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RELATIONSHIPS AMONG PARASITES AND PATHOLOGIES IN SENTINEL BIVALVES: NOAA STATUS AND TRENDS "MUSSEL WATCH" PROGRAM

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ABSTRACT

NOAA's National Status and Trends "Mussel Watch" Program includes a comprehensive survey of the histopathology of sentinel bivalves from the east, west, Gulf, and Great Lakes coasts of the U.S. We analyzed the data for 1995–1998 to identify relationships between various parasites, various pathologies, and between parasite/pathology pairs with the goal of identifying consistencies and differences in these relationships between sentinel bivalves and between major geographic units of the U.S. coastline. The prevalences of parasite, pathology, and parasite-pathology pairs were significantly correlated more frequently for oysters than for mussels. The number of significant correlations within Gulf-coast oysters exceeded the number within east-coast oysters. Correlations were least frequent among east-coast mussels. The incidence of significant negative correlations in prevalence far exceeded the incidence of significant positive correlations in all species and bay regions. Significant relationships in infection intensity occurred much less frequently than for prevalence, but positive correlations occurred more frequently than they did for prevalence. Both trends reinforce the concept that environmental factors controlling transmission are likely distinct from those controlling proliferation. Only a few relationships between parasites were common to more than one sentinel bivalve or more than one coastal region. No single common relationship involved a pathology. However, though commonalities were few, consistent trends in prevalence between mussels and oysters and between coastal regions suggest potentially important large-scale trends among some important parasite groups, particularly gregarines and gut ciliates, gill gregarines and cestodes, prokaryotic inclusions and trematode metacercariae, and *Perkinsus marinus* (Mackin, Owen and Collier, 1950) and gregarines.

Estuarine and coastal marine waters receive many kinds of organic and inorganic contaminants that potentially have adverse effects on biota living in these habitats and possibly on humans who consume them. Sessile bivalve mollusks can be effectively used as bioindicators to monitor the status and trends of coastal water quality. The first national-scale biomonitoring program, the Mussel Watch Monitoring Program, was conducted by the U.S. Environmental Protection Agency (EPA) in the late 1970s (Goldberg et al., 1978, 1983). The modern Mussel Watch Program, developed by the National Oceanic and Atmospheric Administration (NOAA), began in 1986. This program has monitored contaminants of environmental concern yearly since then using, as sentinel organisms, bivalves collected from estuarine and coastal waters along the entirety of the U.S. coastline (O'Connor and Beliaeff, 1995).

The histopathological survey of parasites and pathologies can be an important component of a biomonitoring study of environmental pollution (Yevich and Barszcz, 1983; Gold-Bouchot et al., 1995; Wester et al., 2002). The physiological state of an organism can influence contaminant body burden (e.g., Boyden and Phillips, 1981; Lunsford and Blem, 1982; Jovanovich and 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 and 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 and Couch, 1988; Khan, 1990; Kim et al., 1999, 2001; Wilson-Ormond et al., 2000). A histopathological survey of sentinel bivalve molluscs has been included in the NOAA Mussel Watch Project since 1995 as a consequence. Although many regional surveys have been undertaken (e.g., Burton, 1961; Newman, 1971; Otto et al., 1979; Field et al., 1997; Kube et al., 2002), the Mussel Watch Project is the first nationwide monitoring program to use a quantitative approach to histopathological analysis, including the direct enumeration of parasites and the application of semiquantitative scales for disease intensity and extent of pathologies. The present study builds on the original survey of Yevich and Barszcz (1983) from the original EPA program.

Most bivalve species, and indeed most bivalve individuals, harbor an array of parasites and pathologies. A variety of studies have examined the relationships among parasites, pathologies, and selected morphological conditions (e.g., digestive gland atrophy) within populations, estuaries, or on somewhat larger regional scales (e.g., Gauthier et al., 1990; Bowmer et al., 1991; Figueras et al., 1991; Conn et al., 1994; Comps and Tigé, 1999; Powell et al., 1999a; Kim and Powell, 2004). Little is known about the interaction of parasites within bivalve hosts, however (e.g., Kuris and Lafferty, 1994; Hine, 2002), or their influence on pathologies beyond a few known to be produced by disease (e.g., Ford, 1985; Bower et al., 1999) and parasitic sterilization (e.g., Powell et al., 1999a; Tétreault et al., 2000; Silva et al., 2002). Certainly in the broader context, some co-occurring parasites may interact negatively or positively (Leong and Holmes, 1981; Brattey et al., 1985; Gatto and de Leo, 1998; Poulin and Morand, 2000) and certain pathologies must be related to parasitic assault (e.g., VanBlaricom et al., 1993; Kim and Powell, 2004). The Mussel Watch program is unique in being of continental scale; thereby providing an unparalleled opportunity to examine the relationships of bivalve parasites to each other, their hosts, and the tissue pathologies of their hosts over a number of different regional scales. The objective of this analysis is to examine the relationships between parasitism and pathology in sentinel bivalves on large geographic scales using the 1995–1998 histopathology data from the National Status and Trends Mussel Watch Program.

Materials and Methods

Species Sampled and Sample Collection.—The bivalve samples were collected annually from a network of sites established along the U.S. coastline. Bivalves were dredged or handpicked in intertidal to shallow subtidal areas. Sampling targeted the largest animals available at each site. Each sampled site subsequently was assigned to one of 126 bays [Appendix 1, see Lauenstein et al. (1997) for further details]. A bay typically represents all the sites in a single estuary or a group of neighboring sites on an open coastline.

The introduced zebra mussel, *Dreissena polymorpha* (Pallas, 1771), and quagga mussel, *Dreissena bugensis* Andrusov, 1897, were sampled at sites in the Great Lakes (bays 1–10) and Hudson River (bay 11). Zebra mussels were first discovered in the Great Lakes in 1988 (Hebert et al., 1989). Quagga mussels were found in 1991 (May and Marsden, 1992). Both likely were

introduced from Europe in ship ballast water (Hebert et al., 1989). Both species spread rapidly throughout the Great Lakes system (Griffiths et al., 1991; Strayer, 1991). 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 for this study were *Mytilus edulis* Linnaeus, 1758 sensu stricto, as it is the predominant species from central Maine south (Rawson et al., 2001) to Cape Hatteras (Wells and Gray, 1960) on the east coast. On the west coast, three mussel taxa were collected, *Mytilus californianus* Conrad, 1837 and two species referable to the *M. edulis* complex, *Mytilus galloprovincialis* Lamarck, 1819 and *Mytilus trossulus* Gould, 1850. *Mytilus californianus* was collected at 31 sites mostly located at jetties, points, or capes among the 58 total West coast sites excluding Alaska (Appendix 1; 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 and 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 to 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 analyses.

Four oyster taxa were sampled, *Crassostrea virginica* (Gmelin, 1791), *Crassostrea rhizophorae* Guilding, 1828, *Crassostrea gigas* (Thunberg, 1793), and *Dendostrea sandvichensis* (Sowerby, 1871). *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 and 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 during winter months with each site occupied within 30 d of a defined target date (O'Connor, 1994). Sampling was done in winter to minimize the influence of reproduction on contaminant body burden as bivalves may change their contaminant concentrations by spawning (Jovanovich and Marion, 1987; Ellis et al., 1993). In the Great Lakes, dreissenid mussels were collected in late August through September; winter sampling in the Great Lakes is difficult because the lakes are frequently frozen.

Sample Preparation.—Tissue preparation mostly followed the original NOAA Status and Trends protocols (Ellis et al., 1998a). Due to their small size, dreissenids were preserved whole in their shells in Davidson's fixative without cutting the adductor muscle and remained in the fixative for 1 wk while the degree of decalcification was monitored. If needed, 20–30 ml of acetic acid was added to aid decalcification of shell. When the shell became separated from the soft parts, the fixative was replaced by 70% alcohol for storage.

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 1 wk and then transferred to 70% alcohol for storage. A sharp knife or scalpel was carefully run between the shell and the mantle to separate the meat from the shell. This procedure was repeated for the other shell to completely detach both sides of the mantle from the shell.

For both dreissenids and mytilids, the shell length of each animal was recorded. Byssal threads were completely removed from the byssal gland to avoid problems when sectioning the tissue. A 3–5 mm thick cross-section including digestive gland and gill was removed using a scalpel and placed in a tissue capsule for immediate processing.

For oysters, 12 animals from each site were randomly selected and opened with an oyster knife by cutting the adductor muscle. A small section of mantle tissue (5 × 5 mm) was removed for the culture of *Perkinsus marinus,* the Dermo disease pathogen. A 3–5 mm-thick dorsal-ventral (transverse) cross-section of tissue was removed from five of the animals using scissors. The cross-section was immediately transferred to a tissue capsule and placed in Davidson's fixative for 2 d, followed by storage in 70% alcohol.

