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DISTRIBUTION OF PARASITES AND PATHOLOGIES IN SENTINEL BIVALVES: NOAA STATUS AND TRENDS "MUSSEL WATCH" PROGRAM

YUNGKUL KIM* AND ERIC N. POWELL
Haskin Shellfish Research Laboratory, Rutgers University, 6959 Miller Ave, Port Norris New Jersey 08349

ABSTRACT The 1995–1998 histopathology data from NOAA's Mussel Watch Program were analyzed to: (1) document the occurrence of parasites and pathologies in sentinel bivalves during the 1995–1998 time period, (2) describe and compare the geographic distribution of these parasites and pathologies between different bivalve species and between different geographic regions, and (3) evaluate trends in parasite taxon richness. Parasite taxon richness was higher in oysters than in mytilids and dreissenids. Parasites having higher prevalences in a given host taxon routinely also had higher infection intensities. When different geographic locations were compared, the same trends occurred much more rarely. Oysters were more heavily infected based on total parasite body burden than mytilids, and the frequency of hosts with at least one parasite was higher. Excluding the numerically-dominant gregarines, however, removed the differential between oysters and mytilids, with the exception of East-coast mytilids that were more frequently parasitized than East-coast oysters. Dreissenids had lower prevalence and infection intensity for all parasites than the other host bivalve taxa. Though cestodes offer a discrepancy, most of the more common oyster parasites were unicellular, whereas most of the more common mytilid parasites were multicellular. On the average, parasite distributional patterns along a stretch of coastline were more often clinal in nature in mytilids, in that prevalence and infection intensity tended to change gradually over relatively large distance scales, and more bounded in nature in oysters, in that prevalence and infection intensity tended to change more sharply over shorter distance scales. Latitudinal trends were diametric opposites on the two northern coasts. More parasites occurred in mytilids from northern bays of the East coast, whereas fewer occurred in mytilids from northern bays of the West coast. Mytilids far exceeded oysters in the incidence of pathologies, including digestive gland and gonadal abnormalities and hemocytic infiltration. On the West coast, the vast majority of these pathologies occurred in mussels of the *Mytilus edulis* complex rather than *M. californianus*. All pathologies were more common in mytilids from the northeast coast than in West-coast mytilids. Indeed, discounting the gregarines, northeast coast mytilids combined the highest instances of pathologies with among the highest parasite body burdens of any bivalve taxon and coastal area combination in the Mussel Watch program.

KEY WORDS: mussel, oyster, parasitism, pathology, geographic distribution, sentinel bivalve, prevalence, infection intensity

INTRODUCTION

The National Status and Trends Mussel Watch Program monitors contaminants of environmental concern using, as sentinel organisms, bivalves collected from sites distributed along the entire United States coastline. Siting emphasizes the avoidance of point sources of contamination so that contaminant body burdens are representative of regional norms. The Mussel Watch Program has included a histopathological survey since 1995 to track population health and to assess potential interactions between diseases, parasites, and pathologies and contaminant body burden. Although many regional surveys have been undertaken (e.g., Burton 1961, Newman 1971, Otto et al. 1979, Svärdh 1999, Svärdh & Johannesson 2002), this is the first nationwide monitoring program to use a quantitative approach to histopathological analysis, including the direct enumeration of parasites and pathologies that can be readily tallied and the implementation of semiquantitative scales for infection intensity for dispersed pathologies and ramifying parasites or parasites capable of achieving overwhelming densities (Kim & Powell 2006, Kim et al. 1998).

The impetus for including biological analyses in the Mussel Watch Program was the concern that gametogenic stage might influence contaminant body burden, as some contaminants are preferentially associated with or excluded from gametic tissue (e.g., Jovanovich & Marion 1987, Ellis et al. 1993, Abbe et al. 1994). Accordingly, some biological data have been collected since the inception of the program in 1986 (e.g., Kim & Powell 1998, Kim et al. 1999, 2001). Accumulating support for the interaction of contaminant and parasite body burdens led to the expansion of biological sampling to include histopathological analyses. Parasites, tissue pathologies, and diseases have been suggested as biomarkers for contaminant exposure and environmental stress (Hinton et al. 1992). The physiological state of an organism can influence contaminant body burden (e.g., Boyden & Phillips 1981, Lunsford & Blem 1982, Jovanovich & Marion 1987) and likewise contaminant body burden can influence physiological state (e.g., DiSalvo et al. 1975, Anderson 1977, Axiak et al. 1988, Moore et al. 1989). Physiological processes such as feeding and spawning can significantly influence contaminant uptake and depuration (e.g., Cossa et al. 1980, Mix et al. 1982, Sanders et al. 1989, Páez-Osuna et al. 1995). Parasites, by direct sequestration or through their influence on host physiology, can modulate these processes (e.g., Khan 1987, Bowmer et al. 1991, Chu & Hale 1994, Landsberg 1996, Zimmerman et al. 1999). As a consequence, the expectation that pollution, pathology, and parasitism should have some linkage has been the subject of much study and debate (Laird 1961, Sindermann 1983, Peters 1988, Winstead & Couch 1988, Khan 1990, Kim et al. 1999, 2001, Wilson-Ormond et al. 2000, Wester et al. 2002). One interesting direction of study is the possibility that many pollutants in the natural environment may be more detrimental to parasites than to their hosts (Möller 1987). As an example, Sures et al. (1994) demonstrated that metals, such as lead, were more concentrated within parasite tissues than in tissues of the fish hosts. Rohde (2002) reviewed other examples.

*Corresponding author. E-mail: ykim@hsrl.rutgers.edu

Ultimately the geographic distribution of parasites must follow that of their hosts (Rohde 1993). Thus, factors influencing the geographic distribution of the host, such as temperature (Hedgpeth 1957), are also likely to affect that of the parasites. One expects, then, that the latitudinal gradient should significantly influence parasite infection patterns. Rohde (1992) pointed out that higher numbers of parasitic species normally are found in warmer regions [but see Svärdh and Johannesson (2002) and Powell et al. (1999) for exceptions]. The principal oyster disease-causing organisms, *Perkinsus marinus and Haplosporidium nelsoni*, are strongly temperature-dependent (Soniat & Gauthier 1989, Cook et al. 1998, Paraso et al. 1999) and, therefore, demonstrate latitudinal gradients in prevalence and infection intensity (Powell et al. 1992a, Kim et al. 1998) and respond predictably in extending their range and intensity in response to warming trends (Soniat et al. 2006, Cook et al. 1998, Hofmann et al. 2001). Adult oyster size varies with the latitudinal gradient (Hofmann et al. 1994), as do other biological variables, such as feeding rate (Powell et al. 1992b), that may ultimately influence parasite distributional patterns by, in the latter example, influencing the rate at which waterborne pathogens are accumulated (e.g., Ford & Tripp 1996, Ford et al. 1999a). Provincial boundaries, determined primarily by the latitudinal temperature gradient (Engle & Summers 1999, Llansó et al. 2002, Rohde 2002), should then exert a strong influence on parasite distributional patterns, even when host ranges cross provincial boundaries, as do the principal Mussel Watch sentinel bivalves. However, parasite ranges may be restricted in comparison with the range of their host (George-Nascimento 2000, Kruess & Tscharntke 2000, Rohde 2002) and variations in host abundance may create discontinuities in what otherwise might be continuous distributional patterns as host density often strongly influences parasite occurrence (Blower & Roughgarden 1987, 1989, Woolhouse & Chandiwana 1990).

The geographic scale of the Mussel Watch Program provides an opportunity to examine the distribution of parasites over a broad geographic range. The objectives of this analysis of Mussel Watch data are to: (1) document the occurrence of parasites and pathologies in sentinel bivalves during the 1995–1998 time period, (2) describe and compare the geographic distribution of these parasites and pathologies between different bivalve species and between different geographic regions within the same bivalve species, (3) determine the influence of provincial boundaries on these distributional patterns, and (4) evaluate, using prevalence data, trends in parasite taxon richness. Documenting the ranges of parasites is important because climatic changes are significantly altering the ranges of some parasites with concomitant effects on host population dynamics (Cook et al. 1998, Harvell et al. 1999, Sunila et al. 1999, Hayes et al. 2001) and because trends in biodiversity include the species richness of the parasitic fauna as well as that of their hosts (Hawkins 1990, Sousa 1991, Thomas et al. 1997).

MATERIALS AND METHODS

Species Sampled and Sample Collection

The bivalve samples were collected annually from a network of sites along the United States coastline. Sampling targeted the largest animals at each site. Each sampled site subsequently was assigned to one of 126 bays [Table 1; see Lauenstein et al. (1997)

TABLE 1.

Bay systems sampled by the National Status and Trends Mussel Watch Program. Allocation of sampling sites to bays is detailed in the Appendix of Kim and Powell (2006).

Bay Group	Bay Name	State
1	Green Bay	WI
2	Lake Michigan, west	WI
3	Lake Michigan, east	MI
4	Traverse Bay	MI
5	Saginaw Bay	MI
6	Lake Erie, west	MI
7	Lake Erie, east	OH
8	Niagara River	NY
9	Lake Ontario, west	NY
10	Lake Ontario, east	NY
11	Hudson River	NY
12	Penobscot Bay	ME
13	Merriconeag Sound	ME
14	Cape Arundel	ME
15	Great Bay	NH
16	Cape Ann	MA
17	Nahant Bay	MA
18	Boston Harbor	MA
19	Massachusetts Bay	MA
20	Duxbury Bay	MA
21	Cape Cod	MA
22	Buzzards Bay	MA
23	Narragansett Bay	RI
24	Block Island Sound	RI
25	Long Island Sound, east	CT
26	Long Island Sound, mid	CT
27	Long Island Sound, west	CT
28	Port Jefferson	NY
29	Gardiners Bay	NY
30	Moriches Bay	NY
31	Fire Island	NY
32	Hudson/Raritan Estuary	NY
33	New York Bight	NJ
34	Barnegat Inlet	NJ
35	Absecon Inlet	NJ
36	Delaware Bay, downestuary	NJ
37	Housatonic River	CT
38	Port Jefferson	NY
39	Delaware Bay, midestuary	NJ
40	Delaware Bay, upestuary	NJ
41	Chesapeake Bay, upestuary	MD
42	Chesapeake Bay, Choptank reach	MD
43	Potomac River	MD
44	Rappahannock River	VA
45	Chesapeake Bay, downestuary	VA
46	Chesapeake Bay, mouth	VA
47	Chincoteague Bay	VA
48	Pamlico Sound, north	NC
49	Pamlico Sound, south	NC
50	Beaufort Inlet	NC
51	Cape Fear	NC
52	Winyah Bay	SC
53	Charleston Harbor	SC
54	Savannah River	GA
55	Sapelo Sound	GA
56	St. Johns River	FL
57	Matanzas River	FL

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TABLE 1.
continued

Bay Group	Bay Name	State
58	Indian River	FL
59	Biscayne Bay	FL
60	Florida Keys	FL
61	Florida Bay	FL
62	Puerto Rico	PR
63	Everglades	FL
64	Naples Bay	FL
65	Charlotte Harbor	FL
66	Tampa Bay	FL
67	Cedar Key	FL
68	Apalachee Bay	FL
69	Apalachicola Bay	FL
70	St. Andrews Bay	FL
71	Choctawhatchee Bay	FL
72	Pensacola Bay	FL
73	Mobile Bay	AL
74	Mississippi Sound	MS
75	Lake Borgne	LA
76	Breton Sound	LA
77	Pass a Loutre	LA
78	Tiger Pass	LA
79	Barataria Bay	LA
80	Terrebonne Bay	LA
81	Atchafalaya Bay	LA
82	Vermilion Bay	LA
83	Joseph Harbor	LA
84	Calcasieu Lake	LA
85	Sabine Lake	LA
86	Galveston Bay	TX
87	Brazos River	TX
88	East Matagorda Bay	TX
89	West Matagorda Bay	TX
90	San Antonio Bay	TX
91	Copano/Aransas Bay	TX
92	Corpus Christi Bay	TX
93	Laguna Madre	TX
94	San Diego Bay	CA
95	Mission Bay	CA
96	Oceanside	CA
97	Santa Catalina Island	CA
98	Anaheim Bay	CA
99	Marina Del Rey area	CA
100	Santa Cruz Island	CA
101	Santa Barbara	CA
102	Point Conception	CA
103	San Luis Obispo Bay	CA
104	Monterey Bay	CA
105	San Francisco Bay	CA
106	Tomales/Bodega Bay	CA
107	Point Arena/Delgada	CA
108	Eureka	CA
109	Point St. George	CA
110	Coos Bay	OR
111	Yaquina Bay	OR
112	Tillamook Bay	OR
113	Columbia River	OR
114	Willapa Bay	WA
115	Strait of Juan de Fuca	WA
116	Puget Sound, north	WA
117	Hood Canal	WA
118	Puget Sound, south	WA
119	Sinclair Inlet	WA
120	Elliott Bay	WA
121	Whidbey Island	WA
122	Bellingham Bay	WA
123	Nahku Bay	AK
124	Prince William Sound	AK
125	Cook Inlet/Gulf of Alaska	AK
126	Hawaii	HI

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TABLE 1.
continued

for site descriptions; see Kim and Powell (2006) for details on the allocation of sites to bays.]. A ''bay'', as termed herein, represents all sites in a single estuary, estuarine reach of a large estuary, or group of neighboring sites on an open coastline. Table 1 shows the locations of each bay.

The introduced zebra mussel, *Dreissena polymorpha*, and quagga mussel, *D. bugensis*, were sampled at sites in the Great Lakes (Bays 1–10) and Hudson River (Bay 11). Recently, the quagga mussel has displaced the zebra mussel in many areas (Stoeckmann 2003). Rosenberg and Ludyanskiy (1994) discussed the taxonomy. Mussel Watch sites include all Great Lakes except Lake Superior (Lauenstein et al. 1997).

Mytilid mussel taxa were collected from the Northeast (Bays 12–36) and West (Bays 94–125) coasts, including Alaska. According to Hilbish et al. (2000), mussels collected on the East coast were *Mytilus edulis sensu stricto*, as *M. edulis* is the predominant species from central Maine south (Rawson et al. 2001) to Cape Hatteras (Wells & Gray 1960). On the West coast, three mussel taxa were collected, *M. californianus* and two species referable to the *M. edulis* complex, *M. galloprovincialis* and *M. trossulus*. *Mytilus californianus* was collected at 31 sites mostly located at jetties, points or capes, among the 58 total West-coast sites excluding Alaska (viz., 27 sites out of 36 in California, two sites among six in Oregon and two sites among 16 in Washington). *Mytilus trossulus* was collected at the vast majority of the more northern stations from Oregon to Alaska. *Mytilus galloprovincialis* was introduced into the eastern Pacific in the 1880s and now occurs from central California to Baja California, with some populations probably farther north (McDonald & Koehn 1988, Koehn 1991, Seed 1992), including a population in Puget Sound established at least by 1988 (Wonham 2004). Thus, *M. galloprovincialis* was collected at some California sites and may have been present in some Puget Sound collections. In addition, some central and northern California sites yielded mussels that probably were hybrids of *M. galloprovincialis* and *M. trossulus* (Hilbish et al. 2000). For some later analyses, the readily distinguishable *M. californianus* was compared with the mytilids referable to the *M. edulis* complex. The continued uncertainty in the taxonomy of the remaining mytilids and the insufficient number of sampled bays where only one species was collected prevented subdivision of the members of the *M. edulis* complex in statistical analysis.

Four oyster taxa were sampled, *Crassostrea virginica, C. rhizophorae, C. gigas*, and *Dendostrea sandvichensis*. *Crassostrea virginica* was sampled from coastal and estuarine areas of

the Mid-Atlantic and southeast coasts (Bays 37–61) and the Gulf of Mexico (Bays 63–93). *Crassostrea rhizophorae* was collected in Puerto Rico (Bay 62), and *C. gigas* and *D. sandvichensis* were collected in Hawaii (Bay 126). Considerable disagreement exists as to the taxonomic status of *C. virginica* and *C. rhizophorae* (Newball & Carriker 1983, Ladrón de Guevara et al. 1996), whereas *C. gigas* and *D. sandvichensis* are clearly distinct from the other two. In total, however, *C. virginica* was collected at 55 of 57 bays where oysters were collected.

To simplify discussion when referring to groups of these taxa, the following inclusive terms will be used: dreissenid in reference to the combination of *D. bugensis* and *D. polymorpha;* oyster jointly for *C. virginica, C. rhizophorae, C. gigas*, and *D. sandvichensis;* mytilid for the combination of *M. edulis, M. californianus, M. galloprovincialis*, and *M. trossulus;* and *M. edulis* complex for the mytilid subset of *M. edulis, M. galloprovincialis*, and *M. trossulus*.

Except in the Great Lakes, the sampling sites were visited annually during winter with each site occupied within 30 days of an annual target date (O'Connor 1994). Sampling was done in winter to minimize the influence of gametogenesis and spawning on contaminant body burden (Jovanovich & Marion 1987, Ellis et al. 1993). Dreissenid mussels were collected in late August through September, because the Great Lakes are frequently frozen over during the winter. As a consequence of sampling program design, subsequent analyses may be biased for those parasites that exhibit a strong seasonal cycle of infection intensity (e.g., Wallet & Lambert 1986, Burreson & Ragone Calvo 1996, Ford et al. 1999a).

Sample Preparation

Tissue preparation followed NOAA Status and Trends protocols (Ellis et al. 1998a). With the exception of *P. marinus* in oysters, all analyses were conducted on five randomly chosen specimens from each site. The anterior-posterior length (e.g., Morales-Alamo & Mann 1989) was measured prior to analysis. Because of their small size, dreissenids were preserved whole in their shells in Davidson's fixative. After one week, 20-to-30 ml of acetic acid were added, if needed, to aid decalcification. When the shell became separated from the soft parts, the fixative was replaced by 70% ethyl alcohol. The adductor muscles of mytilids were cut with a sharp knife so that the valves remained open. The entire animal was placed in Davidson's fixative for one week, then transferred to 70% ethyl alcohol. Prior to embedding, the byssal threads of dreissenids and mytilids were completely removed from the byssal glands to avoid problems when sectioning the tissue and a 3–5 mm thick transverse cross-section including digestive gland and gill tissue was removed using a scalpel. For oysters, 12 animals from each site were randomly selected and opened with an oyster knife. A small section of mantle tissue (5 mm $\times$ 5 mm) was removed for the culture of *Perkinsus marinus*, the Dermo disease pathogen. A 3-to-5 mm-thick transverse cross-section of tissue was removed from five of these animals using scissors, transferred to a tissue capsule, and placed in Davidson's fixative for two days, followed by 70% ethyl alcohol. Oyster, mytilid, and dreissinid tissue sections were placed in a tissue capsule, embedded in paraffin, and then sectioned at 5 μm. Tissue sections were stained in a pentachrome series and mounted in Permount (Ellis et al. 1998a).

Parasite/Pathology Quantification

Tissues examined included gill, mantle, gonad and gonoducts, digestive gland tubules, stomach/intestine, and connective tissue. For oysters, *P. marinus* was assayed by the more precise thioglycollate method of Ray (1966) following Powell and Ellis (1998). All other parasites and pathologies were scored microscopically for intensity either quantitatively or on a semiquantitative scale. Quantitative scores were used for parasites, pathologies, and selected morphological conditions, including prokaryotic inclusions (rickettsia, chlamydia, etc.), ciliates, gregarines, nematodes, cestodes, and metacercariae of trematodes, that could be tallied individually, following procedures described by Ellis et al. (1998b) and Kim et al. (2006b). Ciliates were quantified by tissue type (*viz*., gill and digestive tract), as were the gregarines (*viz*., body, gill, and mantle), based on observations of at least moderate tissue specificity of some species (Sprague & Orr 1955). Each nematode cross-section observed was counted, although a single individual may be responsible for a number of tissue cross-sections. Certain tissue pathologies and tissue components were also quantified by direct counts, including cases of hemocytic infiltration that were scored separately as focal and diffuse (Kim & Powell 2004), granulocytomas (Lowe & Moore 1979), and ceroid bodies (Mackin 1951, Stein & Mackin 1955).

