port-of-origin ballast water and sediments. The United Nations International Maritime Organization has ratified international protocols for ballast control.
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Regulation of Lymphoid-Specific Immunoglobulin μ Heavy Chain Gene Enhancer by ETS-Domain Proteins

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The enhancer for the immunoglobulin μ heavy chain gene (*IgH*) activates a heterologous gene at the pre-B cell stage of B lymphocyte differentiation. A lymphoid-specific element, μB, is necessary for enhancer function in pre-B cells. A μB binding protein is encoded by the *PU.1/Spi-1* proto-oncogene. Another sequence element, μA, was identified in the μ enhancer that binds the product of the *ets*-1 proto-oncogene. The μA motif was required for μB-dependent enhancer activity, which suggests that a minimal B cell–specific enhancer is composed of both the PU.1 and Ets-1 binding sites. Co-expression of both PU.1 and Ets-1 in nonlymphoid cells trans-activated reporter plasmids that contained the minimal μ enhancer. These results implicate two members of the Ets family in the activation of *IgH* gene expression.

Transcription of the immunoglobulin (Ig) heavy chain gene (*IgH*) is activated at the pre-B cell stage of B cell differentiation. The μ enhancer (μE), residing in the *IgH* gene, is a lymphocyte-specific regulatory element (*1, 2*) that enhances transcription in transfection assays but is also sufficient to activate a heterologous gene in the pre-B cells of transgenic mice (*3–7*). Thus, the μ enhancer may regulate *IgH* locus activation during B cell ontogeny, perhaps by inducing sterile μ transcripts that may be required for the initiation of gene rearrangements (*8–10*).

The μ enhancer is a composite of multiple positive- and negative-acting sequence

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