Tissue samples were embedded in paraffin after dehydration and clearing. The tissue-paraffin block was then placed in a freezer overnight before sectioning. The paraffin-embedded tissue blocks were first sliced at 20 μm to expose an entire tissue cross-section, and then sectioned at 5 μm. Tissue sections were deparaffinized and hydrated using a xylene-ethanol series. Following hydration, slides were stained in a pentachrome series, dehydrated in a series of acetic acid dips followed by acetone, cleared in xylene and mounted in Permount (Ellis et al., 1998a).

Parasite/Pathology Quantification.—Tissue sections were examined under the microscope using a 10× ocular and a 10× objective. When necessary, a 25× or 40× objective was used for closer examination. Major tissue types examined included gill, mantle, gonad and gonoducts, digestive gland tubules, stomach/digestive gland, and connective tissue. For oyster taxa, rather than histology, *Perkinsus marinus* (Mackin, Owen and Collier, 1950) was assayed by the more precise thioglycollate method (Powell and Ellis, 1998). All parasites and pathologies were scored for intensity based on either a quantitative or semi-quantitative scale. Quantitative scores were used for parasites, pathologies, and selected morphological conditions that could be tallied individually, including prokaryotic inclusion bodies (rickettsia, chlamydia, etc.), various ciliates, gregarines, other protozoans, nematodes, encysted cestodes and metacercariae of trematodes, copepods and other unidentified organisms. For these categories, the total number of occurrences was recorded following procedures described by Ellis et al. (1998b) and Kim et al. (2006). Ciliates were quantified by tissue type (viz., gill and digestive tract), as were the gregarines (viz., body, gill, and mantle). 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 and Powell, 2004), granulocytomas (Lowe and Moore, 1979), and ceroid bodies or pigment cells (Mackin, 1951; Stein and Mackin, 1955). Occasionally, a ceroid body appeared fractured or split; in this case only one fragment was counted.

Some parasites and morphological conditions were assigned to semi-quantitative scales depending on the intensity or extensiveness of the affected area. Definitions of scale values can be found in Ellis et al. (1998b) and Kim et al. (2006). Semi-quantitative scales were used for such parasites as invasive trematodes and the disease-producing protozoans, *P. marinus* and *Haplosporidium nelsoni* (Haskin, Stauber and Mackin, 1966). A semi-quantitative 0 to 4-point scale was used for invasive trematode sporocysts of the families Fellodistomidae and Bucephalidae due to the extensiveness of infections and the difficulty in obtaining quantitative counts of the large branching sporocysts. Intensity of *P. marinus* infection was assigned to each tissue sample based on the number or coverage of hypnospores observed in the tissue using the semi-quantitative 0 to 5-point scale of Mackin as modified by Craig et al. (1989). MSX disease caused by *H. nelsoni* normally starts in the gill epithelium, so gill tissue was

carefully examined to score early infections accurately. Disease intensity was scored on a 0 to 4-point scale. For each specimen examined, neoplasms and unusual digestive tubules were recorded as either 1 (present) or 0 (absent). Abnormal gonadal development, characterized by unusual development at the base of the follicles and by presence of foreign cells and cellular debris in the follicles, was given a semi-quantitative 0 to 4-point score related to the spatial coverage of the condition (Kim et al., 2006). For digestive gland atrophy, a condition caused by a variety of stressors most likely related to poor nutrition (Palmer, 1979; Winstead, 1995; Kim and 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., 2006).

Statistical Analysis.—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:

$$prevalence = \frac{number\ animals\ affected}{number\ animals\ analyzed}.$$

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

$$infection\ intensity = \frac{\sum_{i=1}^{n} number\ of\ ocurrences\ of\ parasite\ or\ pathology}{number\ affected\ individuals}.$$

For conditions rated using semi-quantitative 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 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 and Powell, 2004), confounds prevalence and infection intensity:

$$weighted\ prevalence = prevalence \times infection\ intensity$$

and, as a consequence, was not used in statistical analyses.

The protocol for the biological component of the Mussel Watch Program stipulates analysis of five individuals per site. In this study, a designated bay (Appendix 1) usually contained more than one site. The value of prevalence or infection intensity assigned to each bay was the arithmetic mean of all the animals analyzed from each sampled site in the bay averaged over the 1995–1998 period.

Pathologies were grouped into two categories: major and tissue. Major pathologies included neoplasms, unusual digestive tubules, and gonadal abnormalities. Tissue pathologies included focal and diffuse hemocytic infiltration and granulocytomas. Parasitic taxa were analyzed individually. Bays were grouped into a series of regions. In most cases, these were the east-coast mytilid sites, bays 12–36; the east-coast oyster sites, bays 37–61; the Gulf-coast oyster sites, bays 63–93; the west-coast mytilid sites, bays 94–125; and the Great Lakes/Hudson River dreissenid sites, bays 1–11. In a few cases, only east-coast oyster sites south of Cape Hatteras were analyzed, bays 48–61. Correlation analysis relied on the Spearman rank test (Sokal and Rohlf, 1998).

We identified 15 different parasite, pathology, and morphology types, yielding 105 total possible pairwise comparisons. Some conditions did not occur in some bay groups. For example, six of the possible 15 did not occur in east-coast mussels. The number of pairwise comparisons was correspondingly reduced (to 36 in this example). In addition, for prevalence, double-zero pairs were deleted from analyses because the meaning of a double zero is ambiguous. In some cases, double zeros occur simply because the bay was beyond the range of both parasites. In other cases, they occur if no affected animals were found for either condi-

tion in an area where each could occur. For infection intensity, only bay pairs in which both conditions occurred could be used for analysis because an infection intensity of zero is not defined. Thus, the number of data pairs was often much below the number of data pairs analyzed for prevalence. Also, we chose not to conduct pairwise comparisons where the number of data pairs was less than ten. Finally, we included the three pairwise comparisons among the three gregarine categories, body, mantle and gill, as independent tests. The taxonomic distinctiveness among these three gregarine categories is unclear (Sprague, 1949; Landau and Galtsoff, 1951; Sprague and Orr, 1952; Feng, 1956); they were significantly correlated in most tests. Thus, the number of significant differences may be unfairly inflated by three, assuming taxonomic equivalency.

As many correlations were conducted, some may have been significant by chance. Accordingly, we focused on groups of correlations in which the frequency of significant correlations exceeded that expected by chance and discounted the remainder. The binomial test was used to evaluate the frequency of occurrence of significant correlations. For any given set of correlations, the least significant probability at $\alpha = 0.05$ was used for calculation of the binomial probabilities. As this approach penalizes the integrity of significant results more significant than this level, on occasion we use the binomial test to further investigate the likelihood of outcomes at greater significance levels.

Results

Correlations within Bay Groups—*Prevalence.*—The 4-yr bay averages of prevalence and infection intensity are shown in Tables 1 and 2. Dreissenids had few parasites, as is expected for newly invaded species (Torchin et al., 2002), and were not analyzed further.

Parasite, pathology, and parasite-pathology pairs were significantly correlated more frequently for oysters than for mussels (Table 3). The number of significant correlations within Gulf-coast oysters exceeded the number within east-coast oysters and the number within west-coast mussels exceeded the number within east-coast mussels. The incidence of significant negative correlations far exceeded the incidence of significant positive correlations in all species and bay regions (Table 3).

Only two significant correlations were found for east-coast mytilids. Encapsulated trematode metacercariae were negatively correlated with prokaryotic inclusion bodies and with trematode sporocysts. The frequency of significant results, two of 34 tests, is nevertheless greater than would be expected by chance at the least significant probability level observed (binomial test, $p = 0.01$, $q = 0.99$, $P < 0.005$). Thus, significant relationships between parasite, pathology, and parasite/pathology pairs did not occur commonly in east-coast mussels, but those that did were definitive.

Thirteen correlations were significant for east-coast oysters, three of which were contributed by pairwise comparisons among the gregarines. Negative correlations included those for prokaryotic inclusions with gill gregarines, with cestodes, and with gut ciliates; those for *H. nelsoni* with gill gregarines, with mantle gregarines, with gill ciliates, with nematodes, and with cestodes; and one between gut ciliates and nematodes (Table 3). Interestingly, *P. marinus* failed to produce any significant correlations with other parasites or pathologies in oysters from the east coast. The frequency of occurrence of significant results, 13 of 89, is significantly more than expected by chance (binomial test, $p = 0.05$, $q = 0.95$; $P < 0.0001$). Of these, only four were positive and only a single significant correlation was positive, excluding the pairwise comparisons among the gregarines, that one being between gill gregarines and cestodes. This frequency of occurrence of positive correlations, four in 13, may

Table 1. Average prevalence of parasites and pathologies for each region-species group. -, not present.