Some parasites and morphological conditions, such as ramifying trematode sporocysts and the disease-producing protozoans, *P. marinus* and *Haplosporidium nelsoni*, were assigned to semiquantitative scales depending on the intensity or extensiveness of the affected area. A 0-to-4-point scale was used for ramifying trematode sporocysts of the families Fellodistomidae and Bucephalidae because of the extensiveness of infections and the difficulty in obtaining quantitative counts of the large branching sporocysts (Ellis et al. 1998b, Kim et al. 2006b). Intensity of *P. marinus* infection was assigned using the 0-to-5-point scale of Mackin as modified by Craig et al. (1989) (Ashton-Alcox et al. 2006). *Haplosporidium nelsoni* infection intensity was scored on the 0-to-4-point scale of Kim et al. (2006b) adapted from Ford and Figueras (1988). For each specimen examined, the presence of neoplasms and unusual digestive tubules was recorded. Abnormal gonadal development, characterized by unusual development at the base of the follicles or by presence of foreign cells and cellular debris in the follicles, was given a 0-to-4-point score related to the spatial coverage of the condition (Kim et al. 2006a). For digestive gland atrophy, a condition known to be caused by a variety of stressors most likely related to poor nutrition (Palmer 1979, Winstead 1995, Kim & Powell 2004), the average degree of thinning of the digestive tubule walls was assigned a numerical rating on a 0-to-4-point scale (Kim et al. 2006b).

Statistical Analysis

Definitions

Two descriptions of parasite/pathology occurrence were used in this study: prevalence and infection intensity. Prevalence, the fraction of individuals with the parasite or pathology, was calculated as:

$$Prevelance = \frac{number\ animals\ affected}{number\ animals\ analysed}. \quad (1)$$

Infection intensity, the average number of occurrences of a parasite or pathology in the affected individuals only, was calculated as:

$$\textit{infection intensity} = \frac{\sum_{i=1}^{n} \left(\begin{array}{c} \textit{number of occurrences of} \\ \textit{parasite or pathology} \end{array} \right)}{\textit{number affected individuals}}. \quad (2)$$

For conditions rated using semiquantitative scales, the scale rating replaced the number of occurrences in this calculation. If a parasite or condition did not occur in a bay, infection intensity [Eq. (2)] was undefined for that bay. A value of zero was not assigned. Weighted prevalence or mean abundance, a measure often used in the bivalve literature (e.g., Ford 1988, Kim & Powell 2004), confounds prevalence and infection intensity:

$$\textit{weighted prevalence} = \textit{prevalence} \times \textit{infection intensity} \quad (3)$$

and, as a consequence, is not presented.

Parasite/Pathology Groupings

The protocol for the biological component of the Mussel Watch Program stipulates analysis of five individuals per site. In this study, a designated bay (Table 1) usually contained more than one site. The value of prevalence or infection intensity assigned to each bay was the arithmetic mean of all animals analyzed from each site over the 1995–1998 period. Bays were grouped into a series of regions: East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125; and Great Lakes/Hudson River dreissenid sites, Bays 1–11.

The shear number of samples obtained yearly by the Mussel Watch Program prevented detailed identification of most parasites. As a consequence, parasites were identified, tallied, and analyzed statistically by major taxon following the strategy adopted by Yevich and Barszcz (1983) in the first Mussel Watch Program (Farrington et al. 1983). In addition, total parasite body burden was calculated as the sum of all quantified parasites; that is, all parasites not evaluated using a semiquantitative scale. These included, for mytilid taxa, the gregarines, ciliates, procaryote inclusions, trematode metacercariae, coccidians, copepods, xenomas (cells distended with numerous gill ciliates as described in Otto et al. (1979)), pinnotherid crabs, and other unidentified organisms; for oyster taxa, the gregarines, all ciliates, cestodes, nematodes, prokaryotic inclusions, unencysted trematode metacercariae, copepods, xenomas, pinnotherid crabs, and other unidentified organisms; and for dreissenid taxa, nematodes, individual trematodes, and other unidentified organisms. Because of the numerical dominance of the gregarines in oyster taxa, a modified total parasite body burden was also calculated as the sum of the quantitative counts of the remaining parasite groups. A group of consistently rare parasites was tallied together for convenience of analysis, but also because the distribution of rare species is inherently interesting (Laird 1961, Rabinowitz et al. 1986, Haukisalmi et al. 1988). This sum excluded common taxa such as gregarines, ciliates, nematodes, cestodes and prokaryotic inclusions. The category 'total protozoans' included all ciliates, coccidians in mytilid mussels, and xenomas. Pathologies were grouped into major pathologies, including neoplasms, unusual digestive tubules, and gonadal abnormalities, and tissue pathologies, including focal and diffuse hemocytic infiltration and granulocytomas as described in Villalba et al. (1997). Taxon richness was the sum of the total number of different types of parasites observed in each bay over the four years.

Statistical Approach

Geographic areas of significantly higher or lower parasitism were distinguished by organizing bays along a Gabriel-connected graph (Gabriel & Sokal 1969). This method provides an unbiased 'road map' connecting the sampled bays. Two bays ($\overline{AB}$) are connected if no third bay (C) is present that forms an obtuse angle when connected between the other two ($\angle ACB$). Bay-to-bay distances in kilometers were calculated along this Gabriel network by Marble's (1967) method. Regional statistics were calculated for each bay by defining a bay group as all bays within a 300-km distance of the given bay along the Gabriel network. This group of bays was compared with all bays along a defined stretch of coastline (e.g., the northeast coast) by first computing the "global" median for prevalence or infection intensity for all bays in that geographic region. The frequency at which the prevalences or infection intensities for the bays encompassed in the 300-km group exceeded this 'global' median was compared with the frequency at which the prevalence or infection intensity exceeded the 'global' median for the entire coastline using a binomial test. Because of the many ties at the median, the global probability was not always 0.5. The comparison was quantified for each 300-km bay group using the Z statistic computed from the normal approximation to the binomial distribution:

$$Z = \frac{X - np}{\sqrt{np(1-p)}} \quad (4)$$

where n is the total number of bays, p is the 'global' probability, and X is the number of observations in a bay group where the variable was greater than the 'global' median. One such statistic was computed for each sampled bay. The significance level for each Z statistic was computed as described by Conover (1980).

To identify significant differences among different host bivalve taxa (e.g., mytilids, oysters, dreissenids) and within the same host taxon collected from different coasts (i.e., East, West, Gulf, Great Lakes), values for each bay were ranked and analyzed by ANOVA followed by an *a posteriori* Tukey's Studentized Range Test. For infection intensity obtained by direct count, bivalve length was used as a covariate because larger animals inherently should have higher counts, as the analyzed tissue cross-section is larger.

RESULTS

Overview

Average prevalences and infection intensities are rendered in Tables 2 and 3 and discussed in greater detail in Kim and Powell (2006). Prokaryotic inclusions have been reported widely in oysters from the East and Gulf coasts and in mussels from the East and West coasts (e.g., Yevich & Barszcz 1983, Gulka & Chang 1984, Couch 1985, Gauthier et al. 1990, Figueras et al. 1991). In this study, prokaryotic inclusions were recorded in both mytilids and oysters and from samples collected on the East, West, and Gulf coasts. Prokaryotic inclusions were not observed in dreissenids. No effort was made to distinguish

TABLE 2.

Average taxon richness and prevalence of parasites and pathologies for each region or taxon group.

Taxon/Type	Dreissenids	East-coast		Gulf-coast Oysters	West-coast	
		Mytilids	Oysters		*M. edulis* complex	*M. californianus*
Taxon Richness	0.2609	3.0192	5.7170	7.2192	2.3878	2.4444
Prokaryotic Inclusion	—	0.0548	0.0392	0.0555	0.0429	0.0200
Haplosporidium spp.	—	—	0.0838	—	—	—
Perkinsus marinus	—	—	0.4496	0.6035	—	—
Gill Ciliate	—	0.3612	0.0692	0.0587	0.2862	0.0663
Digestive Tract Ciliate	—	0.0020	0.1300	0.1213	0.0057	0.0037
Body Gregarine	—	—	0.4958	0.5281	0.0519	0.1853
Gill Gregarine	—	—	0.4658	0.6210	0.1024	0.2895
Mantle Gregarine	—	—	0.3563	0.4377	0.0095	0.1311
Trematode Sporocyst	—	0.1116	0.0029	0.0068	0.0024	0.0026
Trematode Metacercariae	—	0.3712	—	—	0.0010	0.0274
Nematode	0.0009	—	0.0346	0.1397	—	—
Cestode	—	—	0.1496	0.0961	—	—
Major Pathology	0.0318	0.4628	—	0.0074	0.3405	0.0442
Tissue Pathology	0.0409	0.3300	0.1621	0.1390	0.0800	0.1032

—, not present.

rickettsia from *Chlamydia* or mycoplasms (Harshbarger et al. 1977). Prokaryotic inclusions normally were observed within the epithelial cells of the digestive system. In some mytilids, prokaryotic inclusions were associated with the gill or renal tissues. Inclusions found in the digestive tract were usually roundish and those in the gill and kidney rather amorphous in shape. No apparent pathological effects or host responses to prokaryotic infection were detected, as is typical for bivalves (Otto et al. 1979, Figueras et al. 1991, Villalba et al. 1997, but see Wu & Pan 2000), but not necessarily for molluscs in general (e.g., Moore et al. 2000, Caceres-Martinez & Tinoco-Orta 2001).

Gregarines are widely distributed in oysters along the East and Gulf coasts (Landau & Galtsoff 1951, Otto et al. 1979, Gauthier et al. 1990). Kim et al. (1998) also observed gregarines in mytilid mussels from the West coast. Mud and stone crabs are known final hosts (Prytherch 1940). In this study, gregarines, likely *Nematopsis* spp., were observed in mytilids and oysters in the connective tissue around the visceral mass of the body, in the gills, and in the mantle connective tissues. No host tissue reaction or discernible pathological effects were observed, in agreement with Cheng (1967).

Perkinsus marinus is abundant in oysters from the East (Ford & Tripp 1996, Kim et al. 1998) and Gulf (Craig et al. 1989, Kim et al. 1998) coasts. In this study, *P. marinus* was observed in oysters from all but one site along the East and Gulf coasts. Abscessed digestive epithelia with cavities containing parasitic cells, ceroid bodies, and hemocytes were observed frequently in infected oysters. Necrotic mantle tissue with increased fibrosis and occlusion of blood vessels was also seen (Mackin 1951).

TABLE 3.

Average infection intensity of parasites and pathologies for each region or taxon group.

Taxon/Type	Dreissenids	East-coast		Gulf-coast Oysters	West-coast	
		Mytilids	Oysters		*M. edulis* complex	*M. californianus*
Prokaryotic Inclusion	—	5.16	6.74	6.99	6.50	4.31
Haplosporidium spp.	—	—	2.23	—	—	—
Perkinsus marinus	—	—	1.47	1.98	—	—
Gill Ciliate	—	3.83	9.57	5.00	3.00	3.86
Digestive Tract Ciliate	—	1.00	7.14	3.43	1.00	3.00
Body Gregarine	—	—	19.64	10.08	4.32	7.86
Gill Gregarine	—	—	13.34	61.01	5.96	4.83
Mantle Gregarine	—	—	9.09	8.39	1.78	18.59
Trematode Sporocyst	—	1.69	1.00	3.07	3.00	3.00
Trematode Metacercariae	—	2.75	—	—	1.00	1.04
Nematode	1.00	—	2.93	2.01	—	—
Cestode	—	—	1.78	1.51	—	—
Ceroid Bodies	9.54	28.20	112.28	104.44	10.16	15.08
Digestive Gland Atrophy	1.79	2.65	2.65	2.33	2.70	2.44
Tissue Pathology	1.17	2.38	1.40	1.39	1.62	1.34

—, not present.

Haplosporidium nelsoni, first reported in Delaware Bay oysters in the late 1950s (Haskin et al. 1965), has extended its range from Maine to Florida (Kern 1988, Ford & Tripp 1996). In this study, MSX was found only on the East coast, mostly from Delaware Bay to Georgia. Multinucleated plasmodia were observed in epithelial cells and connective tissues of the gills and digestive tract. Heavy infections were associated with hemocytic infiltration into the site of infection and tissue necrosis (see also Farley 1968, Ford 1985). A second *Haplosporidium, H. costale*, occurs in oysters from high salinity sites. Although most infections observed in this study are likely *H. nelsoni*, the possibility that *H. costale* was present in some cases cannot be excluded (Sunila et al. 2002, Burreson & Ford 2004).

Ciliates are widely reported in the gills or digestive tract of oysters (Otto et al. 1979, Couch 1985, Gauthier et al. 1990) and mussels (Figueras et al. 1991, Kim et al. 1998, Moret et al. 1999). Ciliates occurring between gill filaments or attached to gill surfaces were one of the most commonly observed parasites in mytilids and oysters. Ciliates were also found in the gut lumen or attached to the digestive tract epithelia. Otto et al. (1979), Figueras et al. (1991) and Villalba et al. (1997) reported no notable pathology in bivalves harboring ciliates. Ciliate infections were not observed to elicit any obvious pathological conditions or host responses in this study.

Branching sporocysts and cercariae of larval trematodes have been reported in mytilids and oysters on the East and Gulf coasts (e.g., Stunkard & Uzmann 1959, Lang & Dennis 1976, Tripp & Turner 1978, Hillman et al. 1988), but typically at prevalences much below those observed in deep-sea mussels and some other bivalves (Powell et al. 1999). Those reported in oysters are probably juvenile *Bucephalus*. Those reported in mytilids are probably juvenile *Proctoeces* (Tripp & Turner 1978). [Adult *Proctoeces* were also found in gonadal ducts of oysters from Florida, Alabama, and Mississippi (Winstead & Couch 1981, Couch 1985, Winstead et al. 1998); these were tallied separately and individually in this study]. Carnivorous fish are the final host of bucephalid trematodes (Hopkins 1954). Fellodistomid trematodes such as *Proctoeces* can complete their entire life cycle in a single invertebrate host. Bottom fishes are alternative final hosts (Stunkard & Uzmann 1959). In this study, ramifying sporocysts were observed in mytilids on the East and West coasts and in oysters on the East and Gulf coasts. Infections occurred principally in the visceral connective tissues of the digestive gland and the gonad, destroying gametic tissue and often causing host sterilization. In advanced stages of infection, sporocysts were observed infiltrating gill and mantle tissue and most other organs (see also Cheng & Burton 1965, Powell et al. 1999). We observed little or no aggregation of host hemocytes around healthy sporocysts (see also Cheng & Burton 1965); however hemocytes were occasionally observed around dead or degenerating parasites (see also Teia dos Santos & Coimbra 1995).

Encapsulated trematode metacercariae, presumably gymnophallids (Bower et al. 1994), were observed in mytilid mussels. Metacercariae were observed in all tissues of mytilids: mantle, visceral connective tissue, foot, byssal gland and gill. In most cases, no conspicuous host response was observed. Hemocytes, however, occasionally infiltrated and surrounded, especially dead or dying, worms. Metacercariae, presumable *Proctoeces*, were observed occasionally free in the gonoducts of oysters.

Larval cestodes occur in oysters throughout much of their range (Cheng 1966, Sindermann & Rosenfield 1967, Cake 1977, Couch 1985). Elasmobranchs, such as sharks, skates, or rays, are known final hosts (Cake 1977). Encysted cestodes were observed in either connective tissue around the digestive gland and gut or in the gills of oysters in this study. Cestode infection did not seem to significantly damage the oyster. The formation of cestode cysts, characterized by encapsulation of larval cestodes by layers of connective tissue fibers (Cheng 1966), was observed routinely. Encapsulated larval cestodes often appeared to be disintegrating and in the process of resorption by the host. Interestingly, larval cestodes were not observed in mussels, a fact that we also glean, from the absence of literature reports, to be typical.

Most reports of larval nematodes in Mussel Watch taxa are from oysters (Burton 1961, Couch 1985, Gauthier et al. 1990). (Larval nematodes in mytilid mussels reported by Kim et al. (1998) are here correctly identified as trematode metacercariae.) All nematodes reported in molluscs are larval stages (Cheng 1978, Lichtenfels et al. 1980). Adults are found in predators of molluscs (Cheng 1978), such as elasmobranchs (Millemann 1963) and sea turtles (Berry & Cannon 1981). In this study, larval nematodes were found localized in vesicular connective tissues of the digestive gland in oysters, as described by Burton (1961) and Couch (1985), destroying adjacent host tissues. In some cases, hemocytic infiltration was associated with the worm (see also Couch 1985, Kim & Powell 2004).

In most cases, possible etiologic agents of the pathologies observed in this study were uncertain. Major pathologies included neoplasms, abnormal digestive tubules, and gonad abnormalities. Neoplasms are occasionally reported in oysters (e.g., Harshbarger et al. 1979, Couch 1985) and more commonly in mussels (Mix 1983, Elston et al. 1988), particularly on the West coast. Neoplasms were occasionally observed in mytilids in this study. Neoplastic cells characterized by high nucleus-to-cytoplasm ratios (Ford et al. 1997) filled the vesicular connective tissues of the infected mytilids. All five cases of disseminated sarcomas observed in this study were from mytilids. A second major pathology often observed in mytilids was degenerated and/or necrotic digestive glands. This condition was characterized by digestive tubules in unusually poor condition with loss of their normal integrity and structure, and sometimes with vacuolated epithelia. Individual digestive tubules sometimes were not discernible from each other. A final major pathology, abnormal gonadal development, was observed commonly in mytilids. Often abnormal gonads were characterized by unusual development of gametes at the base of the follicles. The germ cells resembled those of a germinoma (Peters et al. 1994) and were differentiated from normal cells by being either enlarged or by appearing to have an enlarged nucleus. In other cases, underdeveloped gonadal follicles were observed. These follicles were small and occupied a smaller portion of the mantle tissue. Follicles sometimes were filled with cellular debris. Abnormal gonadal development often was associated with hemocytic infiltration into the surrounding tissues. This condition was distinguished from gonadal resorption typically observed at the end of the gametogenic cycle (Newell 1989, see also Kim & Powell 2004).

Other tissue pathologies included focal and diffuse hemocytic infiltration and tissue necrosis. In focal infiltration, hemocytes are found congregated in a localized area. In diffuse infiltration, hemocytes are noticeably abundant over a large tissue area (Sindermann 1970, Couch 1985, Ellis et al. 1998b). In this study, most cases of hemocytic infiltration and necrosis

characterized by death/decay of cells/tissues were observed in the visceral connective tissue and sometimes associated with the presence of parasites. Granulocytomas occurred mainly in the digestive gland of mytilids, as reported by Villalba et al. (1997).

Differences in Distribution Among Bivalve Taxa and Locations

Parasite Taxon Richness

Taxon richness differed significantly among host bivalve taxa (ANOVA, $P < 0.0001$). Oysters harbored significantly more types of parasites than mytilids and dreissenids. Mytilids had significantly higher taxon richness than dreissenids (Table 2). Taxon richness varied significantly between geographic locations (ANOVA, $P < 0.0001$). Gulf-coast oysters had more parasitic taxa than other locations, averaging over seven per bay (Table 2). Taxon richness of East-coast bivalves was significantly higher than in bivalves from the West coast. On the East coast, oysters had significantly higher taxon richness than *M. edulis*. Oysters averaged 5.7 taxa versus 3.0 for *M. edulis* (ANOVA, $P < 0.0001$; Tukey test, $P < 0.05$). Taxon richness was not significantly different between East- and West-coast mytilids (ANOVA, $P > 0.05$); therefore, the increase in taxon richness on the East coast was due primarily to the combination of oyster and mussel sites with oysters contributing the higher numbers. However, Gulf-coast oysters still had significantly higher taxon richness than East-coast oysters (ANOVA, $P = 0.004$; Tukey test, $P < 0.05$). The *M. edulis* complex and *M. californianus* on the West coast did not differ significantly in taxon richness (ANOVA, $P > 0.05$).