Taxon/type	Dreissenids	East-coast		Gulf-coast	West-coast	
		Mytilids	Oysters	Oysters	*Mytilus edulis* complex	*Mytilus californianus*
Prokaryotic inclusion	-	0.055	0.039	0.056	0.043	0.020
Haplosporidium nelsoni	-	-	0.084	-	-	-
Perkinsus marinus	-	-	0.45	0.60	-	-
Gill ciliate	-	0.36	0.069	0.059	0.29	0.066
Gut ciliate	-	0.0020	0.13	0.12	0.0057	0.0037
Body gregarine	-	-	0.50	0.53	0.052	0.19
Gill gregarine	-	-	0.47	0.62	0.10	0.29
Mantle gregarine	-	-	0.36	0.44	0.0095	0.13
Trematode sporocyst	-	0.11	0.0029	0.0068	0.0024	0.0026
Trematode metacercariae	-	0.37	-	-	0.0010	0.027
Nematode	0.0009	-	0.035	0.14	-	-
Cestode	-	-	0.15	0.096	-	-
Ceroid bodies	0.36	0.61	0.88	0.90	0.26	0.50
Digestive gland atrophy	0.97	1.00	0.99	0.96	1.00	1.00
Major pathology	0.032	0.46	-	0.0074	0.34	0.044
Tissue pathology	0.041	0.33	0.16	0.12	0.080	0.10

Table 2. Average infection intensity of parasites and pathologies for each region-species group. -, not present.

Taxon/type	Dreissenids	East-coast		Gulf-coast	West-coast	
		Mytilids	Oysters	Oysters	*Mytilus edulis* complex	*Mytilus californianus*
Prokaryotic inclusion	-	5.16	6.74	6.99	6.50	4.31
Haplosporidium nelsoni	-	-	2.23	-	-	-
Perkinsus marinus	-	-	1.47	1.98	-	-
Gill ciliate	-	3.83	9.57	5.00	3.00	3.86
Gut 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
Major pathology	1.00	1.56	-	1.00	1.71	1.10
Tissue pathology	1.17	2.38	1.40	1.39	1.62	1.34

occur by chance; however, excluding the gregarines, the frequency of one in 10 is unlikely to occur by chance (binomial test, $p = q = 0.50$; $P < 0.01$). Thus, significant relationships between parasite, pathology, and parasite/pathology pairs commonly occurred in east-coast oysters and were significantly more likely to be negative than positive.

Table 3. Parasite, pathology, and parasite/pathology pairs yielding significant correlations (α = 0.05) for prevalence using the Spearman's Rank correlation test.

Bivalve group	Variable 1	Variable 2	Positive correlation	Negative correlation
Gulf-coast oysters	Major pathology	Gill ciliate		0.04
	Major pathology	Cestode		0.04
	Gut ciliate	Tissue pathology		0.03
	Gut ciliate	Body gregarine		0.003
	Gut ciliate	Gill gregarine		0.006
	Gut ciliate	Mantle gregarine		0.01
	Gut ciliate	Cestode		0.0002
	Gill ciliate	Nematode		0.003
	Gill ciliate	Cestode		0.02
	Nematode	Cestode		0.03
	Nematode	*Perkinsus marinus*		0.02
	Tissue pathology	Gill gregarine	0.003	
	Tissue pathology	Cestode	0.005	
	Body gregarine	Gill gregarine	0.002	
	Body gregarine	Mantle gregarine	0.0001	
	Body gregarine	*Perkinsus marinus*	0.002	
	Gill gregarine	Mantle gregarine	0.002	
	Gill gregarine	Cestode	0.02	
	Gill gregarine	*Perkinsus marinus*	0.0003	
	Mantle gregarine	*Perkinsus marinus*	0.001	
	Perkinsus marinus	Ceroid bodies	0.03	
East-coast mytilids	Prokaryotic inclusion	Trematode metacercariae		0.01
	Trematode sporocyst	Trematode metacercariae		0.0008
East-coast oysters	Prokaryotic inclusion	Gill gregarine		0.04
	Prokaryotic inclusion	Gut ciliate		0.03
	Prokaryotic inclusion	Cestode		0.02
	Haplosporidium nelsoni	Gill gregarine		0.03
	Haplosporidium nelsoni	Mantle gregarine		0.05
	Haplosporidium nelsoni	Gill ciliate		0.0009
	Haplosporidium nelsoni	Nematode		0.01
	Haplosporidium nelsoni	Cestode		0.01
	Nematode	Gut ciliate		0.005
	Mantle gregarine	Body gregarine	0.0001	
	Gill gregarine	Body gregarine	0.0001	
	Gill gregarine	Mantle gregarine	0.0004	
	Gill gregarine	Cestode	0.02	

Twenty-one correlations were significant for Gulf-coast oysters, including positive correlations for *P. marinus* with body, gill, and mantle gregarines and between *P. marinus* and ceroid bodies. Significant negative correlations included correlations between cestodes and nematodes, cestodes and gut ciliates, nematodes and *P. marinus*, nematodes and gill ciliates, and between gut ciliates and all gregarine groups. Significant correlations did not exist between trematode sporocysts in oysters from either the east or Gulf coasts and any other parasite or pathology. The frequency of significant results, 21 of 89, is significantly greater than expected by chance (binomial test, $p = 0.04$, $q = 0.96$; $P < 0.0001$). Of these, ten were positive correlations,

Table 3. Continued.

Bivalve group	Variable 1	Variable 2	Positive correlation	Negative correlation
West-coast mytilids	Prokaryotic inclusion	Major pathology		0.001
	Prokaryotic inclusion	Tissue pathology		0.04
	Prokaryotic inclusion	Body gregarine		0.003
	Prokaryotic inclusion	Mantle gregarine		0.03
	Prokaryotic inclusion	Trematode metacercariae		0.003
	Major pathology	Body gregarine		0.05
	Major pathology	Mantle gregarine		0.01
	Major pathology	Trematode metacercariae		0.002
	Major pathology	Ceroid bodies		0.007
	Trematode sporocyst	Mantle gregarine		0.05
	Body gregarine	Gill ciliate		0.0007
	Gill gregarine	Gill ciliate		0.02
	Gill gregarine	Gut ciliate		0.03
	Mantle gregarine	Gill ciliate		0.0001
	Mantle gregarine	Gut ciliate		0.01
	Trematode metacercariae	Gill ciliate		0.05
	Mantle gregarine	Trematode metacercariae		0.05
	Body gregarine	Gill gregarine	0.0001	
	Mantle gregarine	Gill gregarine	0.0009	

including three for the pairwise comparisons among the gregarines, a frequency not unexpected by chance. The frequency of positive correlations among all significant correlations, after excluding the gregarines, seven of 18, is also likely by chance (binomial test at $p = q = 0.50$; $P > 0.05$). Thus, negative correlations occurred more often in oysters from the Gulf coast, but not significantly more often than positive correlations.

Nineteen significant correlations occurred in west-coast mytilids, including those between both gill and gut ciliates and the gregarines, between mantle gregarines and trematode metacercariae, and between prokaryotic inclusions and the gregarines and trematode metacercariae. Major pathologies were significantly negatively correlated with prokaryotic inclusions, several groups of gregarines, and trematode metacercariae (Table 3). The frequency of occurrence of significant results, 19 of 64, is greater than expected by chance (binomial test, $p = 0.05$, $q = 0.95$; $P < 0.0001$). Of these all were negative, except those between the gregarines, a result unlikely to occur by chance (binomial test, $p = q = 0.50$; $P < 0.0001$). Thus, like east-coast oysters, significant relationships between parasite, pathology, and parasite/pathology pairs were very common and significantly more likely to be negative.

The Gulf and east coasts offer very different oyster habitats. Some oyster parasites are unique to one of the two coasts. The same is true of the east and west coast mytilids, to which can be added the difference in species that occur on the two coasts. Consequently, one might not expect to find equivalent relationships between parasite, pathology, or parasite-pathology pairs on multiple coasts. Nevertheless, several relationships did occur on multiple coasts. Both east and west coast mytilids showed a negative association between prokaryotic inclusions and trematode metacercariae. Both oysters from the Gulf and west coast mytilids demonstrated negative correlations between gill gregarines and gut ciliates, and between mantle gregarines and gut ciliates.

Infection Intensity.—Significant relationships in infection intensity between parasite, pathology, and parasite/pathology pairs occurred much less frequently than for prevalence (Table 4). This was true on all coasts and for all taxa. In addition, unlike prevalence, significant positive correlations occurred more frequently than significant negative correlations. The ratio between positive and negative correlations, all coasts combined, 10:3, is an unlikely outcome by chance (binomial test, $p = q = 0.50$; $P < 0.05$).

No significant correlations between parasites, pathologies, or parasite/pathology pairs were found for east-coast mytilids (Table 4). Four significant correlations occurred for east-coast oysters, three positive and one negative. Positive correlations were found between both body and mantle gregarines and *P. marinus*. A negative correlation occurred between gut ciliates and gill gregarines. Unlike for prevalence, significant relationships did not occur for prokaryotic inclusions, *H. nelsoni*, or cestodes in east-coast oysters. The frequency of occurrence of significant differences, four in 54, is greater than expected by chance (binomial test, $p = 0.03$, $q = 0.97$; $P < 0.05$). The split between positive and negative correlations, 3:1, may have occurred by chance ($P > 0.05$).