Prevalence

Prevalence, when used for total parasite body burden, measures the frequency of occurrence of hosts infected with at least one quantifiable parasite. Hosts parasitized at least once were significantly more common in oysters than in mytilids or dreissenids, and significantly more common in mytilids than in dreissenids (Fig. 1, Table 4). Gulf-coast oysters were parasitized significantly more frequently than East-coast, West-coast, or Great Lakes bivalves (Table 4). East- and West-coast bivalves were similar in the frequency of infection. Most of these differences likely originate in the different taxa collected on each coast; however, no significant difference was detected between *M. edulis* and oysters from the East coast (ANOVA, $P > 0.05$).

After excluding the gregarines, parasitized animals still were significantly more common in mytilids and oysters than in dreissenids (Fig. 1, Table 4). Mytilids and oysters were not significantly different from each other, however; thus, the gregarines were primarily responsible for the higher prevalence of parasitism in oysters. East- and Gulf-coast bivalves were parasitized significantly more frequently than West-coast bivalves, but East-coast and Gulf-coast bivalves were not significantly different from each other (Table 4). On the East coast, *M. edulis* were significantly more frequently infected by parasites than East-coast oysters once the gregarines were excluded (ANOVA, $P = 0.0003$). Thus, inclusion or exclusion of the gregarines substantially altered the outcome of comparisons between bivalve taxa and between geographic locations.

Rare parasites were observed in all bivalve taxa (Fig. 1), but more commonly in mytilids and oysters than in dreissenids (Table 4). The frequencies of occurrence in mytilids and oysters were not significantly different. Rare parasites infected bivalves most often on the West and Gulf coasts (Table 4). East-coast *M. edulis* and East-coast oysters did not differ significantly in the frequency of infection (ANOVA, $P > 0.05$).

Prokaryotic inclusions were found more frequently in oysters than in mytilids (Fig. 2, Table 4). Prokaryotic inclusions were not detected in the dreissenids. Prokaryotic inclusions were observed more commonly in Gulf-coast oysters than East- and West-coast bivalves (Table 4). The frequency of prokaryotic infection was not significantly different between East-coast *M. edulis* and East-coast oysters (ANOVA, $P > 0.05$).

Gregarines were not detected in East-coast *M. edulis* or in the dreissenids (Fig. 3). The geographic distribution among coasts differed significantly (Table 4), because gregarines were significantly more common in oysters in comparison with West-coast mytilids as a whole and also at the tissue level. Gregarines in the body, gill, and mantle tissues all were significantly more common in oysters than in West-coast mytilids (Table 4, Fig. 4).

Dermo disease caused by *P. marinus* was limited to oysters and was observed more commonly in Gulf-coast oysters than in East-coast oysters (Fig. 2, Table 4). Haplosporidian infection was observed only in East-coast oysters (Fig. 2).

Protozoans including ciliates were absent in the dreissenids. The prevalence of protozoa including ciliates, but excluding gregarines, haplosporidians, and apicomplexans, did not differ significantly between mytilids and oysters (Fig. 3, Table 4), nor did prevalence differ significantly in bivalves from the East, West, and Gulf coasts. On the East coast, *M. edulis* were infected significantly more frequently by nongregarine protozoa than oysters, however (ANOVA, $P = 0.007$).

Looking within the protozoa, gill ciliates were more commonly found in mytilids than in oysters (Table 4, Fig. 5). East-coast bivalves were more frequently infected by gill ciliates than Gulf-coast bivalves (Table 4). Bivalves from the West coast fell in-between. East-coast *M. edulis* harbored ciliates in gills more frequently than East-coast oysters (ANOVA, $P = 0.0001$). In contrast, digestive tract ciliates were significantly more common in oysters than in mytilids (Fig. 5, Table 4) and, as a consequence, were more common in Gulf-coast oysters than East- and West-coast bivalves and more frequently encountered in East-coast oysters than in East-coast mytilids (ANOVA, $P = 0.0001$).

Ramifying trematode sporocysts infected mytilids significantly more frequently than oysters (Fig. 6, Table 4) overall and on the East coast (ANOVA, $P = 0.0001$). Trematode sporocysts were not observed in dreissenids. Prevalences were higher in East-coast bivalves than in West- and Gulf-coast bivalves because of the high infection rate in East-coast mytilids (Table 4). Encapsulated trematode metacercariae were observed only in mytilids (Fig. 6, Table 4). East-coast *M. edulis* were more frequently infected by trematode metacercariae than the mytilids from the West coast. Cestodes were not observed in mytilids or dreissenids (Fig. 6), but were similarly common in oysters from the Gulf and East coasts (Table 4). Nematodes occurred at lower prevalences in dreissenids than in oysters (Table 4, Fig. 5). Nematodes were observed significantly more frequently in Gulf-coast oysters than in East-coast oysters (Table 4).

Major pathologies including neoplasms, unusual digestive tubules, and gonadal abnormalities were present in all bivalve taxa, but were more common in the mytilids (Fig. 7, Table 4) and found significantly more frequently in West-coast mytilids. The prevalence of major pathologies was significantly higher in *M. edulis* than in oysters on the East coast (ANOVA,

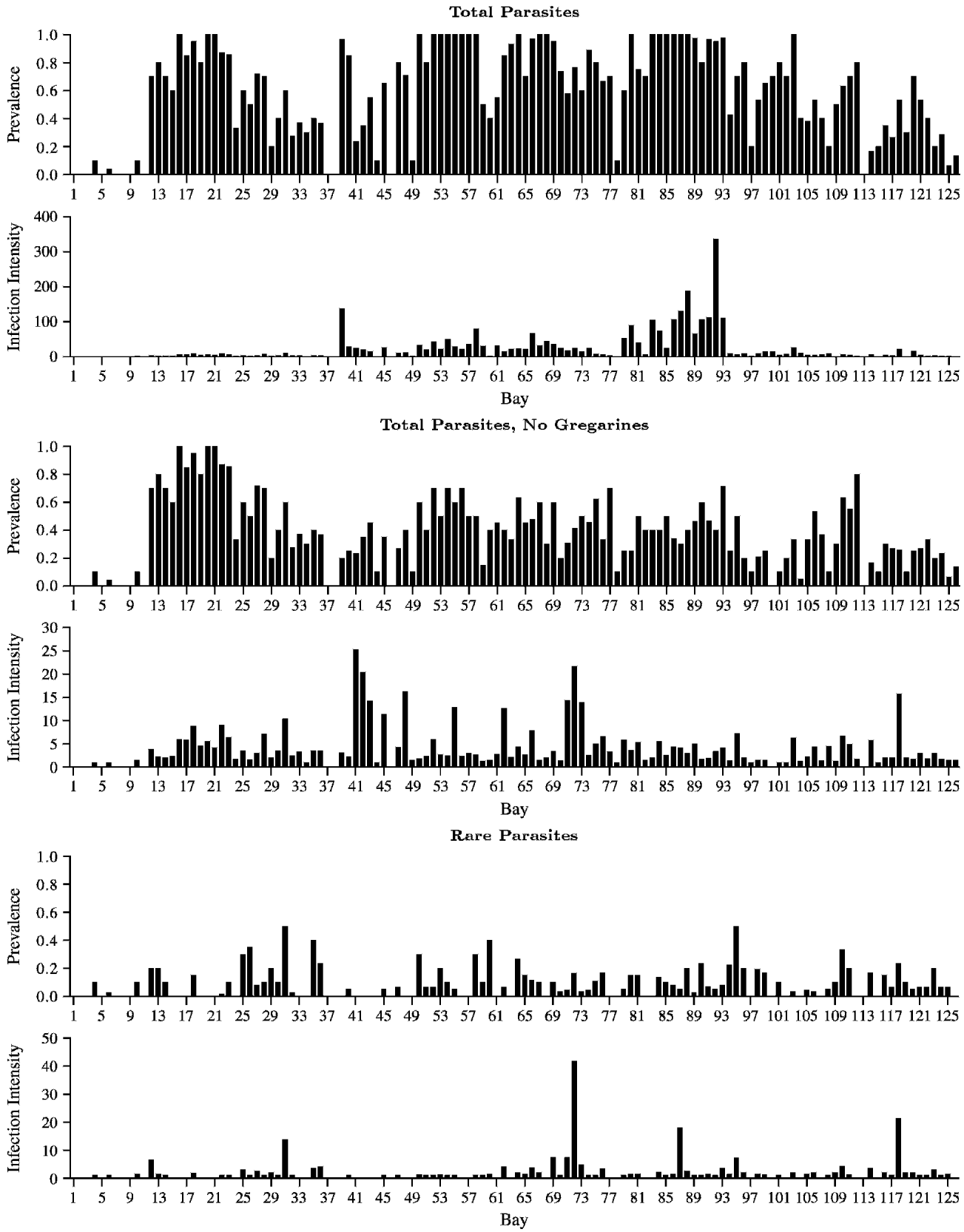

Figure 1. Prevalence and infection intensity for total quantifiable parasite body burden, total quantifiable parasite body burden except the gregarines, and rare parasites. Prevalence measures the frequency of hosts with at least one quantifiable parasite of any quantitated taxon. Great Lakes/Hudson River dreissenid sites, Bays 1–11; East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125.

TABLE 4.

Results of ANOVA and *a posteriori* Tukey Studentized Range tests comparing parasite or pathology prevalence and infection intensity between bivalve taxa and geographic location. For the Tukey tests, same letters within rows within bivalve taxa or location are not significantly different at $\alpha = 0.05$. Comparisons of Tukey results between rows or between bivalve taxa and locations are invalid. Inferences from these ANOVA and Tukey comparisons should issue forth after recognition that some taxa are restricted to certain locations; thus, these two main effects are to some degree confounded.

	Bivalve				Location				
	ANOVA	Tukey Test			ANOVA	Tukey Test			
Variable	*P* value	Mytilid	Oyster	Dreissenid	*P* value	East coast	West coast	Gulf coast	Great Lakes
Total parasites									
Prevalence	0.0001	B	A	C	0.0001	B	B	A	C
Intensity	0.0001	B	A	C	0.0001	AB	B	A	C
Total, no gregarines									
Prevalence	0.0001	A	A	B	0.0001	A	B	A	C
Intensity	0.01	A	A	B	0.002	A	AB	A	B
Rare parasites									
Prevalence	0.01	A	A	B	0.02	AB	A	A	B
Intensity	NS				NS				
Total gregarines									
Prevalence	0.0001	B	A		0.0001	B	B	A	
Intensity	0.0001	B	A		0.0001	A	B	A	
Total protozoans									
Prevalence	NS				NS				
Intensity	NS				NS				
Total prokaryotes									
Prevalence	0.0001	B	A		0.0006	B	B	A	
Intensity	NS				NS				
Gregarines, body tissue									
Prevalence	0.0001	B	A		0.0001	B	B	A	
Intensity	0.03	B	A		0.04	A	B	AB	
Gregarines, gill tissue									
Prevalence	0.0001	B	A		0.0001	B	B	A	
Intensity	0.0001	B	A		0.0001	A	B	A	
Gregarines, mantle tissue									
Prevalence	0.0001	B	A		0.0001	B	B	A	
Intensity	NS				NS				
Perkinsus marinus									
Prevalence					0.03	B		A	
Intensity					0.02	B		A	
Ciliates, gill									
Prevalence	0.0001	A	B		0.007	A	AB	B	
Intensity	NS				NS				
Ciliates, digestive tract									
Prevalence	0.0001	B	A		0.0001	B	C	A	
Intensity	NS				NS				
Trematode sporocysts									
Prevalence	0.003	A	B		0.003	A	B	B	
Intensity	NS				0.0006	B	A	A	
Trematode metacercariae									
Prevalence					0.0001	A	B		
Intensity					0.002	A	B		
Cestodes									
Prevalence					NS				
Intensity					NS				
Nematodes									
Prevalence	0.004		A	B	0.0001	B		A	B
Intensity	NS				0.03	A		AB	B
Major pathologies									
Prevalence	0.0001	A	B	B	0.0001	AB	A	C	BC

continued on next page

TABLE 4.

continued

	Bivalve				Location				
	ANOVA	Tukey Test			ANOVA	Tukey Test			
Variable	*P* value	Mytilid	Oyster	Dreissenid	*P* value	East coast	West coast	Gulf coast	Great Lakes
Hemocytic infiltration									
Prevalence	0.004	A	A	B	0.0001	A	BC	AB	C
Intensity	0.009	A	AB	B	0.02	A	AB	AB	B
Ceroid bodies									
Intensity	0.0001	B	A	C	0.0001	A	B	A	B
Digestive gland atrophy									
Intensity	0.0001	A	A	B	0.0001	A	A	B	C

NS, nonsignificant at $\alpha = 0.05$. Blank indicates that no test was possible because the parasite was confined to one taxon or, for the Tukey test, the prior ANOVA was not significant.

$P = 0.0001$), as expected from these overall trends and significantly higher in bivalves from the East coast than in bivalves from the Gulf coast.

Tissue pathologies, mostly focal and diffuse hemocytic infiltration, but also including instances of tissue necrosis, were equally common in mytilids and oysters, but occurred significantly less commonly in dreissenids (Fig. 7, Table 4). Tissue pathologies were significantly more common in East-coast bivalves than West-coast bivalves. Gulf-coast bivalves fell in between. On the East coast, tissue pathologies were significantly more common in *M. edulis* than in oysters (ANOVA, $P = 0.0002$).

Infection Intensity

Gulf-coast bivalves had significantly higher total body burdens of quantifiable parasites than West-coast and Great Lakes bivalves (Fig. 1, Table 4). Bivalves on the East and West coasts had significantly higher body burdens than Great Lakes bivalves, but the former two were not significantly different (Table 4). On the East coast where both *M. edulis* and eastern oysters were collected, total parasite body burden was significantly higher in oysters (ANOVA, $P = 0.0001$).

As in prevalence, the gregarines strongly influenced these trends. Discounting the gregarines, not surprisingly, East- and Gulf-coast bivalves still had significantly higher total parasite body burdens than the dreissenids in the Great Lakes, but East- and Gulf-coast bivalves no longer differed significantly from each other (Table 4, Fig. 1). West-coast bivalves fell in between the East/Gulf and Great Lakes groups (Table 4). Infection intensity of *M. edulis* on the East coast was not significantly different from that in East-coast oysters (ANOVA, $P > 0.05$).

Neither the infection intensity of rare parasites nor total protozoans differed significantly among different host taxa or different locations (Figs. 1 and 3, Table 4). Rare parasites were significantly more common in East-coast *M. edulis* than in East-coast oysters (ANOVA, $P = 0.009$), however the infection intensity of total protozoans did not differ significantly (ANOVA, $P > 0.05$). Infection intensities of gill and digestive tract ciliates and prokaryotic inclusion bodies also were similar among all bivalve taxa and all locations (Figs. 2 and 5, Table 4). Infection intensity of *P. marinus* was significantly higher in Gulf-coast oysters than East-coast oysters (Fig. 2, Table 4), however.

West-coast mytilids had significantly lower gregarine body burdens than oysters collected on the East and Gulf coasts; the latter two were not significantly different (Fig. 3, Table 4). East-coast oysters had significantly higher infection intensities of gregarines in body tissue than West-coast mytilids; Gulf-coast oysters fell in between (Fig. 4, Table 4). The infection intensity of gill gregarines, though still significantly lower in West-coast mytilids, did not differ between East- and Gulf-coast oysters (Fig. 4, Table 4). Mantle gregarines did not differ significantly in infection intensity between host taxon or location (Fig. 4, Table 4).

The infection intensity of trematode sporocysts did not differ significantly among bivalve taxa (Fig. 6, Table 4); however, East-coast bivalves had significantly lower infection intensities than the similar levels found in West- and Gulf-coast bivalves (Table 4), even though prevalences were much higher. *Mytilus edulis* and oysters from the East coast did not differ significantly (ANOVA, $P > 0.05$). East-coast mytilids had significantly higher numbers of trematode metacercariae than West-coast mytilids (Fig. 6, Table 4). Nematode infection intensities were not significantly different among bivalve taxa nor were cestode infection intensities between East- and Gulf-coast oysters (Figs. 5 and 6, Table 4).

Hemocytic infiltration and other tissue pathologies were significantly more numerous in mytilids than dreissenids: oysters occupied an intermediate position (Fig. 7, Table 4). These pathologies were significantly more numerous in East-coast bivalves than Great Lakes bivalves (ANOVA, $P = 0.02$): West- and Gulf-coast bivalves occupied an intermediate position (Table 4).

Ceroid bodies were significantly more numerous in oysters than in mytilids or dreissenids, and more common in mytilids than in dreissenids (Fig. 7, Table 4). Consequently, Gulf- and East-coast bivalves were characterized by a significantly greater number of ceroid bodies per tissue cross-section (Table 4). Digestive gland atrophy was less severe in dreissenids than in mytilids or oysters: the latter two were not significantly different from each other (Fig. 7, Table 4). Digestive gland atrophy was more severe in East- and West-coast bivalves than in oysters from the Gulf coast, but digestive gland atrophy was of similar severity in East-coast mytilids and East-coast oysters ($P > 0.05$).

Comparisons Within Congeneric Taxa

Mytilids on the East and West Coast

The fraction of hosts with at least one quantifiable parasite was significantly higher in East-coast *M. edulis* than

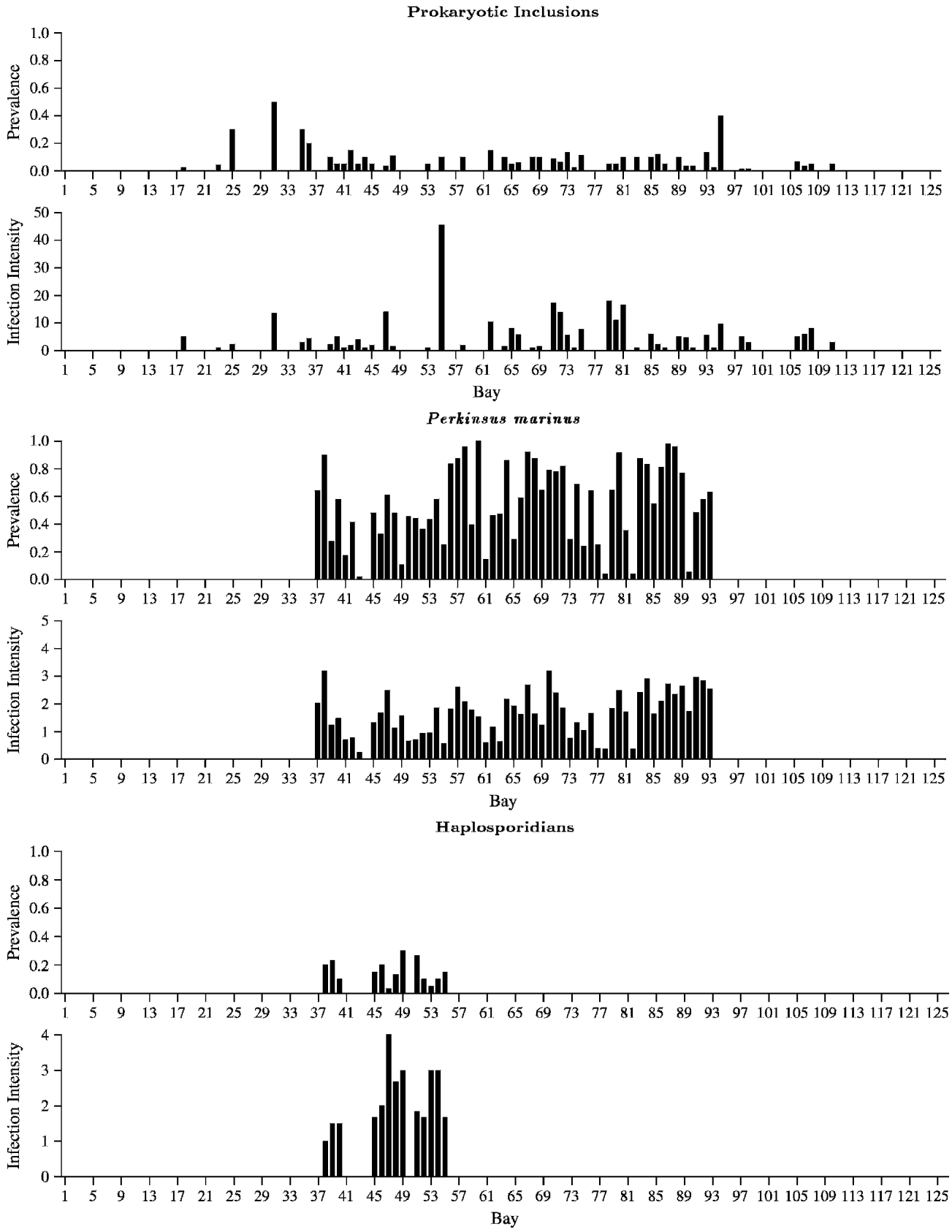

Figure 2. Prevalence and infection intensity of prokaryotic inclusions, *Perkinsus marinus*, and the haplosporidians. Great Lakes/Hudson River dreissenid sites, Bays 1–11; East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125.