Significant positive correlations for infection intensity occurred in Gulf-coast oysters between gill gregarines and *P. marinus* and between gill gregarines and tissue pathologies. Both were also true for prevalence. However, unlike prevalence, no significant relationships with major pathologies were obtained. A significant negative association occurred between body gregarines and gut ciliates. Unlike prevalence, however, no significant correlations existed between cestodes and nematodes in oysters from the Gulf coast. The frequency of occurrence of significant correlations, four of 66, is no greater than expected by chance (binomial test, $p = 0.05$, $q = 0.95$; $P > 0.05$). The distribution of positive and negative correlations, 3:1, likewise could have occurred by chance.

With the exception of body and gill gregarines, no significant correlations were found in mytilids from the west coast between different parasite types, whereas

Table 4. Parasite, pathology, and parasite/pathology pairs yielding significant correlations ($\alpha = 0.05$) for infection intensity using the Spearman's Rank correlation test.

Bivalve group	Variable 1	Variable 2	Positive correlation	Negative correlation
Gulf-coast oysters	Body gregarine	Gut ciliate		0.01
	Tissue pathology	Gill gregarine	0.02	
	Perkinsus marinus	Gill gregarine	0.01	
	Cestode	Ceroid bodies	0.05	
East-coast oysters	Gill gregarine	Gut ciliate		0.03
	Body gregarine	Mantle gregarine	0.0004	
	Body gregarine	*Perkinsus marinus*	0.02	
	Mantle gregarine	*Perkinsus marinus*	0.03	
West-coast mytilids	Major pathology	Body gregarine		0.04
	Digestive gland atrophy	Major pathology	0.004	
	Digestive gland atrophy	Tissue pathology	0.03	
	Body gregarine	Gill gregarine	0.004	
	Body gregarine	Ceroid bodies	0.0001	

prevalence produced a number of significant correlations between parasite pairs. Major pathologies were negatively correlated with body gregarines, as was also found with prevalence. Digestive gland atrophy was positively associated with both types of pathologies. A significant positive correlation existed between body gregarines and ceroid bodies (Table 4). The frequency of occurrence of significant correlations, five of 25, is much greater than expected by chance (binomial test, $p = 0.04$, $q = 0.96$; $P < 0.0001$). However, the ratio of negative to positive correlations, 1:4, may have occurred by chance ($P > 0.05$).

In no case did the same significant correlation in infection intensity between parasite, pathology, or parasite/pathology pair occur on more than one coast.

Correlations within West-Coast Mussel Taxa.—Because several mussel taxa were collected on the west coast, significant correlations might have been produced by trends only in one taxon or by common trends among taxa. On the west coast, *M. californianus* was more commonly taken in the south (viz., southern California), whereas *M. trossulus* and *M. galloprovincialis* were more commonly taken in the north (viz., Oregon to Alaska). However, sufficient sampling intensity existed to compare *M. californianus* with the remaining combined mytilid taxa for only a few parasite, pathology, and parasite/pathology pairs.

Prevalences of body and mantle gregarines were negatively correlated with gill ciliates in both *M. californianus* and the *M. edulis* complex (Table 5). In other cases, significant correlations in prevalence were present in one taxon, but not the other. Prevalence of gill gregarines was negatively correlated with prevalence of gill ciliates only in the *M. edulis* complex. A significant negative correlation between the prevalences of prokaryotic inclusions and major pathologies and between the prevalences of prokaryotic inclusions and trematode metacercariae occurred only in *M. californianus*, as did a negative association between the prevalence of tissue pathologies and gill ciliates and between the prevalence of prokaryotic inclusions and gregarines in body and mantle tissue. Prevalences of gregarines in body and gill were positively correlated with that of major pathologies in the *M. edulis* complex but not in *M. californianus*, whereas prevalences of gill ciliates and trematode metacercariae were negatively correlated with major pathologies only in *M. californianus*.

The frequency of significant correlations in *M. californianus*, 11 of 56, is significantly greater than expected by chance (binomial test, $p = 0.05$, $q = 0.95$; $P < 0.0001$). For the *M. edulis* complex, the frequency of significant correlations, six of 52, is also greater than expected by chance (binomial test, $p = 0.05$, $q = 0.95$; $P < 0.02$).

The number of pairwise comparisons was severely restricted for infection intensity. Of the few possible pairwise comparisons, none was significant for the *M. edulis* complex. For *M. californianus*, two of 17 were significant, a frequency not significantly different from chance.

Correlations within Southeast-Coast Oysters.—On the east coast, Cape Hatteras is a well-known provincial boundary and, as a consequence of an expected change in distributional pattern for parasites across this boundary, an additional set of analyses was conducted focused on east-coast oysters from Cape Hatteras south. In this more circumscribed region, as in Gulf-coast oysters, a significant positive correlation existed between the prevalence of gregarines and *P. marinus* (Table 6) and between the prevalence of the three gregarine categories. Negative correlations included ones for nematodes with gut ciliates, for *H. nelsoni* with gill gregarines, and for *H. nelsoni* with nematodes. Of the 85 correlations conducted, 10 were signifi-

Table 5. Parasite, pathology, and parasite/pathology pairs yielding significant correlations (α = 0.05) for the two mytilid taxa on the west coast, *Mytilus californianus* and the *Mytilus edulis* complex, for prevalence and infection intensity using the Spearman's Rank correlation test.

Bivalve group	Variable 1	Variable 2	Positive correlation	Negative correlation
M. californianus				
Prevalence	Major pathology	Prokaryotic inclusion		0.004
	Major pathology	Gill ciliate		0.008
	Major pathology	Trematode metacercariae		0.05
	Tissue pathology	Gill ciliate		0.02
	Body gregarine	Gill ciliate		0.006
	Mantle gregarine	Gill ciliate		0.006
	Body gregarine	Prokaryotic inclusion		0.005
	Mantle gregarine	Prokaryotic inclusion		0.01
	Trematode metacercariae	Prokaryotic inclusion		0.004
	Body gregarine	Gill gregarine	0.0001	
	Mantle gregarine	Gill gregarine	0.03	
Infection intensity	Gill gregraine	Digestive gland atrophy		0.04
	Body gregarine	Gill gregarine	0.001	
M. edulis complex				
Prevalence	Gill ciliate	Body gregarine		0.003
	Gill ciliate	Gill gregarine		0.0007
	Gill ciliate	Mantle gregarine		0.007
	Major pathology	Gill gregarine	0.01	
	Major pathology	Body gregarine	0.02	
	Gill gregarine	Mantle gregarine	0.05	

cant; a frequency much greater than expected by chance (binomial test, $p = 0.05$, $q = 0.95$; $P < 0.005$). Four correlations were negative, six positive, a ratio not significantly different from chance. Infection intensity yielded three significant correlations. The frequency, three of 32, is unlikely to be found by chance (binomial test, $p = 0.01$, $q = 0.99$; $P < 0.0001$). All were positive, an unlikely event (binomial test, $p = q = 0.50$; $P < 0.05$).

Discussion

Prevalence.—Prevalences of pathologies, parasites, and pathology/parasite pairs in sentinel bivalves were significantly correlated at a much greater frequency than anticipated by chance in all taxa and on all coasts. Most of these correlations were negative. In fact, the frequency of negative correlations was greater than the frequency of positive correlations in all but the east-coast oysters restricted to the Carolinian Province (Cape Hatteras south). Significant correlations were common in east- and Gulf-coast oysters and both mussel taxa on the west coast. East-coast mytilids did not produce many correlations between parasites/pathologies, nor did dreissenids. For mytilids on the east coast, only two relationships were recognized in prevalence, both negative, between prokaryotic inclusions and trematode metacercariae and between trematode sporocysts and trematode metacercariae. Dreissenids had a limited number of parasites despite the variety of parasites in dreissenids in their home range (Kinkelin et al., 1968; Wallet and Lambert, 1986; Bowmer et al.,

Table 6. Parasite, pathology, and parasite/pathology pairs yielding significant correlations (α = 0.05) for east-coast oysters from sites south Cape Hatteras for prevalence and infection intensity using the Spearman's Rank correlation test.

Bivalve group	Variable 1	Variable 2	Positive correlation	Negative correlation
Prevalence	Tissue pathology	Prokaryotic inclusion		0.05
	Gill gregarine	*Haplosporidium nelsoni*		0.03
	Nematode	*Haplosporidium nelsoni*		0.006
	Nematode	Gut ciliate		0.04
	Body gregarine	Gill gregarine	0.0007	
	Body gregarine	Mantle gregarine	0.0001	
	Body gregarine	*Perkinsus marinus*	0.004	
	Gill gregarine	*Perkinsus marinus*	0.003	
	Gill gregarine	Mantle gregarine	0.006	
	Mantle gregarine	*Perkinsus marinus*	0.009	
Infection intensity	Body gregarine	Mantle gregarine	0.01	
	Body gregarine	*Perkinsus marinus*	0.01	
	Mantle gregarine	*Perkinsus marinus*	0.005	

1991; Karatayev et al., 2000, 2002), probably due to their recent introduction into the U.S. (Hebert et al., 1989; May and Marsden, 1992). The few significant relationships in east-coast mytilids are not similarly explained, as these animals were parasitized by a range of organisms and commonly so in some cases (Table 1). Interestingly, no pathologic conditions produced significant correlations with other biological variables in east-coast mytilids even though such correlations were relatively common in west-coast mytilids.

The simplest explanation for the infrequent occurrence of positive correlations is that two conditions, parasites and/or pathologies, usually respond dissimilarly to environmental trends. Most parasites respond to temperature and salinity as typical estuarine/marine organisms do (e.g., Jordan, 1995; Cook et al., 1998; Harvell et al., 2002). The relationship of pathologies to the same environmental variables is less clear; some, such as hemocytic infiltration, may have multiple causes, whereas others may be linked to specific diseases (e.g., Peters, 1998; Figueras et al., 1991; Kim and Powell, 2004). Nevertheless, the expectation that positive correlations in prevalence should occur as a consequence of similar environmental requirements is surprisingly unfulfilled. The few positive correlations are dominated by co-occurring prevalences of the gregarines in body, mantle, and gill tissue. As these may be taxonomically identical organisms, this co-occurrence is not unanticipated. The only protozoan-metazoan pair showing a positive association was gill gregarines and cestodes in oysters, interestingly from both the east and Gulf coasts. The only other noteworthy positive correlation occurred between *P. marinus* and the gregarines, but only in the Gulf and southeast. Both are extremely common in Gulf- and southeast-coast oysters and are distributed in a similar way within the estuarine salinity gradient.

Why negative correlations should be so common, by comparison, is less clear, but three possibilities bear examination. (1) If provincial boundaries or climatic clines were responsible, in that two parasites trended oppositely with latitude for example or were differentially distributed about a provincial boundary, one would anticipate a greater equivalency between positive and negative correlations. In the one obvious test, we removed oyster sites north of Cape Hatteras, a well-known provincial

boundary, and retested just the southern sites. Although some negative correlations were thereby removed, others remained, most notably those between the nematodes and gut ciliates, the nematodes and *H. nelsoni*, and the gill gregarines and *H. nelsoni*. Thus, the explanation for negative correlations would appear to be more complex than simple obverse latitudinal trends. (2) Local environmental variability may differentially affect parasites and the complexity of local variability might minimize the chance that two parasites would behave similarly over larger spatial scales, particularly for prevalence where multiple hosts or complex transmission routes play an important role. In this way, the frequency of negative correlations might be enhanced. Craig et al. (1989), for example, did not find a significant correlation between salinity and *P. marinus* in Gulf-coast oysters from Mussel Watch collections probably because bay-wide average prevalences were controlled by factors other than the within-bay salinity gradient (Powell et al., 1992; Wilson et al., 1992; Kim and Powell, 1998). Kesting and Zander (2000) found that local conditions influence the parasite fauna of the Baltic at least as much as the salinity gradient. Soniat et al. (1998) showed that *P. marinus* prevalence and infection intensity were manifestations of the multi-year time-history of environmental change, not just responsive to conditions at or near the time of sampling. Thus, a more complex relationship with local environmental variability and the time-history of environmental change cannot be discounted as the source of negative correlations. (3) The final alternative is a negative interaction between parasites whereby one interferes with the establishment of the other in the host. Such interactions are not commonly reported among bivalve parasites. Nevertheless, these analyses suggest that further investigation of such interactions might be fruitful.

Where significant, major pathologies, neoplasms, gonad abnormalities, and the like, were consistently negatively correlated with parasites. This was true in oysters and mussels. As contaminant exposure is implicated in some of these pathological conditions (e.g., Hinton et al., 1992; Weis et al., 1995; Landsberg, 1996), a negative impact of contaminant exposure on some components of the parasitic fauna might be inferred.

Surprisingly few significant correlations occurred with hemocytic infiltration, often associated with the occurrence of some parasites and diseases (e.g., Bower et al., 1999; Choi et al., 2002; Kim and Powell, 2004). Two were positive, in Gulf-coast oysters infected with gill gregarines and cestodes, as might be expected. Two, however, were negative, with gut ciliates in Gulf-coast oysters and prokaryotic inclusions in west-coast mytilids.

Infection Intensity.—Fewer potential correlations could be tested for infection intensity because all double-zero and single-zero prevalence pairs were necessarily excluded and this reduced data density considerably. Nevertheless, surprisingly few significant correlations were observed and, of these, the vast majority was positive. The rarity of significant relationships in infection intensity certainly accrues from the rarity of positive correlations in prevalence. Negative correlations predominated for prevalence and these would only under unusual circumstances be expected to yield a positive correlation with infection intensity, at least for those parasites such as *P. marinus*, the ciliates, the prokaryotes, and the invasive trematodes that proliferate after infection. That such parasites did not yield negative correlations with infection intensity reinforces the distinctiveness of the proliferation and transmission

processes that void the cavalier use of weighted prevalence that confounds the two. Weighted prevalence has not been analyzed as a consequence in this study.

The few significant positive correlations, however, correspond closely with the significant positive correlations in prevalence. These instances are dominated by the gregarines and *P. marinus*, and thus may be manifestations of the underlying association of both parasites with the salinity gradient. An interesting exception is the negative correlation between gut ciliates and the gregarines that occur in oysters on both the east and Gulf coasts. Noteworthy correlations also occur on the west coast between major pathologies and digestive gland atrophy, as digestive gland morphology is responsive to environmental stress in bivalves (Axiak et al., 1988; Hinton et al., 1992; Gold-Bouchot et al., 1995; Da Ros et al., 1998).

The three putative gregarine groups, differentiated by tissue location, consistently gave significant positive correlations among themselves for prevalence; yet only two cases exist for infection intensity, in east-coast oysters and in West-coast mytilids. As gregarines were not observed in east-coast mussels, a total of nine possible correlations exist among the east- and Gulf-coast oysters and west-coast mussels. Both frequencies of occurrence of significant correlations, eight of nine for prevalence and two of nine for infection intensity, diverge from chance (binomial test, $p = 0.05$, $q = 0.95$; $P < 0.01$, $P < 0.05$, respectively). The paucity of significant correlations in infection intensity suggests that some taxonomic distinctiveness exists between these gregarine categories, as suggested by Sprague (1949) and Sprague and Orr (1952), or at least that the progression of infection differs manifestly between tissue types.

Trends Among Taxa and Between Coasts.—Only a few relationships between parasites and pathologies were common to more than one coast. These included negative associations between prevalences of prokaryotic inclusions and trematode metacercariae in east- and west-coast mytilids, and negative correlations between prevalences of gill and mantle gregarines with gut ciliates in oysters from the Gulf coast and mytilids from the west coast. Positive relationships for prevalences among the gregarines were common to east-coast oysters, Gulf-coast oysters and, west-coast mytilids. Gill gregarines and cestodes were positively correlated in east- and Gulf-coast oysters. When the analysis of east-coast oysters was restricted to Cape Hatteras south, a few additional common trends on both coasts were obtained, particularly between *P. marinus* and the gregarines. No commonalities were present for infection intensity among host taxa, for any parasite, pathology, or parasite/pathology pair.

Overall, correlations between parasites and pathologies in the same bivalve taxon from different coasts occurred infrequently, suggesting that similar parasitic taxa from different coasts may respond differently to environmental conditions or that parasitic taxa may be inherently different in their interactions with each other. Infrequent occurrences between taxa on different coasts might be anticipated and this anticipation was met. However, though few, the common findings between mussels and oysters suggest potentially important trends among major parasite groups, particularly the gregarines and gut ciliates, gill gregarines and cestodes, and *P. marinus* and the gregarines. It is noteworthy that not a single common occurrence involved a pathology.

In east-coast oysters, *H. nelsoni*, a parasite restricted to the east coast, accounted for a substantial fraction of all significant negative correlations in prevalence. *Haplosporidium nelsoni* is a dominant disease-causing organism in the mid-Atlantic region

(Ford and Tripp, 1996) and becomes less influential further south (e.g., Crosby and Roberts, 1990). Restricting analysis to east-coast oyster sites south of Cape Hatteras continued to document many of these correlations, however. Negative correlations included ones for *H. nelsoni* with gill gregarines and gill ciliates. As gills have been considered as an initial site of infection for *H. nelsoni* (Ford et al., 1999; Powell et al., 1999b), the negative correlations suggest that the presence of gill parasites might discourage infection, or vice versa.