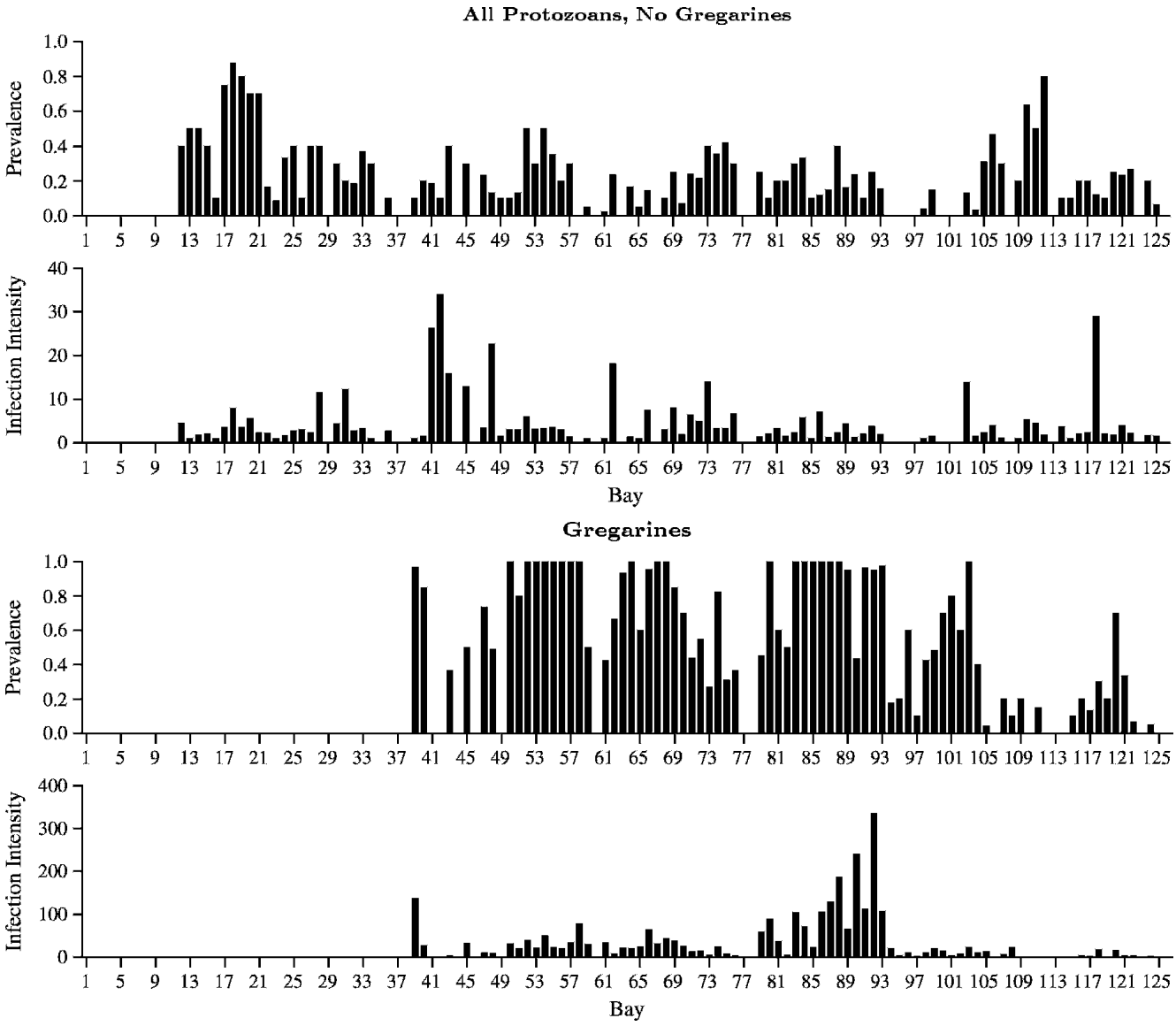

Figure 3. Prevalence and infection intensity of gregarines and all protozoans, exclusive of the gregarines. Great Lakes/Hudson River dreissenid sites, Bays 1–11; East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125.

in the West-coast mytilids (Table 5, Fig. 1). This trend was even more evident after discounting the gregarines (Fig. 1, Table 5). Infection intensity did not differ significantly, however, when the body burden of all quantifiable parasites was tallied (Fig. 1, Table 5), unless the gregarines were excluded: body burdens were higher for the remaining quantifiable parasites for *M. edulis* on the East coast.

The overall trend was established by coherent trends in the majority of parasitic taxa. Protozoans and the numerically important contributor, gill ciliates, were more frequently observed in East-coast *M. edulis* than West-coast mytilids, but infection intensity was not significantly different (Figs. 3 and 5, Table 5). In contrast, neither prevalence nor infection intensity of digestive tract ciliates differed between East-coast *M. edulis* and West-coast mytilids (Fig. 5).

Like most protozoans, trematode metacercariae were more commonly observed in East-coast *M. edulis* than in West-coast mytilids (Fig. 6). In this case, infection intensity was also significantly higher (Table 5). Like the protozoans and trematode metacercariae, East-coast *M. edulis* had higher prevalences of trematode sporocysts than West-coast mytilids (Fig. 6). Unlike the protozoans, infection intensity was also significantly higher (Table 5).

Neither the frequency nor the intensity of infection of rare parasites differed significantly between *M. edulis* from the East coast and mytilids from the West coast (Fig. 1). The same was true for prokaryotic inclusions (Fig. 2). In a trend opposite to most parasitic taxa, gregarines were not found in East-coast *M. edulis*, but were commonly observed in West-coast mytilids (Fig. 3).

Trends in the occurrence of pathologies followed trends in the occurrence of most parasitic taxa. Both major and tissue pathologies were significantly more common in East-coast *M. edulis* than West-coast mytilids (Fig. 7, Table 5). The frequency of occurrence of hemocytic infiltration and other tissue pathologies was also higher in East-coast *M. edulis*. No differences in the severity of digestive gland atrophy were

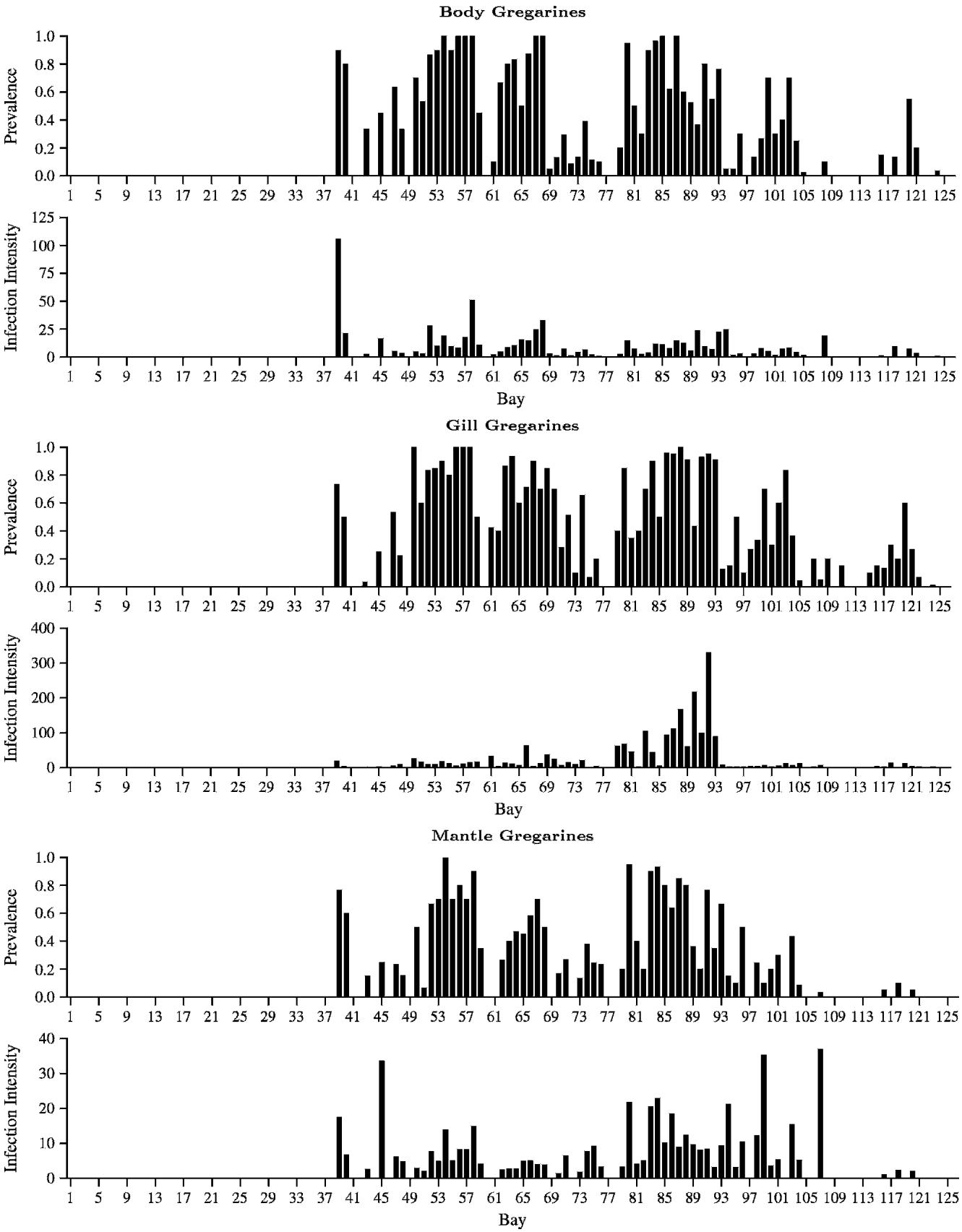

Figure 4. Prevalence and infection intensity of gregarines in the body, gill, and mantle tissues of bivalves. Great Lakes/Hudson River dreissenid sites, Bays 1–11; East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125.

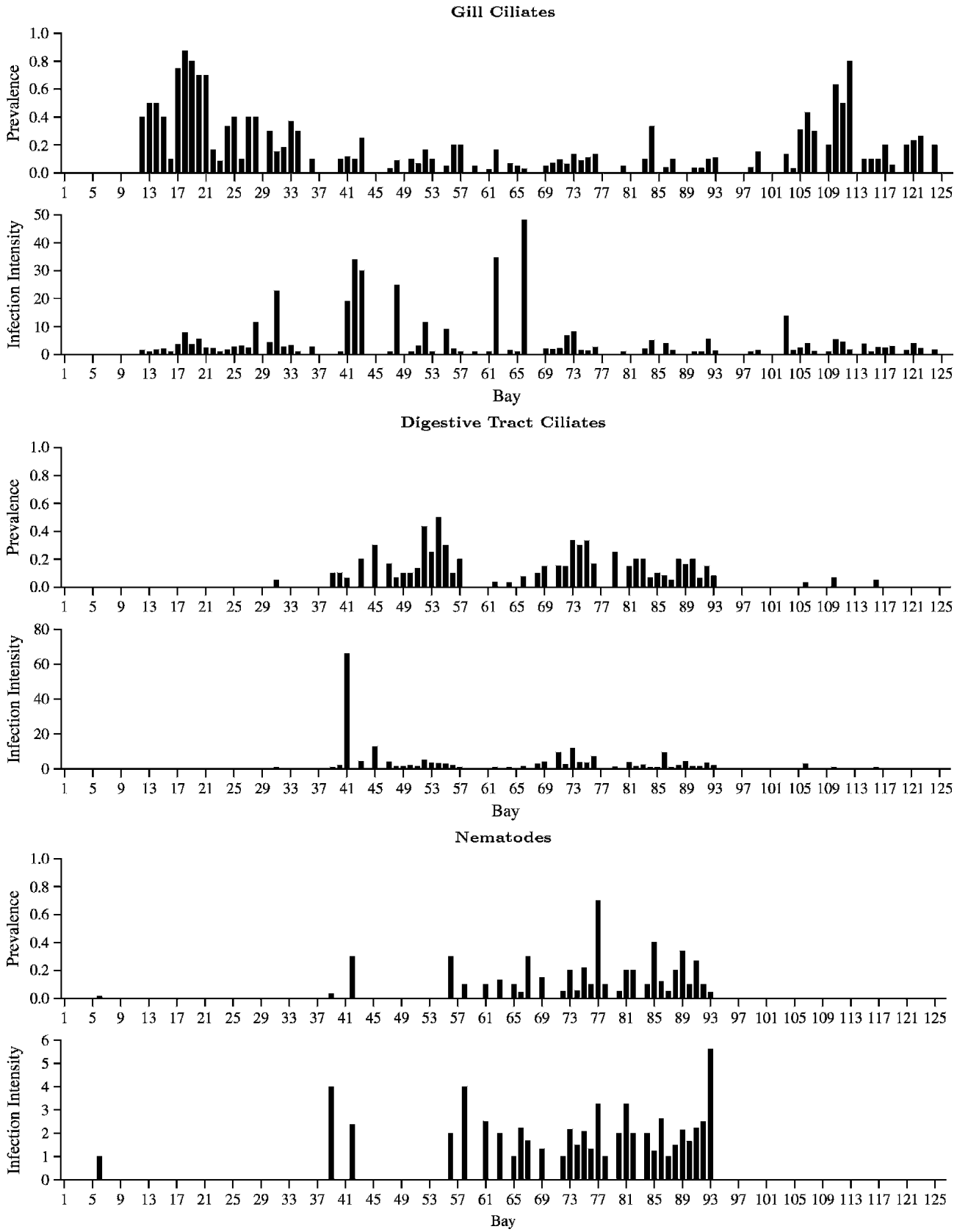

Figure 5. Prevalence and infection intensity of ciliates in the gill tissue and digestive tract, and prevalence and infection intensity of nematodes in bivalves. Great Lakes/Hudson River dreissenid sites, Bays 1–11; East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125.

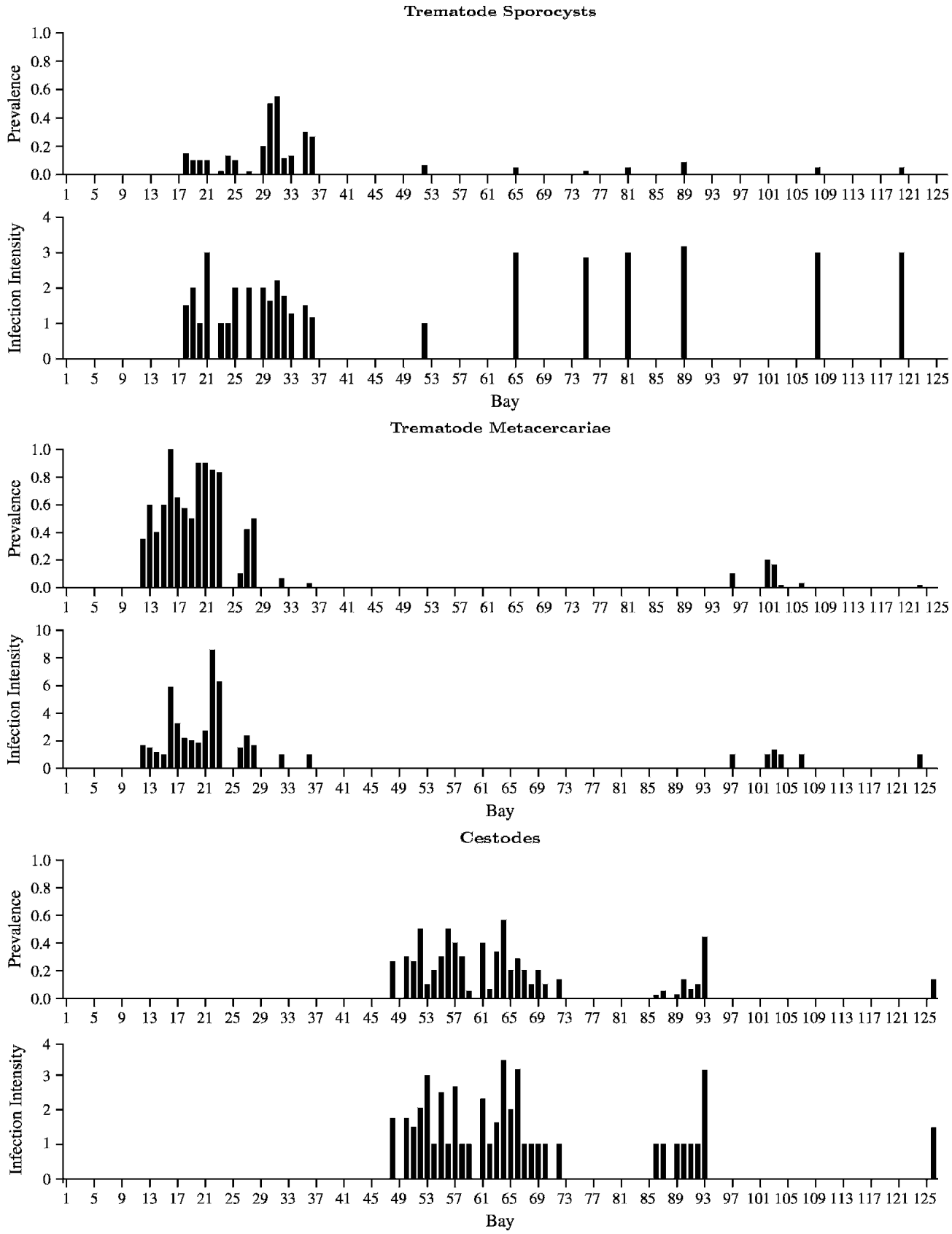

Figure 6. Prevalence and infection intensity of ramifying trematode sporocysts, encapsulated trematode metacercariae, and cestodes in the tissues of bivalves. Great Lakes/Hudson River dreissenid sites, Bays 1–11; East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125.