Surprisingly, no relationships were found between parasites/pathologies and *P. marinus* prevalence in oysters from the east coast, although they were common occurrences for Gulf oysters, particularly with the gregarines and nematodes. Restricting analysis to latitudes south of Cape Hatteras revealed that *P. marinus* prevalence was correlated with other parasites on the southeast coast of the U.S., as in the Gulf. Thus, the relationship between *P. marinus* and other parasites was different for the northern oyster sites on the east coast. Possibly, this is due to the time of collection as *P. marinus* infection intensity is low during the winter and false negatives from the thioglycollate assay are therefore common occurrences at this time (e.g., Choi et al., 1989; Hofmann et al., 1995; Robledo et al., 1998).

Gauthier et al. (1990) reported a positive association between *P. marinus* and the gregarines in oysters from the Louisiana coast of the Gulf of Mexico. In this study, the majority of positive relationships between parasites in Gulf-coast oysters, exclusive of those among the gregarine categories themselves, were also positive associations between *P. marinus* and the gregarines, suggesting that the presence of either parasite taxon may influence the susceptibility of the host to the other or that both, being high salinity-high temperature parasites, are following very similar environmental cues.

The positive association between tissue pathologies and cestodes in Gulf-coast oysters was expected as larval cestode infections in oysters elicit host cellular reactions (Cheng, 1966). Kim et al. (1998) reported that weighted prevalences of digestive tract ciliates were negatively associated with cestodes in Gulf-coast oysters. The same relationship was found in prevalence between the two parasites from the same region in this study. Mackin (1951) noted that ceroid bodies increased in number as *P. marinus* proliferates. Stein and Mackin (1955) also reported significantly more ceroid bodies in oysters heavily infected by *P. marinus* than in uninfected or lightly infected oysters. This study, however, did not find a positive association between infection intensity of *P. marinus* and the abundance of ceroid bodies in Gulf-coast oysters.

Caveats and Retrospections.—Excluding the Great Lakes sites, the Status and Trends Mussel Watch Program samples during the winter months. The seasonal cycle of many of these parasites, if one exists, is unknown, but some parasites, such as *H. nelsoni* and *P. marinus*, are strongly influenced by temperature change. Thus, the results of the comparisons investigated here may be biased to some unknown degree by the time of collection. Nevertheless, some interesting geographic patterns are apparent. Of these, the infrequency of significant correlations in east-coast mytilids is perhaps the most noteworthy; oysters in general and mytilids on the west coast demonstrated many more significant correlations. Why parasitic taxa so rarely demonstrate significant interactions in east-coast mytilids is unknown. Correlations in prevalence are overwhelmingly negative regardless of bivalve taxon or geographic region, suggesting that further investigation into the interaction of certain parasite taxa might be advantageous. Correlations in infection intensity are much

less frequent than for prevalence and this reinforces the belief that environmental factors controlling transmission are likely distinct from those controlling proliferation. It is noteworthy that the cases of significant correlations in infection intensity are overwhelmingly associated with parasites that do not proliferate after infection. Finally, common relationships between bivalve taxa or geographic regions were infrequent, as perhaps might be expected. However, the few that did occur, including those between the gregarines and gut ciliates, between gill gregarines and cestodes, and between *P. marinus* and the gregarines, point to common processes of infection between taxa and regions that bear further investigation.

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Appendix 1. Assignments into bay groups, and information on study site, bivalve taxa, and frequency of sampling for this study.

					Sample year			
Bay group	Site code	Site name	State	Taxon code*	1995	1996	1997	1998
1	GBBS	Green Bay, Bayshore Park	WI	DR		X		X
2	LMMB	Lake Michigan, Milwaukee Bay	WI	DR		X		X
	LMNC	Lake Michigan, North Chicago	IL	DR		X		X
	LMCB	Lake Michigan, Calumet Breakwater	IL	DR				X
3	LMHB	Lake Michigan, Holland Breakwater	MI	DR		X		X
	LMMU	Lake Michigan, Muskegon	MI	DR		X		X
4	TBLL	Traverse Bay, Leelanau State Park	MI	DR		X		X
5	LHTB	Lake Huron, Thunder Bay	MI	DR		X		X
	SBSP	Saginaw Bay, Sandpoint	MI	DR	X	X		X
	SBSR	Saginaw Bay, Saginaw River	MI	DR	X	X		X
	LHBR	Lake Huron, Black River Canal	MI	DR	X	X		X
6	LESP	Lake Erie, Stony Point	MI	DR	X		X	
	LERB	Lake Erie, Reno Beach	OH	DR	X		X	
	SBPP	Lake Erie, Peach Orchard Pt.	OH	DR	X		X	
	LEOW	Lake Erie, Old Woman Creek	OH	DR	X	X	X	
	LELR	Lake Erie, Lorain	OH	DR	X		X	
7	LEAB	Lake Erie, Ashtabula	OH	DR	X		X	
	LEDK	Lake Erie, Dunkirk	NY	DR	X		X	
8	NRNF	Niagara River, Niagara Falls	NY	DR	X			
9	LOOC	Lake Ontario, Olcott	NY	DR	X		X	
	LORC	Lake Ontario, Rochester	NY	DR	X		X	
10	LOOS	Lake Ontario, Oswego	NY	DR	X		X	
	LOCV	Lake Ontario, Cape Vincent	NY	DR	X		X	
11	HRCI	Hudson River, Cruger Island	NY	DR	X		X	
12	PBPI	Penobscot Bay, Pickering Island	ME	ME	X		X	
	PBSI	Penobscot Bay, Sears Island	ME	ME	X		X	
13	MSSP	Merriconeag Sound, Stover Point	ME	ME	X		X	
14	CAKP	Cape Arundel, Kennebunkport	ME	ME	X		X	
15	GBDP	Great Bay, Dover Point	NH	ME			X	
16	CAGH	Cape Ann, Gap Head	MA	ME	X		X	
17	SHFP	Salem Harbor, Folger Point	MA	ME	X		X	
	MBNB	Massachusetts Bay, Nahant Bay	MA	ME	X		X	
18	BHDI	Boston Harbor, Deer Island	MA	ME	X		X	
	BHDB	Boston Harbor, Dorchester Bay	MA	ME	X		X	
	BHHB	Boston Harbor, Hingham Bay	MA	ME	X		X	
	BHBI	Boston Harbor, Brewster Island	MA	ME	X		X	
19	MBNR	Massachusetts Bay, North River	MA	ME	X		X	
20	DBCI	Duxbury Bay, Clarks Island	MA	ME	X		X	
21	CCNH	Cape Cod, Nauset Harbor	MA	ME	X		X	
22	BBCC	Buzzards Bay, Cape Cod Canal	MA	ME		X		X
	BBWF	Buzzards Bay, West Falmouth	MA	ME		X		X
	BBNI	Buzzards Bay, Naushon Island	MA	ME		X		X
	BBGN	Buzzards Bay, Goosebury Neck	MA	ME		X		X
	BBRH	Buzzards Bay, Round Hill	MA	ME		X		X
	BBAR	Buzzards Bay, Angelica Rock	MA	ME		X		X

Appendix 1. Continued.

Bay group	Site code	Site name	State	Taxon code*	Sample year			
					1995	1996	1997	1998
23	NBDI	Narragansett Bay, Dyer Island	RI	ME	X		X	
	NBPI	Narragansett Bay, Patience Island	RI	ME	X	X	X	
	NBDU	Narragansett Bay, Dutch Island	RI	ME	X	X	X	
24	BIBI	Block Island Sound, Block Island	RI	ME	X	X	X	
25	LICR	Long Island Sound, Connecticut River	CT	ME		X		X
26	LINH	Long Island Sound, New Haven	CT	ME		X		X
	LIHR	Long Island Sound, Housatonic River	CT	ME		X		X
27	LISI	Long Island Sound, Sheffield Island	CT	ME		X		X
	LIMR	Long Island Sound, Mamaroneck	NY	ME		X		X
	LITN	Long Island Sound, Throgs Neck	NY	ME		X		X
	LIHH	Long Island Sound, Hempstead Harbor	NY	ME		X		X
	LIHU	Long Island Sound, Huntington Harbor	NY	ME		X		X
28	LIPJ	Long Island Sound, Port Jefferson	NY	ME		X		X
29	LIGB	Long Island, Gardiners Bay	NY	ME		X		X
30	MBTH	Moriches Bay, Tuthill Point	NY	ME		X		X
31	LIFI	Long Island, Fire Island Inlet	NY	ME		X		X
	LIJI	Long Island, Jones Inlet	NY	ME		X		X
32	HRJB	Hudson/Raritan Estuary, Jamaica Bay	NY	ME	X		X	
	HRUB	Hudson/Raritan Estuary, Upper Bay	NY	ME	X			
	HRLB	Hudson/Raritan Estuary, Lower Bay	NY	ME	X		X	
	HRRB	Hudson/Raritan Estuary, Raritan Bay	NJ	ME	X		X	
33	NYSH	New York Bight, Sandy Hook	NJ	ME	X		X	
	NYLB	New York Bight, Long Branch	NJ	ME	X		X	
	NYSR	New York Bight, Shark River	NJ	ME	X		X	
34	BIBL	Barnegat Inlet, Barnegat Light	NJ	ME		X		X
35	AIAC	Absecon Inlet, Atlantic City	NJ	ME		X		X
36	DBCM	Delaware Bay, Cape May	NJ	ME	X	X		X
	DBCH	Delaware Bay, Cape Henlopen	DE	ME	X	X		X
37	LIHO	Long Island Sound, Housatonic River	CT	CV				X
38	LIPO	Long Island Sound, Port Jefferson	NY	CV				X
39	DBFE	Delaware Bay, False Egg Island Point	NJ	CV		X		X
	DBBD	Delaware Bay, Ben Davis Pt. Shoal	NJ	CV	X	X		X
40	DBAP	Delaware Bay, Arnolds Point Shoal	NJ	CV		X		X
	DBKI	Delaware Bay, Kelly Island	DE	CV		X		X
41	CBBO	Chesapeake Bay, Bodkin Point	MD	CV	X		X	
	CBMP	Chesapeake Bay, Mountain Point Bar	MD	CV	X			
	CBHP	Chesapeake Bay, Hackett Point Bar	MD	CV	X		X	
42	CBCP	Chesapeake Bay, Choptank River	MD	CV	X		X	
	CBHG	Chesapeake Bay, Hog Point	MD	CV			X	
43	PRSP	Potomac River, Swan Point	MD	CV			X	
	PRMC	Potomac River, Mattox Creek	VA	CV	X		X	
	PRRP	Potomac River, Ragged Point	VA	CV	X		X	
44	RRRR	Rappahannock River, Ross Rock	VA	CV	X		X	
45	CBDP	Chesapeake Bay, Dandy Point	VA	CV	X		X	
	CBJR	Chesapeake Bay, James River	VA	CV	X		X	

Appendix 1. Continued.

Bay group	Site code	Site name	State	Taxon code*	Sample year 1995	1996	1997	1998
46	CBCC	Chesapeake Bay, Cape Charles	VA	CV	X		X	
47	QIUB	Quinby Inlet, Upshur Bay	VA	CV	X	X		X
	CBCI	Chincoteague Bay, Chincoteague Inlet	VA	CV	X	X		X
48	RSJC	Roanoke Sound, John Creek	NC	CV	X			
	PSCH	Pamlico Sound, Cape Hatteras	NC	CV	X	X		X
	PSWB	Pamlico Sound, Wysocking Bay	NC	CV	X			
49	PSPR	Pamlico Sound, Pungo River	NC	CV	X			
	PSNR	Pamlico Sound, Neuse River	NC	CV	X		X	
50	BIPI	Beaufort Inlet, Pivers Island	NC	CV		X		X
51	CFBI	Cape Fear, Battery Island	NC	CV	X	X		X
52	WBLB	Winyah Bay, Lower Bay	SC	CV		X		X
	SRNB	Santee River, North Bay	SC	CV	X	X		X
53	CHFJ	Charleston Harbor, Fort Johnson	SC	CV		X		X
	CHSF	Charleston Harbor, Shutes Folly Island	SC	CV		X		X
54	SRTI	Savannah River Estuary, Tybee Island	GA	CV	X		X	
55	SSSI	Sapelo Sound, Sapelo Island	GA	CV	X		X	
	ARWI	Altamaha River, Wolf Island	GA	CV	X		X	
56	SJCB	St. Johns River, Chicopit Bay	FL	CV	X		X	
57	MRCB	Matanzas River, Crescent Beach	FL	CV	X		X	
58	IRSR	Indian River, Sebastian River	FL	CV	X		X	
59	NMML	North Miami, Maule Lake	FL	CV	X		X	
	BBGC	Biscayne Bay, Goulds Canal	FL	CV	X		X	
60	BHKF	Florida Keys, Bahia Honda	FL	CS		X		X
61	FBJB	Florida Bay, Joe Bay	FL	CV	X	X	X	
	FBFO	Florida Bay, Flamingo	FL	CV	X	X	X	X
62	PRBB	Puerto Rico, Bahia de Boqueron	PR	CR		X		X
	PRBM	Puerto Rico, Bahia Montalva	PR	CR				X
	PRBJ	Puerto Rico, Bahia de Jobos	PR	CR		X		X
63	EVFU	Everglades, Faka Union Bay	FL	CV	X	X		X
64	RBHC	Rookery Bay, Henderson Creek	FL	CV		X		X
	NBNB	Naples Bay, Naples Bay	FL	CV	X	X		X
65	CBBI	Charlotte Harbor, Bird Island	FL	CV	X		X	
	CBFM	Charlotte Harbor, Fort Myers	FL	CV	X		X	
66	TBCB	Tampa Bay, Cockroach Bay	FL	CV		X		X
	TBHB	Tampa Bay, Hillsborough Bay	FL	CV		X		X
	TBKA	Tampa Bay, Peter O. Knight Airport	FL	CV		X		X
	TBOT	Tampa Bay, Old Tampa Bay	FL	CV		X		X
	TBPB	Tampa Bay, Papys Bayou	FL	CV		X		X
	TBMK	Tampa Bay, Mullet Key Bayou	FL	CV		X		X
	TBNP	Tampa Bay, Navarez Park	FL	CV		X		X
67	CKBP	Cedar Key, Black Point	FL	CV	X		X	
68	AESP	Apalachee Bay, Spring Creek	FL	CV	X		X	
69	APCP	Apalachicola Bay, Cat Point Bar	FL	CV	X		X	
	APDB	Apalachicola Bay, Dry Bar	FL	CV	X		X	
70	SAWB	St. Andrews Bay, Watson Bayou	FL	CV	X		X	

Appendix 1. Continued.

Bay group	Site code	Site name	State	Taxon code*	Sample year			
					1995	1996	1997	1998
	PCMP	Panama City, Municipal Pier	FL	CV	X		X	
	PCLO	Panama City, Little Oyster Bar	FL	CV	X		X	
71	CBSR	Choctawhatchee Bay, Off Santa Rosa	FL	CV	X	X	X	X
	CBJB	Choctawhatchee Bay, Joe's Bayou	FL	CV		X	X	X
	CBBL	Choctawhatchee Bay, Ben's Lake	FL	CV		X		
	CBPP	Choctawhatchee Bay, Postil Point	FL	CV		X	X	X
	CBBB	Choctawhatchee Bay, Boggy Bayou	FL	CV		X		
72	PBSP	Pensacola Bay, Sabine Point	FL	CV		X		X
	PBIB	Pensacola Bay, Indian Bayou	FL	CV				X
	PBPH	Pensacola Bay, Public Harbor	FL	CV		X		X
73	MBDR	Mobile Bay, Dog River	AL	CV		X		X
	MBHI	Mobile Bay, Hollingers Island	AL	CV		X		X
	MBCP	Mobile Bay, Cedar Point Reef	AL	CV		X		X
74	MSPB	Mississippi Sound, Pascagoula Bay	MS	CV		X		X
	MSBB	Mississippi Sound, Biloxi Bay	MS	CV	X			X
	MSPC	Mississippi Sound, Pass Christian	MS	CV		X		X
75	LPNO	Lake Pontchartrain, New Orleans	LA	CV	X	X		X
	LBGO	Lake Borgne, Gulf Outlet	LA	CV	X	X		X
	LBMP	Lake Borgne, Malheureux Point	LA	CV	X	X		X
76	BSBG	Breton Sound, Bay Gardene	LA	CV	X	X		X
	BSSI	Breton Sound, Sable Island	LA	CV		X		X
77	MRPL	Mississippi River, Pass A Loutre	LA	CV		X		X
78	MRTP	Mississippi River, Tiger Pass	LA	CV		X		X
79	BBMB	Barataria Bay, Middle Bank	LA	CV	X		X	
	BBSD	Barataria Bay, Bayou Saint Denis	LA	CV	X		X	
80	TBLF	Terrebonne Bay, Lake Felicity	LA	CV		X		X
	TBLB	Terrebonne Bay, Lake Barre	LA	CV		X		X
81	CLCL	Caillou Lake, Caillou Lake	LA	CV	X		X	
	ABOB	Atchafalaya Bay, Oyster Bayou	LA	CV	X		X	
82	VBSP	Vermilion Bay, Southwest Pass	LA	CV	X		X	
83	JHJH	Joseph Harbor Bayou, Joseph Harbor Bayou	LA	CV	X		X	
84	CLLC	Calcasieu Lake, Lake Charles	LA	CV		X		X
	CLSJ	Calcasieu Lake, St. Johns Island	LA	CV	X	X		X
85	SLBB	Sabine Lake, Blue Buck Point	LA	CV	X		X	
86	GBHR	Galveston Bay, Hanna Reef	TX	CV	X		X	
	GBYC	Galveston Bay, Yacht Club	TX	CV	X		X	
	GBTD	Galveston Bay, Todd's Dump	TX	CV	X		X	
	GBOB	Galveston Bay, Offatts Bayou	TX	CV	X		X	
	GBCR	Galveston Bay, Confederate Reef	TX	CV	X		X	
87	BRFS	Brazos River, Freeport Surfside	TX	CV	X		X	
	BRCL	Brazos River, Cedar Lakes	TX	CV	X		X	
88	MBEM	Matagorda Bay, East Matagorda	TX	CV	X		X	
89	MBTP	Matagorda Bay, Tres Palacios Bay	TX	CV	X		X	
	MBCB	Matagorda Bay, Carancahua Bay	TX	CV	X		X	

Appendix 1. Continued.