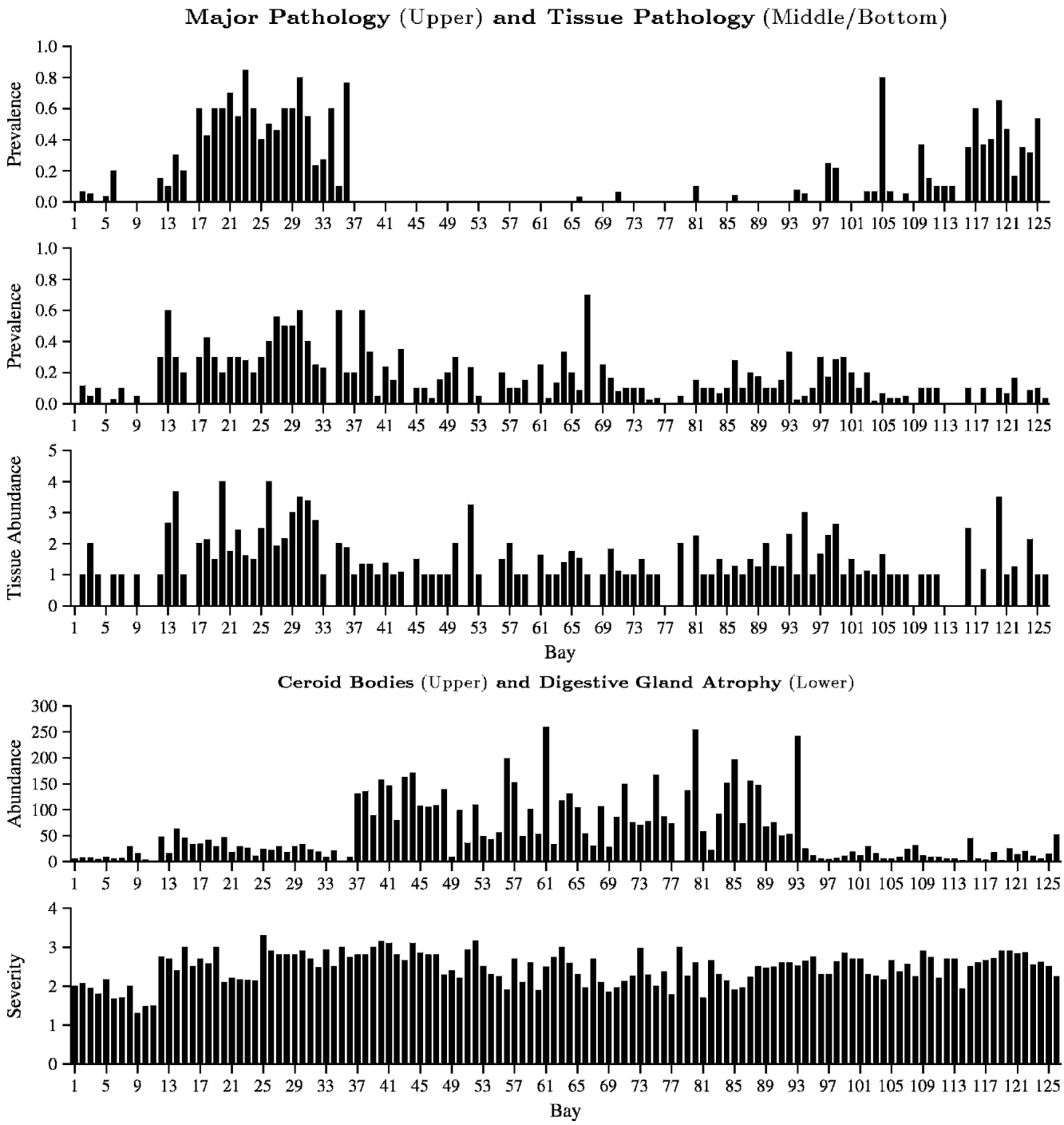

Figure 7. Prevalence of neoplasms, unusual digestive tubules, and gonadal abnormalities, cumulated under the category "major pathology," prevalence and tissue abundance of focal and diffuse hemocytic infiltration and tissue necrosis, cumulated under the category "tissue pathology," the abundance of ceroid bodies, and the severity of digestive gland atrophy in sentinel bivalves. Great Lakes/Hudson River dreissenid sites, Bays 1–11; East-coast mytilid sites, Bays 12–36; East-coast oyster sites, Bays 37–61; Gulf-coast oyster sites, Bays 63–93; West-coast mytilid sites, Bays 94–125.

observed (Fig. 7), but ceroid bodies were significantly more numerous in East-coast *M. edulis* (Fig. 7, Table 5).

Oysters on the East and Gulf Coast

Significantly more Gulf-coast oysters harbored parasites than East-coast oysters (Fig. 1, Table 5). This trend was due solely to the prevalence of gregarines in Gulf-coast oysters, however (Fig. 1, Table 5). Infection intensity did not differ significantly regardless of the inclusion or exclusion of the gregarines (Table 5). The similarity in prevalence and infection intensity between East-coast and Gulf-coast oyster parasites as a whole was followed by most parasitic taxa. The prevalence of

TABLE 5.

Results of ANOVA tests comparing parasite or pathology prevalence and infection intensity between congeneric bivalve taxa.

Variable	Mytilids East *versus* West	Oysters East *versus* Gulf	*M. edulis* complex *versus M. californianus*
Total parasites			
Prevalence	0.01	0.03	NS
Intensity	NS	NS	NS
Total, no gregarines			
Prevalence	0.0001	NS	0.0004
Intensity	0.01	NS	0.008
Rare parasites			
Prevalence	NS	0.03	0.0003
Intensity	NS	0.002	NS
Total gregarines			
Prevalence		NS	0.002
Intensity		NS	NS
Total protozoans			
Prevalence	0.001	NS	0.001
Intensity	NS	NS	0.03
Total prokaryotes			
Prevalence	NS	NS	NS
Intensity	NS	NS	NS
Gregarines, body tissue			
Prevalence		NS	0.03
Intensity		NS	NS
Gregarines, gill tissue			
Prevalence		NS	0.003
Intensity		0.05	NS
Gregarines, mantle tissue			
Prevalence		NS	0.003
Intensity		NS	0.005
P. marinus			
Prevalence		0.03	
Intensity		0.02	
Ciliates, gill			
Prevalence	0.0008	NS	0.005
Intensity	NS	NS	NS
Ciliates, digestive tract			
Prevalence	NS	NS	NS
Intensity	NS	NS	0.0001
Trematode sporocysts			
Prevalence	0.0001	NS	NS
Intensity	0.01	0.009	NS
Trematode metacercariae			
Prevalence	0.0001		0.05
Intensity	0.002		NS
Cestodes			
Prevalence		NS	
Intensity		NS	
Nematodes			
Prevalence		0.0001	
Intensity		0.03	
Major pathologies			
Prevalence	0.0003	NS	0.0001
Hemocytic infiltration			
Prevalence	0.0001	NS	NS
Intensity	0.0005	NS	NS
Ceroid bodies			
Intensity	0.0001	NS	NS
Digestive gland atrophy			
Intensity	NS	0.001	0.004

NS, nonsignificant at $\alpha = 0.05$. Blank indicates that no test was possible because the parasite was absent from one of the groups.

gregarines was not significantly different between Gulf- and East-coast oysters (Table 5), nor were differences observed at the tissue level (Table 5), with one exception. The infection intensity of gregarines found in the gill tissue was significantly higher in Gulf-coast oysters (Fig. 4, Table 5). The prevalence and infection intensity of total protozoans did not diverge significantly, nor did they for prokaryotic inclusions, gill ciliates, digestive tract ciliates, or cestodes (Table 5).

Like gill gregarines, some parasitic taxa were more common in Gulf oysters. Gulf oysters were more frequently infected and infected at a significantly higher level with rare parasites (Fig. 1, Table 5). *Perkinsus marinus* reached higher prevalences and infection intensities in Gulf-coast oysters (Table 5, Fig. 2). Trematode sporocysts were not significantly more prevalent in Gulf-coast oysters, but infection intensities were significantly higher (Fig. 6, Table 5). In the only case where East-coast oysters were more heavily parasitized, although the prevalence of nematodes was significantly higher on the Gulf coast, infection intensity was significantly higher in East-coast oysters (Fig. 5, Table 5).

The rate of occurrence of pathologies did not diverge between oyster populations on the two coasts, nor did the abundance of ceroid bodies. Digestive gland atrophy, however, was significantly more severe in East-coast oysters (Table 5, Fig. 7).

Mytilid Taxa on the West Coast

The two mytilid taxa on the West coast, the *M. edulis* complex and *M. californianus*, were parasitized to a similar degree and the total body burden of quantifiable parasites was not significantly different (Table 5). Discounting the gregarines, however, prevalence and infection intensity were significantly higher in the *M. edulis* complex than in *M. californianus* (Table 5). Rare parasites infected the *M. edulis* complex significantly more frequently, as did the protozoans and the important subcategory of gill ciliates, but for none of these taxa was infection intensity significantly higher (Table 5).

In contrast, some parasitic taxa occurred more commonly in *M. californianus*. Gregarines were more commonly observed in *M. californianus* in all tissue categories, but infection intensity was not significantly higher except in mantle tissue in which gregarines were much more abundant in *M. californianus* (Table 5). Digestive tract ciliates, though also no more prevalent in either mussel taxon, reached higher infection intensities in *M. californianus* (Table 5). The prevalence of trematode metacercariae was significantly higher in *M. californianus*, but infection intensity did not diverge significantly.

In comparison, prokaryotic inclusions and trematode sporocysts were no more frequent in the *M. edulis* complex than in *M. californianus*, nor were infection intensities higher.

In contrast to the tendency for many parasites to occur more commonly in *M. californianus*, the prevalence of major pathologies was significantly higher in the *M. edulis* complex. Neither tissue pathologies nor ceroid bodies were significantly more numerous in either taxon, but the severity of digestive gland atrophy was higher in the *M. edulis* complex.

Geographic Distribution

Approach

Geographic distributions were investigated by comparing the frequency at which prevalence or infection intensity exceeded the global median for a 300-km section of coastline

to the exceedance frequency for all bays on that coastline. This comparison was made by sequentially placing each bay along the coast at the center of a 300-km stretch. We identified three conditions: coastline stretches where (a) the prevalence or infection intensity fell above the global median more frequently than expected by chance, indicating a regional high in prevalence or infection intensity, (b) the prevalence or infection intensity fell below the global median more frequently than expected by chance, indicating a regional low in prevalence or infection intensity, and (c) the prevalence or infection intensity fell near the global median, indicating an average prevalence or infection intensity. We also identified three patterns of geographic change by examining the along-coast trend in the relationship of local frequency to global frequency. (a) In some cases, constancy over a span of bays was identified by a relatively homogeneous level of parasitism, whether above, below or near the global median, along a stretch of coastline. (b) Boundaries were identified as regions of substantial and rapid change; for example, from a prevalence or infection intensity above the global median to below the global median over a short geographic distance. (c) Clines (e.g., Hummel et al. 1995) were recognized by slow steady increases or decreases in prevalence or infection intensity relative to the global median, following a temperature gradient over a long geographic distance, for example.

Northeast Coast

Beginning in central Maine (Bay 12), prevalence and infection intensity of prokaryotic inclusions showed a clinal trend with prevalence and infection intensity below the global median in the north and above the global median in Delaware Bay (Bay 36). Local prevalences and infection intensities did not differ significantly from the median for this stretch of coastline, except at the extremes of the latitudinal range (Figs. 2, 8, and 9), however. The same clinal trend existed for prevalence and infection intensity of trematode sporocysts and this relationship was significant for a number of 300-km sections (Figs. 6 and 10). The geographic trends in the prevalence of gill ciliates and trematode metacercariae were diametric opposites to that of trematode sporocysts and prokaryotic inclusions. Prevalence declined from highs in Maine through Duxbury Bay, MA (Bay 20), to lows south of Moriches Bay, NY (Bay 30) (Figs. 5, 6, 11, and 13). Of the four, trematode sporocysts and gill ciliates were characterized by more rapidly changing distributional patterns in the vicinity of Bays 24 (Block Island Sound) and 27 (western Long Island Sound) than elsewhere. Unlike most parasites, infection intensity of gill ciliates did not show a geographic trend (Figs. 5 and 12).

An interesting deviation from these clinal trends occurred in the region of Gardiners Bay (Bay 29) and Moriches Bay (Bay 30), sometimes including Port Jefferson (Bay 28). Here, in four cases, namely prokaryotic inclusions, trematode sporocysts, gill ciliates, and trematode metacercariae, local highs (gill ciliates and trematode metacercariae) or local lows (prokaryotic inclusions and trematode sporocysts) occurred within the overall clinal trend. Obtaining this coincidence of trends by chance is unlikely (binomial test, $P < 0.025$).

Southeast and Gulf Coasts

The distribution of a few parasitic taxa along the stretch of coastline from Delaware Bay to the southern tip of Florida and throughout the Gulf coast was as simple as the distribution of most parasites in *M. edulis* in the northeast, but most distributional patterns were markedly more complex. The simplest distributional patterns belonged to the nematodes and haplosporidians. The prevalence and infection intensity of nematodes followed a remarkably consistent clinal trend in which both remained below the median for oysters, and occasionally significantly so, but slowly rising, from the northern most sites in Delaware Bay downcoast to the southern tip of Florida and northward along the western coast of Florida to approximately Tampa Bay (Bay 66) (Figs. 5 and 10). Prevalence and infection intensity continued to rise westward across the Gulf significantly exceeding the global median westward of Mississippi Sound (Bay 74) and reaching highest levels south of Galveston Bay (Bay 86). Equally simple was the distribution of the haplosporidians. Prevalence and infection intensity were significantly above the median from New York to Georgia (Figs. 2 and 14).

For the remaining parasitic taxa, geographic trends were complex and consistent trends between taxa were uncommon. Most similar were the trends of the gregarines and cestodes and, to a lesser extent, *P. marinus*. Though differing in specifics, the general pattern for gregarines and cestodes was to attain regional highs from roughly the Cape Hatteras region of North Carolina to approximately the Tampa Bay (Bay 66) region of Florida, regional lows from the western Florida panhandle to western Louisiana, and regional highs south along the Texas coast.

Prevalence and infection intensity of gregarines in body tissue remained below the median, occasionally significantly so, for oysters from Delaware Bay south to Cape Lookout-Cape Fear, NC (Bays 50–51) (Figs. 4 and 15). Prevalence and infection intensity rose rapidly south of Cape Fear, remaining significantly above the median from Winyah Bay (Bay 52) to the Indian River (Bay 58); that is, for much of coastal South Carolina and Georgia into northern Florida. This zone, consistently significant for prevalence, was only spottily significant for infection intensity, although infection intensities averaged above the global median through much of this stretch, and, indeed through most of southern Florida, north to Apalachee Bay (Bay 68). Prevalence and infection intensity were significantly below the global median from about St. Andrews Bay (Bay 70) on the west coast of Florida through Atchafalaya Bay, LA (Bay 81) and rose dramatically to levels significantly above the median for extreme western Louisiana and the entirety of the Texas coast.

Gill gregarines followed much the same geographic pattern, but with a few important nuances. Prevalence and infection intensity of gill gregarines were significantly below the median for oysters from Long Island Sound, CT (Bay 37), to Beaufort Inlet, NC (Bay 50) (Figs. 4 and 16). Prevalence and infection intensity were equivalently high through much of the southeast coast and the western coast of Florida, and equivalently low in southern Florida into Louisiana, rising again in Texas.

Prevalence and infection intensity of mantle gregarines were likewise similar (Figs. 4 and 17). Note, however, that the zone of infection intensities significantly above the global median was much restricted in the southeast and did not extend into western Florida, as it had for gregarines in the gill tissue, and the northern Florida to Louisiana stretch was not characterized by

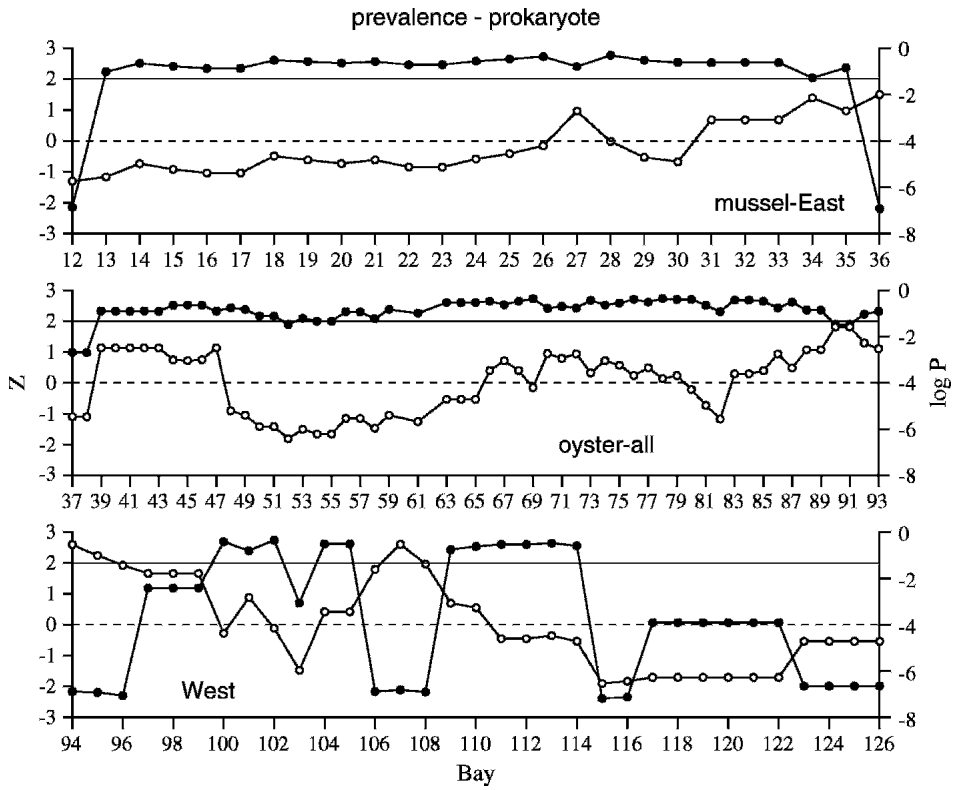

Figure 8. Geographic trends in the prevalence of prokaryotic inclusions. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences for each bay are shown in Figure 2. Bay numbers are interpreted in Table 1.

infection intensities significantly below the global median, as it had been for gill gregarines. Furthermore, infection intensity and prevalence were only rarely significantly below the global median north of Cape Hatteras (Bay 48), whereas gill gregarines were consistently so. Nevertheless, the general pattern followed that of the remaining gregarines.

Prevalence and infection intensity of cestodes likewise followed this same general pattern (Figs. 6 and 18). Cestodes were never observed in oysters north of Cape Hatteras, NC (Bay 48). Prevalence and infection intensity remained significantly above the global median over the southeast and western Florida coasts, and declined westward of Cedar Key, FL (Bay 67), from values significantly above the median to values significantly below the median westward of Pensacola Bay (Bay 72). Prevalence and infection intensity remained significantly below the median from this point into northern Texas (Sabine Lake—Bay 85) and rose gradually from values significantly below the median to values near the median from there to the southern Texas coast.

Prevalence and infection intensity of the oyster pathogen *Perkinsus marinus* remained significantly below the median for oysters from Long Island Sound, CT (Bay 37) to Charleston Harbor (Bay 53), in part due to the winter time of collection; prevalences and infection intensities reach yearly lows during the winter and particularly so in more northern climes (Soniat & Gauthier 1989, Ragone Calvo & Burreson 1994, Ford 1996) (Figs. 2 and 14). Southward, *P. marinus* prevalence and infection intensity rose to values near the global median and then remained above the global median for much of the southeast and western Florida coasts, and significantly so in the Charlotte Harbor, FL (Bay 65) to Choctawhatchee Bay, FL (Bay 71) stretch. Once again, regional lows, though never significantly below the global median, occurred throughout much of the northern Gulf and regional highs in infection intensity, often significantly above the global median, occurred for much of the coast south of Lake Calcasieu (Bay 84). Interestingly, prevalence tended to decline, whereas infection intensity remained high, along the Texas coast (Figs. 2 and 14).

Prokaryotic inclusions follow a divergent geographic pattern for the southeast and Gulf coastlines. Prevalence and infection intensity of prokaryotic inclusions remained above the global median through Bay 47 near Cape Hatteras (Bay 48), quite the opposite of *P. marinus*, the gregarines, and the cestodes. Prevalence and infection intensity dropped, falling for a time below the median for oysters, over much of the southeast and western Florida coasts, then rose above the global median again at Tampa Bay (Bay 66) (Figs. 2, 8 and 9). Prevalence and infection intensity remained above the global median for most bays throughout the remainder of the Gulf of Mexico, rising significantly above the global median for a portion of the Texas coast. Unlike the distribution in mytilids on the East coast, the distribution of prokaryotic inclusions in oysters is not obviously consistent with trends in latitude of collection.

The geographic distribution of ciliates was also divergent from most other parasitic taxa, although the two groups, gill and digestive tract ciliates, followed a relatively similar pattern.

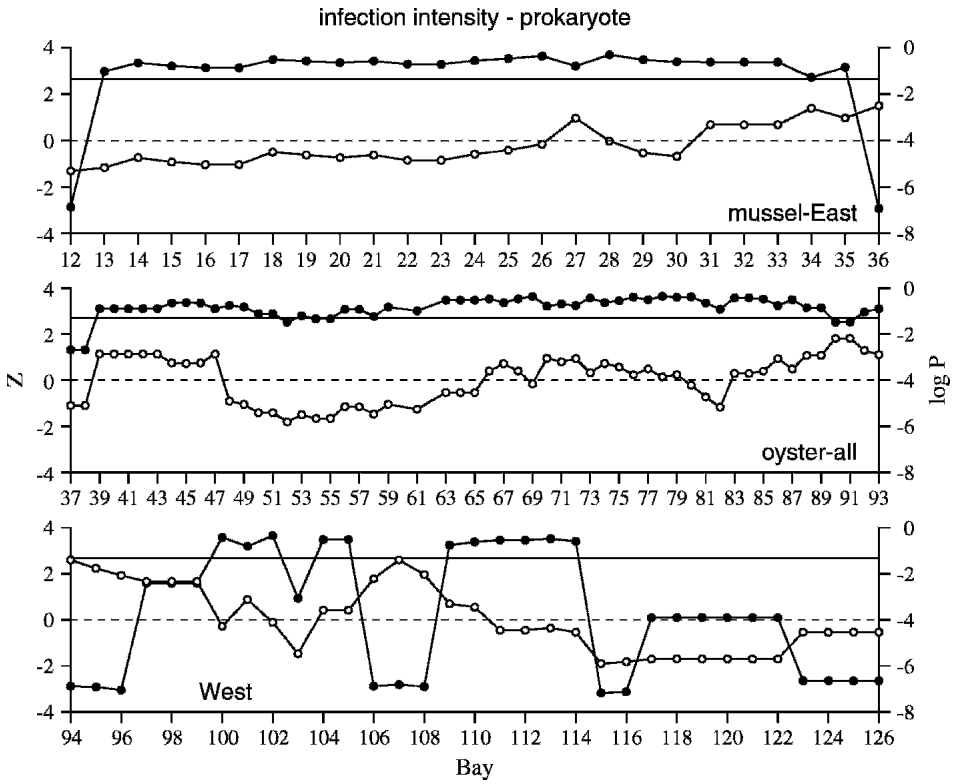

Figure 9. Geographic trends in the infection intensity of prokaryotic inclusions. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Infection intensities for each bay are shown in Figure 2. Bay numbers are interpreted in Table 1.

Prevalence and infection intensity of gill ciliates diverged little from the global median except near Pensacola Bay (Bay 72) in the northeastern Gulf (Figs. 5, 11 and 12). A second regional high, though not significant, occurred along the southeast coast between Cape Fear (Bay 51) and the Matanzas River (Bay 57). The prevalence and infection intensity of digestive tract ciliates remained near the median through Bay 49, south Pamlico Sound near Cape Hatteras, then rose to a regional high in the Cape Fear (Bay 51) to Savannah River (Bay 54) region of the coast, and remained significantly above the global median from there through St. Johns River, FL (Bay 56) (Figs. 5 and 18). Gill ciliates were above the global median throughout much of the same stretch, but in that case, not significantly so. Prevalence and infection intensity of digestive tract ciliates fell significantly below the global median from Biscayne Bay (Bay 59) to Tampa Bay (Bay 66), then exceeded the global median throughout the remainder of the Gulf, and significantly so particularly in the region from Mobile Bay (Bay 73) to Barataria Bay (Bay 79), near but somewhat west of the regional high for gill ciliates.

West Coast

For the gregarines and to a substantial degree the prokaryotic inclusions, prevalences and infection intensities fell from south to north. For prevalence and infection intensity of gregarines in the body, gill, and mantle tissue, values were significantly above the global median from southernmost California north to San Luis Obispo Bay, CA (Bay 103), with extreme values from Santa Cruz Island (Bay 100) to Point Conception (Bay 102) (Figs. 3, 4, and 15–17). Prevalence and infection intensity declined north of this region, reaching significantly low levels from Point Arena/Delgada (Bay 107) north to Willapa Bay (Bay 114) and into Alaska.

For prokaryotic inclusions, prevalence and infection intensity remained significantly above the global median for mytilids from southern California to Cape Blanco, OR (Bay 110) (Figs. 2, 8 and 9), with the exception of a few Californian sites in the vicinity of San Luis Obispo Bay (Bay 103). Prevalence and infection intensity remained low north of this region.

Gill ciliates in large measure followed an opposing trend to the prokaryotic inclusions and the gregarines (Figs. 5, 11, and 12). Prevalence and infection intensity remained significantly below the median for mytilids over southern California, and rose to a regional high from Point Conception, CA (Bay 102), through Tillamook Bay, OR (Bay 112). In this stretch, prevalence and infection intensity often significantly exceeded the global median. North of Tillamook Bay, prevalence and infection intensity declined, but remained near the global median into Alaska. The opposing trend between gill ciliates and prokaryotic inclusions is remarkably similar to that observed along the northeast coast.

Trematode metacercariae were unique on the West coast in not having regional highs at either of the extremes of the latitudinal gradient. Trematode metacercariae were predominately observed in the Point Conception (Bay 102) to Point Arena/Delgada (Bay 107) area on the West coast (Figs. 6 and 13).

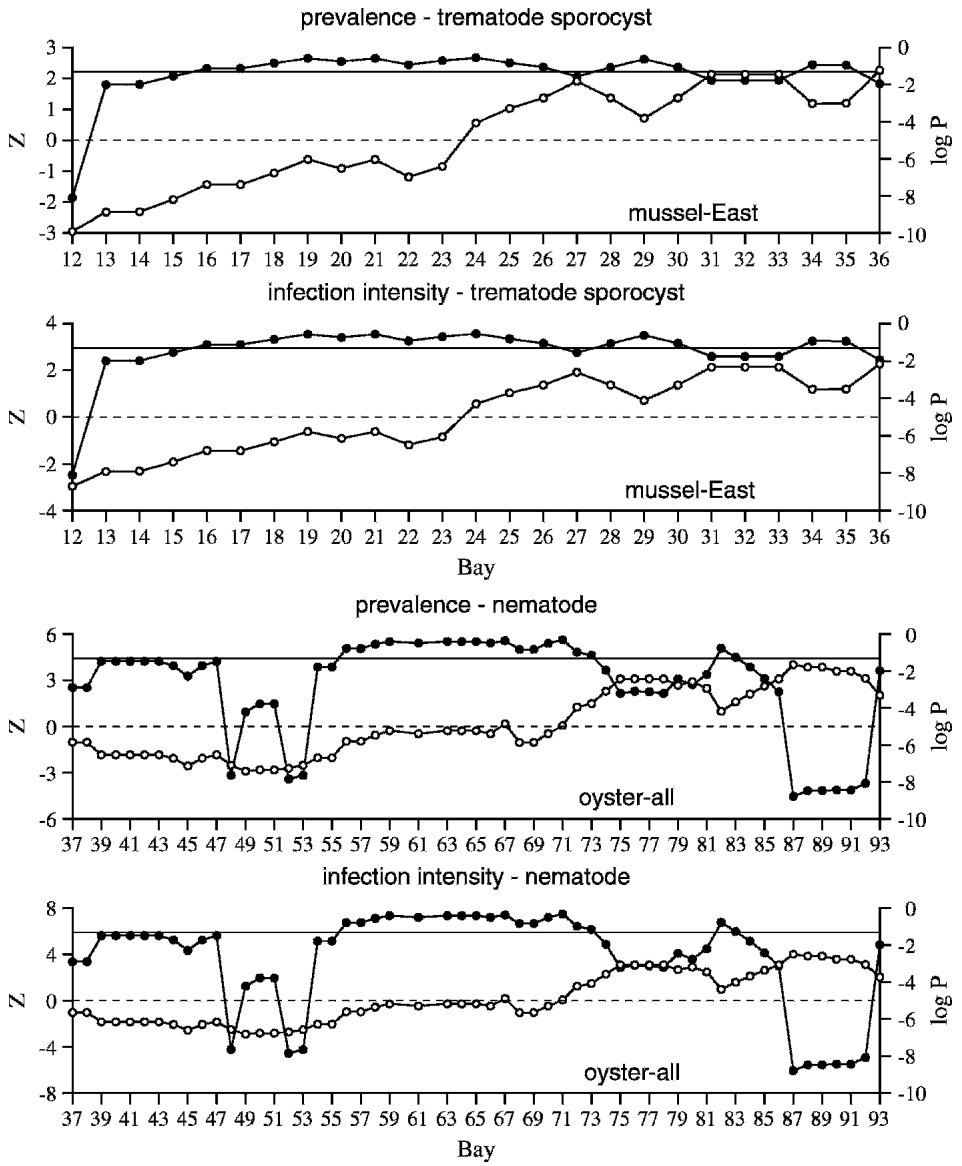

Figure 10. Geographic trends in the prevalence and infection intensity of trematode sporocysts and nematodes. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences and infection intensities for each bay are shown in Figures 5 and 6. Bay numbers are interpreted in Table 1.

DISCUSSION

Taxon Richness of Parasites

Parasite taxon richness was higher in oysters than mytilids and dreissenids. Mytilids harbored significantly more parasitic taxa than dreissenids. Between the two bivalve taxa collected from the East coast, oysters harbored more parasitic taxa than *M. edulis*. Taxon richness was similar between the two West-coast mytilid species, *M. californianus* and the remaining mytilids of the *M. edulis* complex. Taxon richness was highest on the Gulf coast.

Trends in species richness can often originate from sampling artifacts (Green & Young 1993, Griffiths 1999, Kidwell 2002). About as many bays were sampled along the Gulf coast as other coastline sections discriminated in this analysis and the number of bays in which mytilids and oysters were collected is similar (East-mytilid, 25; East-oyster, 25; Gulf, 31; West, 32). Thus, trends are unlikely to be due to differences in sample size. In addition, we tallied taxa observed within each bay system, rather than tallying cumulatively over all bays along a coastline, and, although the total number of animals examined varied between bay systems, no coastal-scale bias in sampling intensity existed at this level. Thus, trends in taxon richness can be interpreted at the biological and geographic level.

Rohde (1992) discussed latitudinal gradients in parasite species diversity and suggested that greater species richness occurs in the tropics probably due to a greater number of free-living species in the tropics providing more opportunities for parasites. In this study, parasite taxon richness was higher along

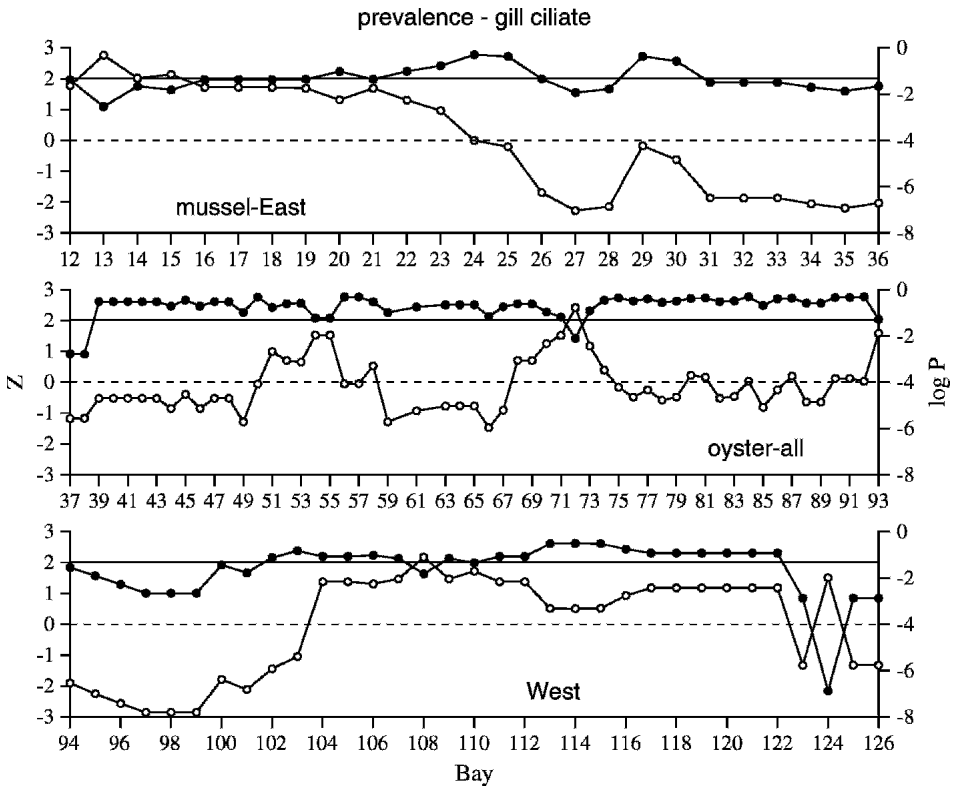

Figure 11. Geographic trends in the prevalence of ciliates in the gill. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences for each bay are shown in Figure 5. Bay numbers are interpreted in Table 1.

the Gulf coast than elsewhere. Some portion of this accrues from a seemingly innately higher parasite burden in oysters in comparison with mussels. However, Gulf-coast oysters also had more diverse groups of parasites than East-coast oysters, and this probably arises because Gulf oysters were sampled from locations at lower latitudes than more than half of the East-coast oyster locations.

The singularly low taxon richness in dreissenids may arise from an inherently low richness of parasitic fauna; however, a more likely origin is the newness of the introduction of these species into U.S. waters (Hebert et al. 1989, May & Marsden 1992). Zebra mussels were first discovered in the Great Lakes in 1988 (Hebert et al. 1989). Quagga mussels were found in 1991 (May & Marsden 1992). Both species spread rapidly throughout the Great Lakes system and then into the major river basins of the central and eastern U.S. (Griffiths et al. 1991, Strayer 1991, Mills et al. 1996). Introduced species often have a more restricted parasitic fauna (Torchin et al. 2002, Marshall et al. 2003). Certainly a wider range of parasites seems to occur in dreissenids in their home range (de Kinkelin et al. 1968, Wallet & Lambert 1986, Bowmer et al. 1991, Molloy et al. 1996, 1997, Laruelle et al. 1999, Karatayev et al. 2000, 2002, 2003).

Trends in Significance of Comparisons

Prevalence and infection intensity are inherently different. Prevalence describes the proportion of individuals in the population infected by a specific parasite and depends on transmission dynamics that integrate a variety of biological and physical processes. Infection intensity is a measure of the intensity of infection solely in infected individuals. For some parasitic taxa, infection intensity is predominately controlled by the chance of multiple infection, a function of transmission dynamics. But, for many parasites, such as the protozoan taxa and the prokaryotes, as well as the ramifying taxa such as trematode sporocysts, infection intensity is dependent on the interaction of the environment and the internal milieu of the host that controls proliferation. Despite the inherent and substantive differences in the two data types, parasites having higher prevalences in a given host taxon routinely also had higher infection intensities when comparisons were made between different host bivalve taxa. When different geographic locations were compared, the same trends occurred much more rarely: only for total protozoans, *P. marinus*, and cestodes, two of which were restricted to oyster hosts.

One interesting result of the analysis of prevalence and infection intensity between bivalve hosts and geographic locations was the occurrence rate of significant results. In every case where a nonsignificant comparison occurred in one, prevalence or infection intensity, but not the other, the nonsignificant result involved a comparison of infection intensity. In fact, comparisons of prevalence yielded 14 significant results out of 15 trials for bivalve host and 16 out of 18 trials for geographic location, whereas the equivalent occurrence rate for comparisons of infection intensity yielded 8 of 16 comparisons as significant for bivalve host and 12 of 19 for geographic location. Whereas

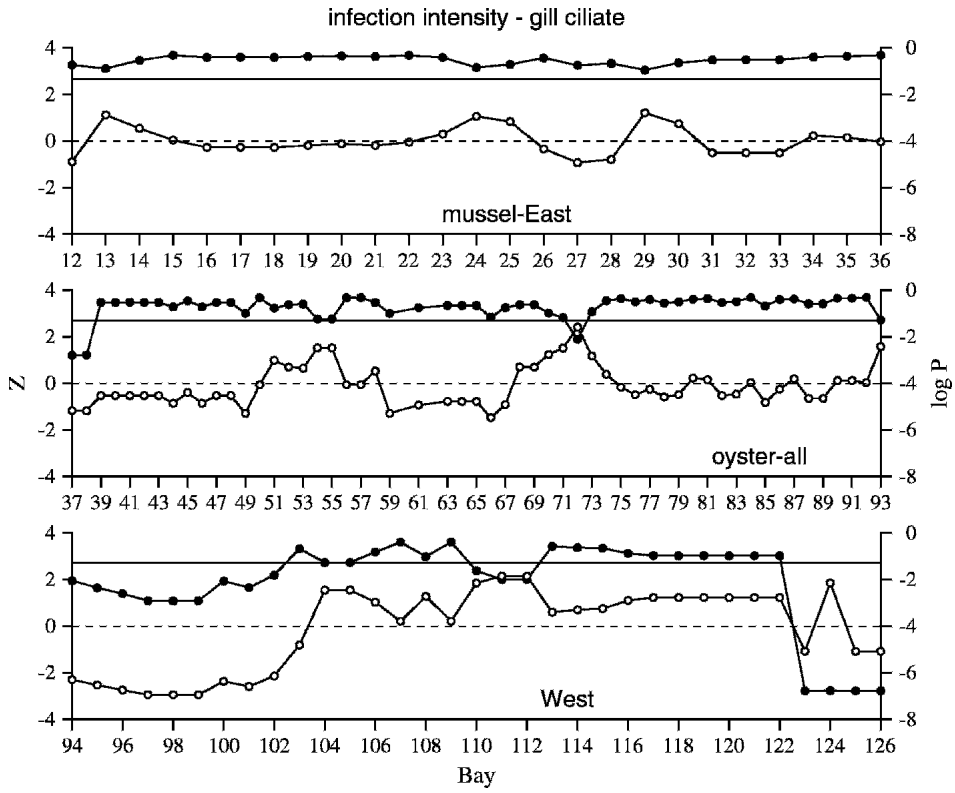

Figure 12. Geographic trends in the infection intensity of ciliates in the gill. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Infection intensities for each bay are shown in Figure 5. Bay numbers are interpreted in Table 1.

all four of these occurrence rates far exceed that of chance (binomial test, $p = 0.05$, $q = 0.95$, $P < 0.0001$), the occurrence rate for prevalence would likewise not be anticipated from that for infection intensity (taxon comparison, binomial test, $p = q = 0.50$, $P < 0.0005$; location comparison, binomial test, $p = 0.63$, $q = 0.37$, $P < 0.02$). Accordingly, significant comparisons of prevalence occurred significantly more often than did significant comparisons of infection intensity.

Several facts offer explanations for these trends. Firstly, the dataset for infection intensity is inherently more meager than that for prevalence because only infected animals were included. Bays with a prevalence of zero were excluded from the comparison because infection intensity is not defined for an uninfected population. Secondly, distribution of infection intensity data is often negative binomial (e.g., Munger et al. 1989, Jones et al. 1991), and this wider and biased variance influences statistical analysis (Terceiro 2003, O'Neill & Faddy 2003). This effect was mostly ameliorated by our use of ranked data in analysis, however. Thirdly, the timing of infection and the internal milieu control, to a large extent, the rate of proliferation, and these processes may vary widely over local and regional scales (e.g., Ford et al. 1999a, 1999b). These additional interactions, beyond those controlling the rate of transmission, introduce additional variability into bay-average infection intensity. Finally, for some parasites, infection intensity mediates mortality and this process removes at differential rates a fraction of the parasitized host population (e.g., Anderson & Gordon 1982, Hethcote & van den Driessche 1995, Powell et al. 1996).