Bay group	Site code	Site name	State	Taxon code*	Sample year 1995	1996	1997	1998
	MBLR	Matagorda Bay, Lavaca River Mouth	TX	CV	X		X	
	MBGP	Matagorda Bay, Gallinipper Point	TX	CV	X		X	
	ESBD	Espiritu Santo, Bill Days Reef	TX	CV		X		X
90	ESSP	Espiritu Santo, South Pass Reef	TX	CV		X		
	SAMP	San Antonio Bay, Mosquito Point	TX	CV	X	X		
	SAPP	San Antonio Bay, Panther Point Reef	TX	CV		X		
91	MBAR	Mesquite Bay, Ayres Reef	TX	CV	X		X	
	CBCR	Copano Bay, Copano Reef	TX	CV	X		X	
	ABLR	Aransas Bay, Long Reef	TX	CV	X		X	
92	CCNB	Corpus Christi, Nueces Bay	TX	CV	X		X	
	CCBH	Corpus Christi, Boat Harbor	TX	CV	X		X	
93	LMAC	Lower Laguna Madre, Arroyo Colorado	TX	CV		X		X
	LMPI	Lower Laguna Madre, Port Isabel	TX	CV	X	X		X
	LMSB	Lower Laguna Madre, South Bay	TX	CV	X	X		X
94	IBNJ	Imperial Beach, North Jetty	CA	MC	X		X	
	PLLH	Point Loma, Lighthouse	CA	MC	X		X	
	SDCB	San Diego Bay, Coronado Bridge	CA	MT	X		X	
	SDHI	San Diego Bay, Harbor Island	CA	MT	X		X	
95	MBVB	Mission Bay, Ventura Bridge	CA	MT	X		X	
	LJLJ	La Jolla, Point La Jolla	CA	MC	X		X	
96	OSBJ	Oceanside, Municipal Beach Jetty	CA	MC	X		X	
97	SCBR	Santa Catalina Island, Bird Rock	CA	MC		X		X
98	NBWJ	Newport Beach, West Jetty	CA	MC		X		X
	ABWJ	Anaheim Bay, West Jetty	CA	MC	X	X		X
	LBBW	Long Beach, Breakwater	CA	MC		X		X
	SPFP	San Pedro Harbor, Fishing Pier	CA	MT		X		X
	PVRP	Palos Verdes, Royal Palms State Park	CA	MC	X	X		X
99	RBMJ	Redondo Beach, Municipal Jetty	CA	MC		X		X
	MDSJ	Marina Del Rey, South Jetty	CA	MT	X	X		X
	TBSM	Las Tunas Beach, Santa Monica Bay	CA	MC		X		X
	PDPD	Point Dume, Point Dume	CA	MC	X	X		X
100	SCFP	Santa Cruz Island, Fraser Point	CA	MC		X		X
101	SBSB	Point Santa Barbara, Point Santa Barbara	CA	MC		X		X
102	PCPC	Point Conception, Point Conception	CA	MC		X		X
103	SLSL	San Luis Obispo Bay, Point San Luis	CA	MC	X	X		X
	SSSS	San Simeon Point, San Simeon Point	CA	MC		X		X
104	PGLP	Pacific Grove, Lovers Point	CA	MC	X		X	X
	MBML	Monterey Bay, Moss Landing	CA	MC	X		X	X
	MBES	Monterey Bay, Elkhorn Slough	CA	MC	X		X	X
	MBSC	Monterey Bay, Point Santa Cruz	CA	MC	X		X	X
105	SFDB	San Francisco Bay, Dumbarton Bridge	CA	MT	X		X	X
	SFSM	San Francisco Bay, San Mateo Bridge	CA	MT	X		X	X
	SFEM	San Francisco Bay, Emeryville	CA	MT	X		X	X
106	TBSR	Tomales Bay, Spenger's Residence	CA	MT	X		X	X

Appendix 1. Continued.

Bay group	Site code	Site name	State	Taxon code*	Sample year 1995	1996	1997	1998
	BBBE	Bodega Bay, Bodega Bay Entrance	CA	MC	X		X	X
107	PALH	Point Arena, Lighthouse	CA	MC	X		X	X
	PDSC	Point Delgada, Shelter Cove	CA	MC	X		X	X
108	HMBJ	Eureka, Humboldt Bay Jetty	CA	MC	X		X	
	EUSB	Eureka, Samoa Bridge	CA	MC	X		X	
109	SGSG	Crescent, Point St. George	CA	MC	X		X	
110	CBCH	Coos Bay, Coos Head	OR	MC		X		X
	CBRP	Coos Bay, Russell Point	OR	MT	X	X		X
111	YBOP	Yaquina Bay, Oneatta Point	OR	MT	X		X	
	YHFC	Yaquina Bay, Fogarty Creek	OR	MC	X		X	
112	TBHP	Tillamook Bay, Hobsonville Point	OR	MT	X		X	
113	CRSJ	Columbia River, South Jetty	OR	MT	X		X	
114	WBNA	Willapa Bay, Nahcotta	WA	MT				X
	GHWJ	Grays Harbor, Westport Jetty	WA	MC	X	X		X
115	JFCF	Strait of Juan de Fuca, Cape Flattery	WA	MC		X		X
116	PSPA	Puget Sound, Port Angeles	WA	MT		X		X
	PSPT	Puget Sound, Port Townsend	WA	MT		X		X
117	PSHC	Puget Sound, Hood Canal	WA	MT	X	X		X
118	SSBI	South Puget Sound, Budd Inlet	WA	MT	X	X		X
	CBTP	Commencement Bay, Tahlequah Point	WA	MT		X		X
	PSSS	Puget Sound, South Seattle	WA	MT		X		
119	SIWP	Sinclair Inlet, Waterman Point	WA	MT		X		X
120	EBDH	Elliott Bay, Duwamish Head	WA	MT		X		X
	EBFR	Elliott Bay, Four-Mile Rock	WA	MT		X		X
121	WIPP	Whidbey Island, Possession Point	WA	MT	X	X		X
	PSEH	Puget Sound, Everett Harbor	WA	MT		X		X
122	BBSM	Bellingham Bay, Squalicum Marina Jetty	WA	MT	X	X		X
	PRPR	Point Roberts, Point Roberts	WA	MT				X
123	KTMP	Ketchikan, Mountain Point	AK	MT	X		X	
	NBES	Nahku Bay, East Side	AK	MT	X		X	
124	PWSH	Prince William Sound, Sheep Bay	AK	MT	X			
	PWKH	Prince William Sound, Knowles Head	AK	MT	X			
	PVMC	Port Valdez, Mineral Creek Flats	AK	MT	X		X	
	UISB	Unakwit Inlet, Siwash Bay	AK	MT	X		X	
	PWDI	Prince William Sound, Disk Island	AK	MT	X			
	GASL	Prince William Sound, Sleepy Bay	AK	MT	X			
125	CIHS	Cook Inlet, Homer Spit	AK	MT	X		X	
	GAWB	Gulf of Alaska, Windy Bay	AK	MT	X			
	GASH	Gulf of Alaska, Shuyak Harbor	AK	MT	X			
126	BPBP	Barbers Point, Barbers Point Harbor	HI	DS				X
	HHKL	Honolulu Harbor, Keehi Lagoon	HI	DS		X		X
	HHKB	Hawaii, Kaneohe Bay	HI	CG		X		X

*DR, *Dreissena* spp.; DS, *Dendostrea sandvichensis;* MC, *Mytilus californianus;* MT, *Mytilus edulis, Mytilus galloprovincialis, Mytilus trossulus,* and hybrids; ME, *Mytilus edulis;* CG, *Crassostrea gigas;* CR, *Crassostrea rhizophorae;* CS, *Chama sinuosa;* CV, *Crassostrea virginica.*