Differences Among Bivalve Taxa

Interestingly, substantial differences exist in the prevalence of parasitism among these sentinel bivalves. Oysters were more heavily infected based on total parasite body burden than mytilids. The frequency of hosts with at least one parasite was higher and the overall parasite body burden was higher. The source of much of this differential, however, was the numerically-dominant gregarines. Excluding this parasite group removed the differential between oysters and mytilids, with one important exception. East-coast mytilids were more frequently parasitized than East-coast oysters, once the gregarines were excluded.

The differential between dreissenids, on the other hand, and the other two bivalve taxa was not similarly ameliorated. Dreissenids had lower prevalence and infection intensity for all parasites than the other host bivalve taxa, and, indeed, for most of the co-occurring individual parasitic taxa. This differential was not necessarily an outgrowth of the lower taxon richness in dreissinids; rather, protozoans, including the gregarines and ciliates, and prokaryotic inclusions were absent from these taxa and thus total parasite body burden was ordained to be low in comparison with the oysters and mytilids. Lack of unicellular parasites is likely a corollary of the invasive stature of the dreissenids because ciliates, at least, are well known parasites in these species' native waters (Laruelle et al. 1999, Karatayev et al. 2002, 2003). However, individual parasitic taxa that did infect the dreissenids were also low in prevalence and in infection intensity. These include nematodes

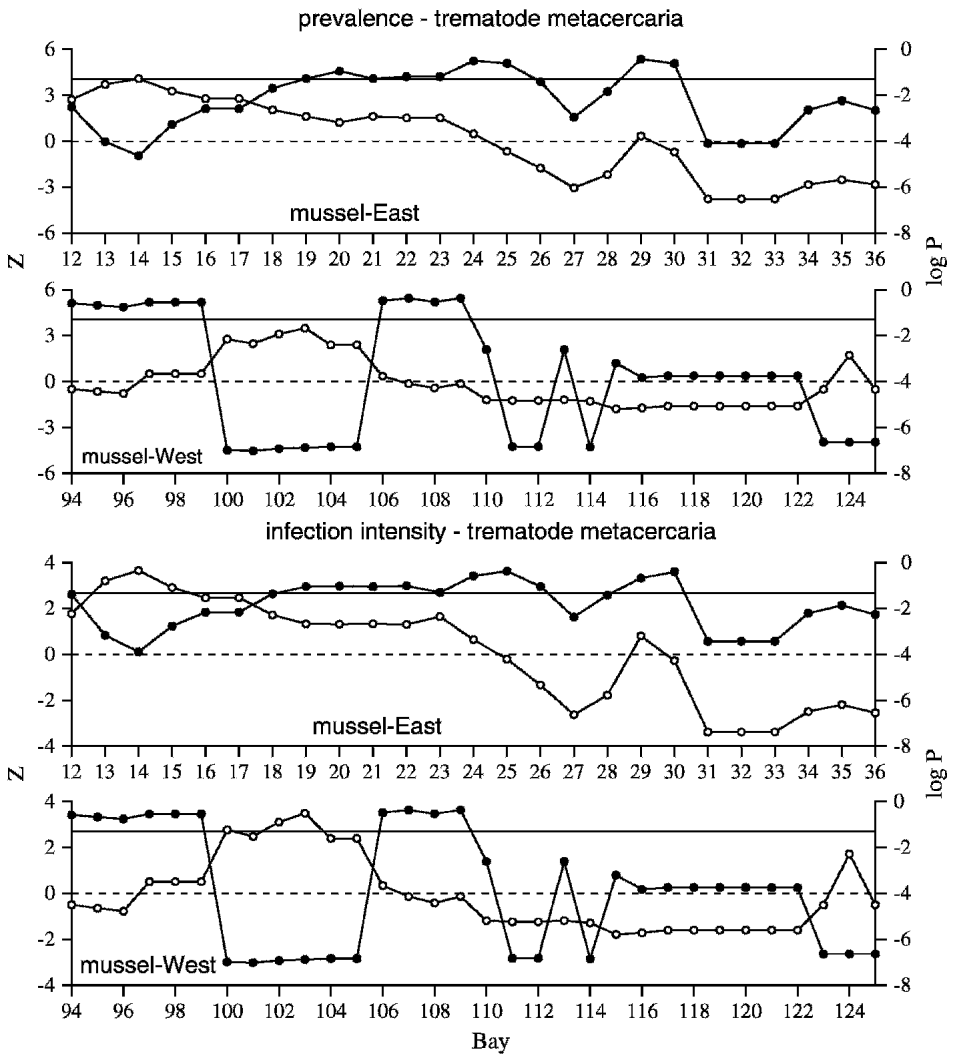

Figure 13. Geographic trends in the prevalence and infection intensity of encapsulated trematode metacercariae. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences and infection intensities for each bay are shown in Figure 6. Bay numbers are interpreted in Table 1.

and a number of rare parasites, suggesting that dreissenid population dynamics might also be important. High growth rates and short life spans offer obvious mechanisms to minimize prevalence and infection intensity of parasites (e.g., Sprung 1995, Stoeckmann 2003).

Differences between oysters and mytilids occurred much more frequently at the level of individual parasites: some parasites were unique to oysters; one was unique to mytilids. Encapsulated trematode metacercariae were not observed in oysters. The parasites unique to oysters included the two dominant disease-causing organisms, *P. marinus* and *H. nelsoni*. However, disregarding these, the cestodes, missing from mytilids on both coasts, and the gregarines, missing from mytilids in the northeast, were also noteworthy.

Cestodes were commonly recorded in oysters from warmer waters: the western Gulf (along the southern Texas coast), the eastern Gulf, and the southeastern coast (from Florida panhandle to North Carolina), but, in this study, cestodes were never found north of North Carolina on the East coast and were not observed in the northern Gulf of Mexico in the vicinity of the Mississippi River from Alabama to Louisiana. This temperature dependency could explain the absence of cestodes in mytilids in the northeast and possibly on the West coast. Cestodes are also commonly observed in surf clams north of Cape Hatteras, but once again, prevalences are highest in the southernmost part of the range (Kim & Powell 2004).

Gregarines were not observed in *M. edulis* from the East coast, but were recorded in all mytilids from the West coast, and in large numbers in oysters from the East and Gulf coasts. In the latter two cases, the parasites tended to be most common in southern climes, but not restricted to areas of warm temperatures. Gregarines are also reported in abalone on the West coast (VanBlaricom et al. 1993). Why the parasite is absent from the northeast mytilids is unclear.

Encapsulated trematode metacercariae were observed only in mytilid mussels. They were observed in all mytilid taxa, however, and on both the East and West coasts, though more commonly on the East coast. On the East coast,

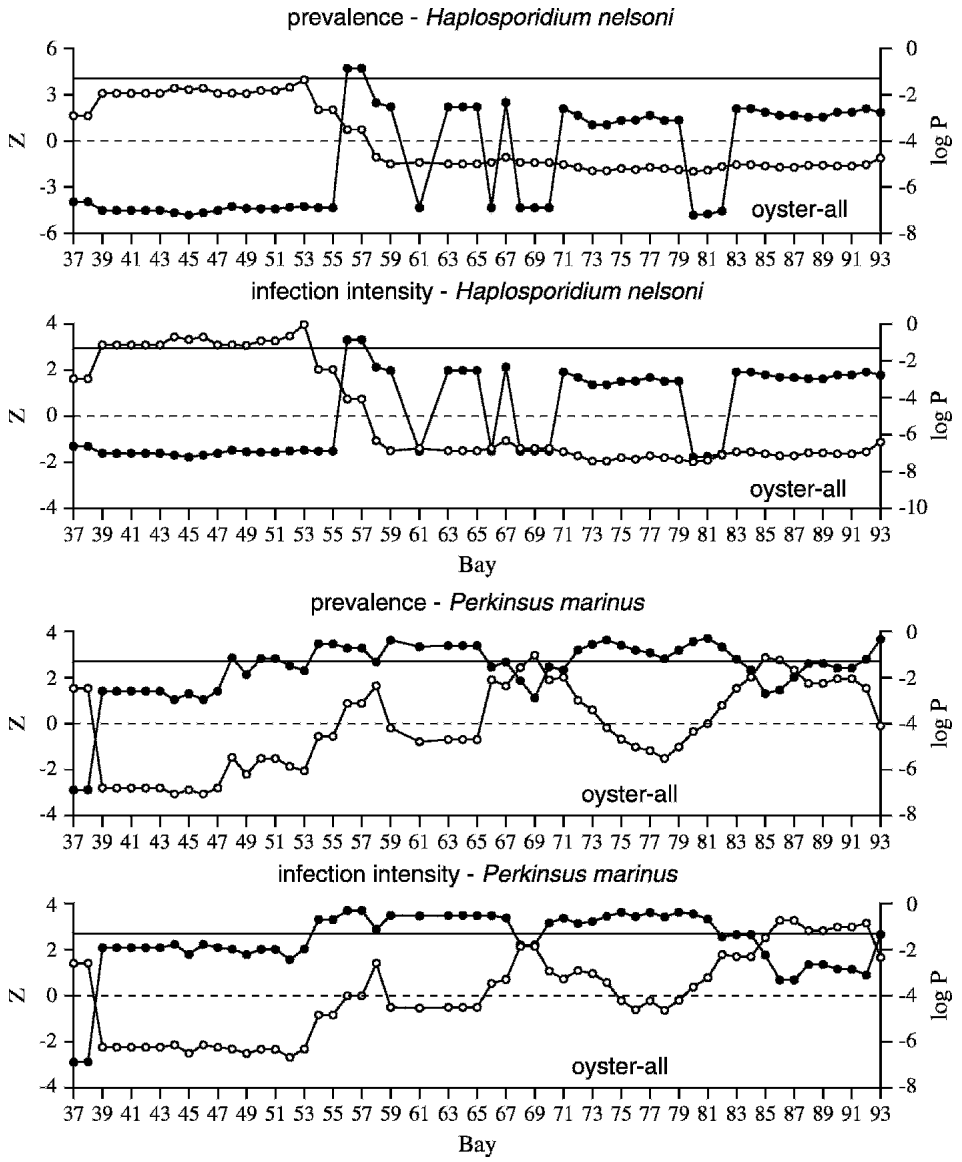

Figure 14. Geographic trends in prevalence and infection intensity of the haplosporidians and *Perkinsus marinus*. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences and infection intensities for each bay are shown in Figure 2. Bay numbers are interpreted in Table 1.

trematode metacercariae were more common in the north. Prevalence and infection intensity declined more or less steadily to the south. In contrast, on the West coast, trematode metacercariae were most common near the center of the latitudinal range.

Added to these obvious differences between mytilids and oysters were a number of other noteworthy trends. Prokaryotic inclusions and digestive tract ciliates were more common in oysters; gill ciliates and trematode sporocysts were more common in mytilids. The comparison for trematode sporocysts was dominated by high prevalences in northeast mytilids. Trematode sporocysts are also very common in deep-sea mussels (Powell et al. 1999). Though cestodes offer a discrepancy, interestingly, most of the more common oyster parasites are unicellular, whereas most of the common mytilid parasites are multicellular.

Mytilus californianus were collected at 31 sites out of 69 total West-coast mussel sites. The two West-coast taxa differed in some important respects. Gregarines were more prevalent in *M. californianus* than in the *M. edulis* complex, as were trematode metacercariae. Though not more prevalent, digestive tract ciliates reached higher infection intensities in *M. californianus*. Gill ciliates more commonly infected the *M. edulis* complex. Also, Caceres-Martinez and Vasquez-Yeomans (1997) reported higher copepod prevalence in *M. galloprovincialis* than in *M. californianus*. In aggregate, this study resolved fifteen significant differences between these two mytilid groups out of a total of 31 possibilities (Table 5), a frequency exceeding that expected by chance (binomial test, $p = 0.05$, $q = 0.95$, $P < 0.0001$). Thus, the parasite and pathology complement of *M. californianus* diverged substantially from the other West-coast mytilids.

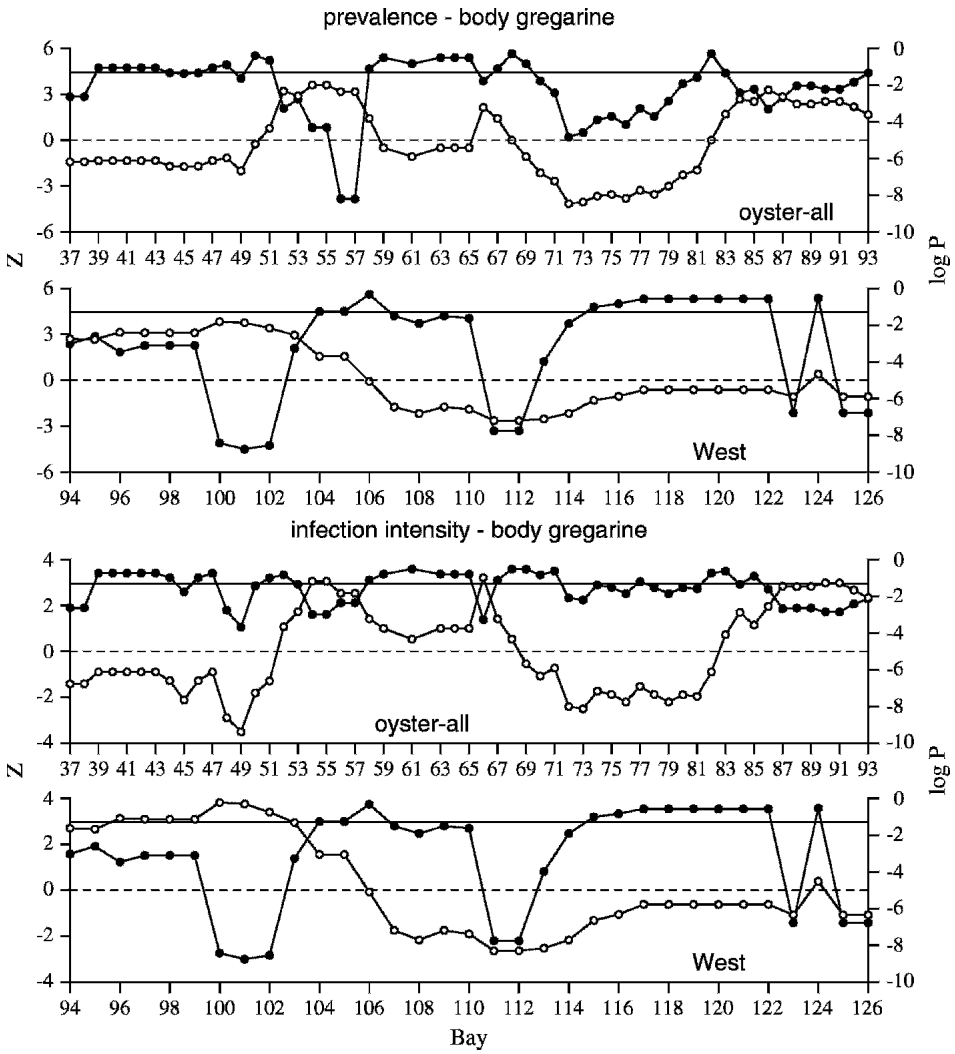

Figure 15. Geographic trends in the prevalence and infection intensity of gregarines in the body tissue. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic Z (○). Solid line indicates a P value of 0.05. Dashed line indicates a Z-value of zero. Prevalences and infection intensities for each bay are shown in Figure 4. Bay numbers are interpreted in Table 1.

East-coast oysters diverged significantly from Gulf-coast oysters in 10 of 35 comparisons (Table 5). This is a significantly lesser frequency than observed between *M. californianus* and the *M. edulis* complex on the West coast (15 of 31) (binomial test, $p = 0.48$, $q = 0.52$, $P < 0.02$). East- and West-coast mytilids differ in 13 cases out of 23, a more frequent rate than observed between East- and Gulf-coast oysters ($P < 0.005$), but not significantly different from that observed between West-coast *M. californianus* and the West-coast *M. edulis* complex. To the extent this analysis permits, these comparisons indicate that differences between taxa are just as likely to be caused by differences between coasts or, at least, taxon and coastline differences are not extraordinarily disparate in their overall impact on parasite complement.

Geographic Trends Between Coasts and Taxa

Oysters routinely harbored more parasites than mytilids. Mytilids far exceed oysters in the incidence of pathologies and the vast majority of these were in *M. edulis* and related taxa rather than, on the West coast, in *M. californianus*. Major pathologies, including digestive gland and gonadal abnormalities, were more common in *M. edulis*, as were instances of hemocytic infiltration, though this differential was less significant. The severity of digestive gland atrophy was similar in both taxa. All pathologies were more common in mytilids from the northeast coast than from the West coast. Whether this high incidence is related to the higher contaminant body burdens noted in mussels from this region is unknown (O'Connor & Beliaeff 1995, O'Connor 1996).

Prevalence data also show that gill ciliates, trematode sporocysts, and trematode metacercariae are principally associated with East-coast *M. edulis* in comparison with the West-coast mytilids. Infection intensities, however, revealed that only trematode metacercariae were more abundant in infected East-coast *M. edulis*; whereas trematode sporocysts more severely infected the many fewer infected West-coast mytilids. Trematode sporocysts were much more broadly distributed in northeast mytilids, but at lower infection intensities. Thus, West-coast mytilid populations were generally

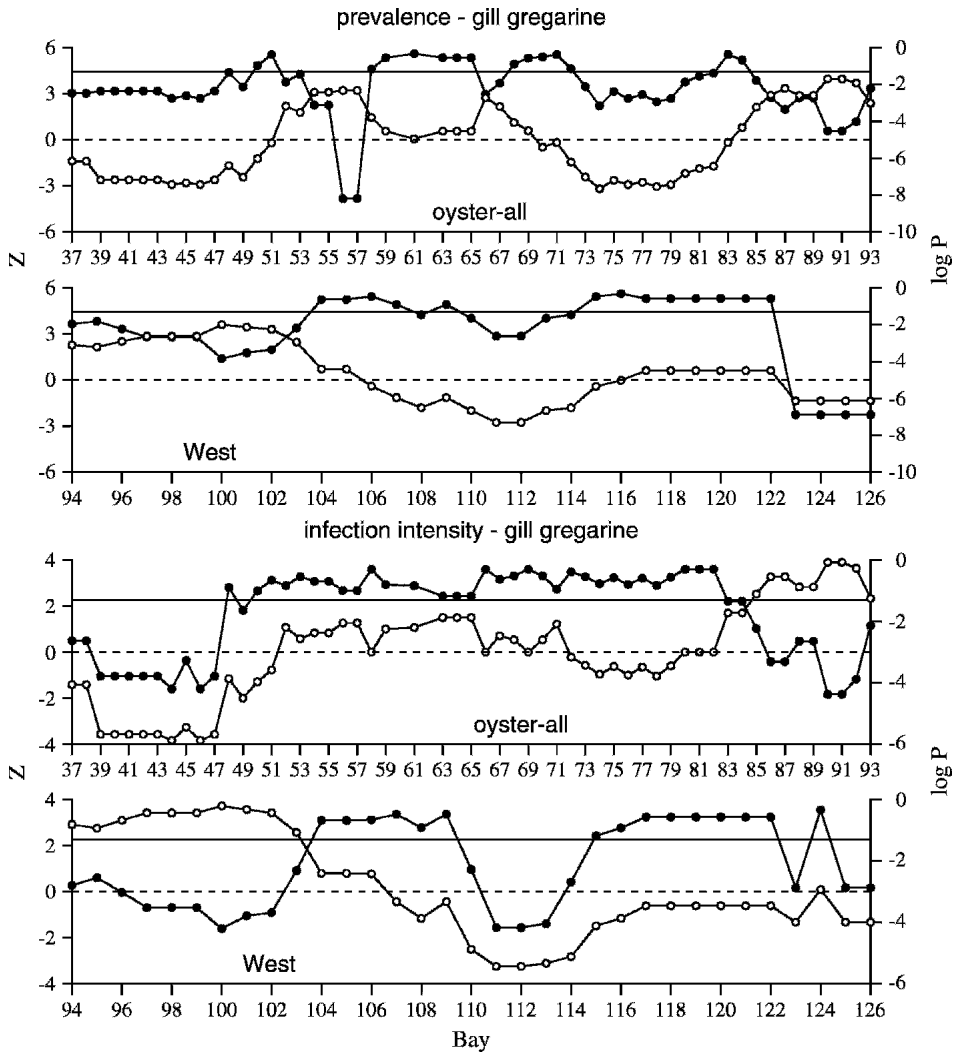

Figure 16. Geographic trends in the prevalence and infection intensity of gregarines in the gill tissue. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences and infection intensities for each bay are shown in Figure 4. Bay numbers are interpreted in Table 1.

lower in prevalence and intensity of infection than East-coast *M. edulis*, a trend that followed the similar tendency for the pathologies.

Ciliates were distinguished by tissue type. Digestive tract and gill ciliates are demonstrably different taxa (e.g., Winstead et al. 2004) and can be expected to have divergent geographic distributions. Ciliates were seen in mytilids and oysters from all three coasts in this study. Their distributions were dramatically divergent. Gill ciliates were most prevalent in mytilids on the East and West coast. Digestive tract ciliates predominated in oysters on the southeast and Gulf coasts.

A more difficult issue is the need to differentiate among gregarines in the body, gill, and mantle tissue. Gregarines were dominant parasites in oysters and important parasites in West-coast mytilids. Sprague (1949) and Sprague and Orr (1952, 1955) suggested that two different species (*Nematopsis ostrearum* and *N. prytherchi*) occur in Gulf oysters, and that *N. prytherchi* tend to concentrate in the gills. Feng (1958) found *N. ostrearum* primarily in mantle tissue of East-coast oysters. Overall, the geographic distribution of the gregarines in the three tissue types was very similar, in terms of prevalence and infection intensity. Some interesting divergences were present, however. Infection intensity of gill gregarines was overwhelmingly highest in oysters from central Texas on the Gulf coast, supporting the suggestion of Sprague and Orr (1952, 1955) that the gregarine in the gill is different from the one in mantle tissue in Gulf-coast oysters. The distribution of gill gregarines also diverged from the others in West-coast mytilids where this parasite was unusually prevalent, in comparison with the other two, along the Washington coastline. The geographic distribution of body and mantle gregarines, in contrast, offered few obvious points of divergence, suggesting that the same parasite infects these tissues within taxon and geographic region, even if the species differed among taxa and coasts.

Temporal Observations

Some temporal consistencies in parasite distributions exist between the 1970s and the present Mussel Watch Projects.

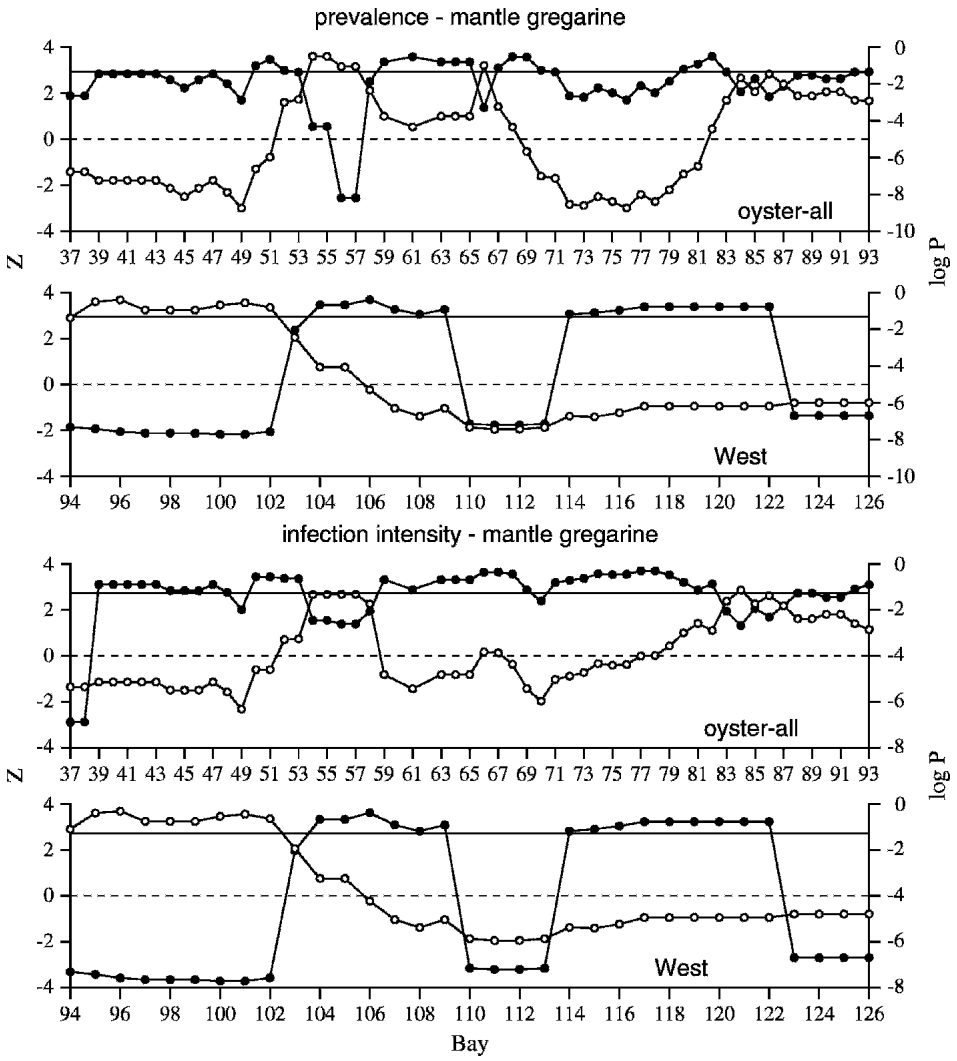

Figure 17. Geographic trends in the prevalence and infection intensity of gregarines in the mantle tissue. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences and infection intensities for each bay are shown in Figure 4. Bay numbers are interpreted in Table 1.

Yevich and Barszcz (1983) reported prokaryotic inclusions in the digestive tract of oysters and in West-coast mytilids, and prokaryotic inclusions in the gills of East-coast *M. edulis* from the 1976 Mussel Watch Program. Prokaryotic inclusions were not observed in this study in the epithelial cells of the digestive tract of East-coast *M. edulis* or in representatives of the *M. edulis* complex on the West coast, but were found in oysters and in *M. californianus* on the West coast. Prokaryotic inclusions associated with the gills were recorded in mytilids from both the East and West coasts, both the *M. edulis* complex and *M. californianus*, but not in oysters. Yevich and Barszcz (1983) reported that trematode sporocysts were most prevalent in East-coast *M. edulis*. Sporocysts of trematodes were more commonly recorded in *M. edulis* from Massachusetts to Delaware on the East coast in this study as well.

Geographic Trends Within Taxa

Hall (1964) classified the shallow-water marine climates on both sides of North America based on the duration of marine temperatures that define (molluscan) provinces within which nearshore communities maintain a characteristic composition. Within the geographic range of this study, according to Hall (1964), generally-accepted major provinces are: Atlantic coast—mild temperate [Virginian—northern boundary at 41°N—Cape Cod (Bay 21)], outer tropical [Carolinian—northern boundary at 35°N—Cape Hatteras (Bay 48)] and inner tropical [Caribbean—northern boundary at 30°N—north of Cape Canaveral (Bay 56)]; Pacific coast—mild temperate [Oregonian—northern boundary at 48°N—Cape Flattery (Bay 115)] and warm temperate [Californian—northern boundary at 34°N—Point Conception (Bay 102)]. Later, Valentine (1966) provided more detailed provincial and subprovincial boundaries on the West coast including Puget Sound (Bays 116–121), Cape Mendocino (Bays 107–108), Monterey Bay (Bay 104), and Point Conception (Bay 102). Wilson et al. (1992) noted geographic boundaries in the Gulf of Mexico at Tampa Bay, FL (Bay 66), in the vicinity of the Mississippi River (Bays 77–78), and between Matagorda Bay and Aransas Bay, TX (Bays

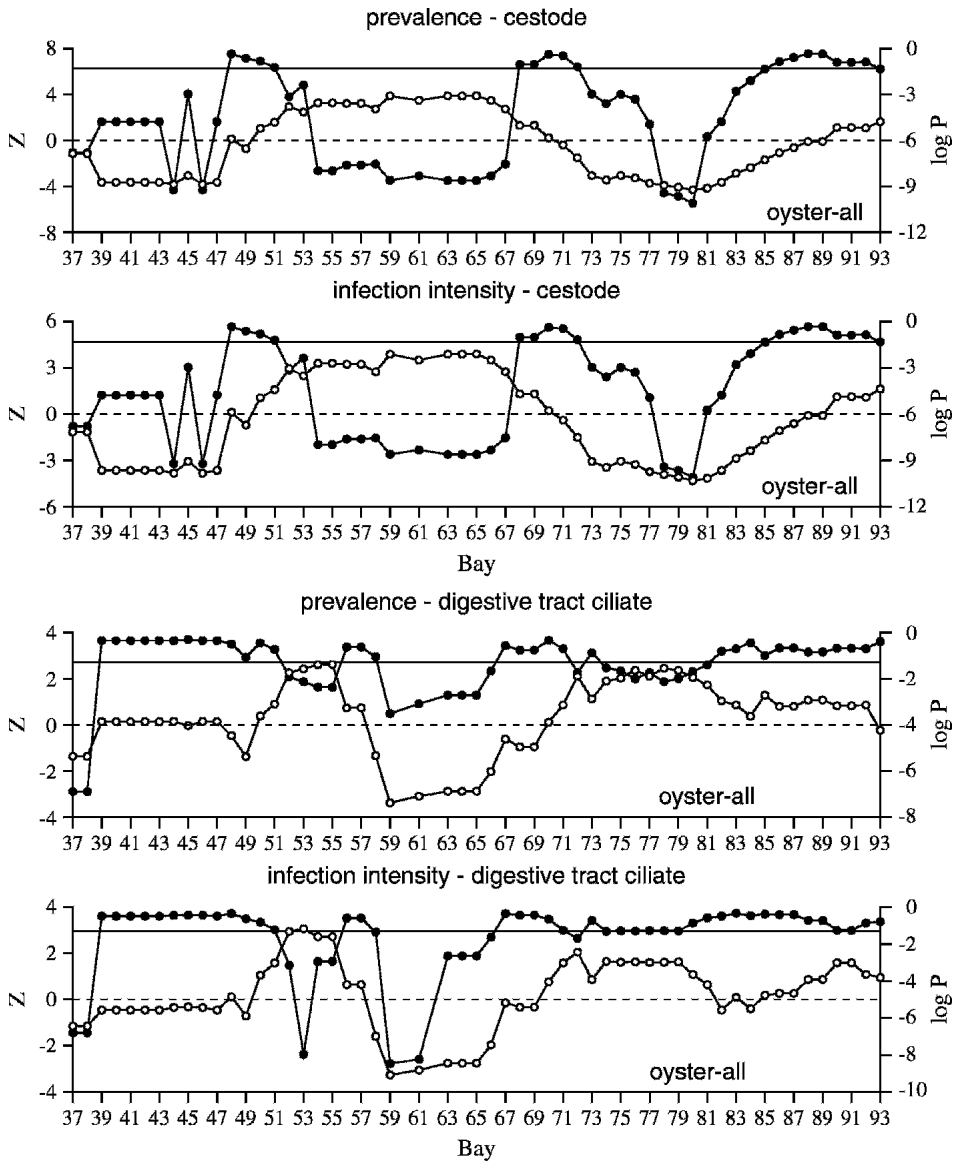

Figure 18. Geographic trends in the prevalence and infection intensity of cestodes and ciliates in the digestive tract. • indicates the significance level for a comparison between the frequency at which bays within a 300-km distance of the central (numbered) bay fell above (or below) the global median and the same frequency for the entire coastline, as measured by the test statistic *Z* (○). Solid line indicates a *P* value of 0.05. Dashed line indicates a *Z*-value of zero. Prevalences and infection intensities for each bay are shown in Figures 5 and 6. Bay numbers are interpreted in Table 1.

89–91) from previous Mussel Watch data and these boundaries are consistent with broad zoogeographic trends in the Gulf of Mexico (Kim & Powell 1998). Hayden and Dolan (1976) emphasized the use of both coastal marine fauna and hydrodynamics of adjacent waters to establish the marine provinces of the coastal environment.

On the average, parasite distributional patterns along a stretch of coastline were more often clinal in nature in mytilids, in that prevalence and infection intensity tended to change gradually over relatively large distance scales, and more bounded in nature in oysters, in that prevalence and infection intensity tended to change more sharply over shorter distance scales and often associated with provincial boundaries. Clinal trends in mytilids along the northeast coast (Bays 12–36), for example, include the steady increase of prokaryotic inclusions and trematode sporocysts from Maine to Delaware and the gradual increase of gill ciliates and trematode metacercariae from Delaware to Maine. Interestingly, summer water temperatures change significantly in the vicinity of Cape Cod, and would be expected to exert an influence on parasite distributions, but none is apparent. No such strong demarcation in temperature occurs during the winter, however (Hutchins 1947), when Mussel Watch sampling occurs. The limited influence of bivalve length (and presumably age) on prevalence and infection intensity of parasites suggests that many of these taxa are short lived and may follow seasonal cycles of infection that would respond to the changing strength of the temperature gradient across Cape Cod in summer and winter, thereby possibly minimizing the importance of Cape Cod as a regional boundary during the winter. It is nevertheless notable that the

prevalences of gill ciliates and trematode sporocysts, unlike trematode metacercariae and prokaryotic inclusions, show a more rapid rate of change west of Block Island and this may be a manifestation of the northern boundary of the Virginian province.

Parasites, with the exception of trematode metacercariae, tended to follow latitudinal trends as well on the West coast, with prevalence and infection intensity changing more or less gradually with changing latitude. Interestingly, more parasites occurred in *M. edulis* from northern bays of the East coast, whereas fewer parasites occurred in mytilids from northern bays of the West coast. Latitudinal trends were diametric opposites on the two northern coasts. We cannot offer an explanation for this phenomenon.

Among oysters, in contrast, only two parasites offered relatively distinct clinal patterns: nematodes and, to a large extent, *Perkinsus marinus*. Results of this study are consistent with previous studies showing that *P. marinus* is abundant in oysters from the East- (Ford & Tripp 1996) and Gulf-coasts (Craig et al. 1989). Prevalence and infection intensity in Gulf-coast oysters were significantly higher than in East-coast oysters. This trend follows average winter temperatures, an important environmental factor controlling Dermo infection (Powell et al. 1996, Cook et al. 1998).

More often, oysters followed a distinctly bounded distributional pattern in that portions of the coastline were characterized by distinctly higher or lower prevalences and infection intensities. Some of these boundaries are generally recognized provincial boundaries (Hall 1964, Valentine 1966). Cape Hatteras, NC (Bay 48), the northern limit of the Carolinian province, is a well-known biogeographic boundary for free-living animals on the Atlantic coast (e.g., Cerame-Vivas & Gray 1966) and parasites are no exception. The Cape Hatteras and Cape Lookout/Cape Fear area was a regional boundary for prokaryotic inclusions, the gregarines, ciliates, and cestodes. The Atlantic coast of Florida in the vicinity of Cape Canaveral was also a regional boundary for gregarines and ciliates. The same location has been identified as an important genetic boundary in oysters (Reeb & Avise 1990). Normally, these rapid changes did not involve the appearance or disappearance of a parasitic taxon, as is often associated with a provincial boundary, but a distinct change in frequency of occurrence or abundance. Changes may have occurred at a lower taxonomic level than resolved in this study, of course; however, it is easily as likely that rapid downcoast changes in prevalence and infection intensity are associated with local environmental processes that are also bounded by these notable provincial geographies.

The Gulf of Mexico can be divided into three broad geographic regions according to the weather patterns: eastern, southern and northwestern, because of the southwest-northeast trending isotherms and isohyets that trend onshore in the northeast region (Douglas & Englehart 1981). These regions were routinely associated with highs and lows in prevalence and infection intensity. North and northeastern Gulf lows in prevalence and infection intensity, for example, were observed for *P. marinus*, gregarines, and cestodes. The obverse, relatively high prevalences and infection intensities, was observed in the same region for digestive tract ciliates. Gill ciliates, though less widespread, also obtained regional highs in the northeastern Gulf. The Tampa Bay area on the Gulf coast of Florida and the Matagorda/Aransas Bay area of Texas divide the temperate and subtropical zones. The Tampa Bay region was noteworthy in differentiating areas of high and low infection for prokaryotic inclusions and the northern Texas coast marked an area of change in prevalence and infection intensity for the majority of Gulf-coast parasites.

On the West coast, the only equivalent bounded distributional pattern belonged to the trematode metacercariae. Cape Mendocino, CA (Bays 107–108), the northern boundary of the distributional high for trematode metacercariae, is also identified as an important provincial boundary by Valentine (1966).

CONCLUSIONS

Temperature is a driving force for most of the parasites examined in this study. In some cases, prevalence and infection intensity are modulated to produce clinal shifts over large regional scales; in other cases, the changes in prevalence and infection intensity are sharper; nevertheless, the underlying influence of temperature cannot be overlooked. Besides these global effects, the coastline trends identify some important more local processes that create local highs and lows in prevalence and infection intensity. Lafferty et al. (2004) stress the complexity of reasons for changes in parasite prevalence and infection intensity. Whereas the large-scale trends are likely to be stable over time, only further study can determine the extent to which the more local trends are. The simple expectation of increased prevalence and infection intensity with decreasing latitude and increasing temperature, inculcated into the overall trend of species richness with latitude (e.g., Rohde 1992, 2002) and anticipated from recent evidences of the effect of global warming (e.g., Cook et al. 1998, Harvell et al. 2002, Danovaro et al. 2004), does not hold up uniformly. A number of parasites show opposing trends in this study and elsewhere (e.g., Paillard 2004). Perhaps most noteworthy among these exceptions are parasites from *M. edulis* on the northeast coast. Prokaryotic inclusions and trematode sporocysts increased in prevalence and infection intensity from north to south, but trematode metacercariae and gill ciliates followed the opposing trend from south to north.

Some more general trends are also potentially important. Among the taxa, oysters were consistently more highly parasitized than mytilids, with a single exception of prevalence in mytilids in the northeast region. Oysters had more types of parasites and body burdens were higher. Much of the latter was due to the numerically dominant gregarines. Nevertheless, the data suggest innate differences between these taxa in their parasite communities. Most common mytilid parasites were multicellular eukaryotes. Most common oyster parasites were unicellular eukaryotes and prokaryotes. In contrast to the oysters and mytilids, taxon richness was low in dreissenid mussels, as anticipated for new invaders, but also low in prevalence and infection intensity suggesting that these taxa are inherently less likely to be highly parasitized than the two marine groups.

Among coasts, of greatest note is the unique combination of high parasite prevalence and high instance of pathology in East-coast mytilids. East-coast *M. edulis* were more commonly infected by more types of parasites than were West-coast mytilids and by far more frequently affected by serious pathological conditions. East-coast mytilids exceeded East-coast oysters in

overall prevalence, despite the higher overall parasite loads in oysters, and far exceeded oysters in the instance of pathologies. Among mytilids, major pathologies were more common in the *M. edulis* complex than in *M. californianus* on the West coast, so the mytilids may be inherently more susceptible to these pathologies; nevertheless, East-coast mytilids exceeded West-coast mytilids in this regard. Why parasitism and pathology are so high in the northeast region is not yet known.

ACKNOWLEDGMENTS

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