

Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions

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Abstract

Invasions by non-indigenous species (NIS) are recognized as important stressors of many communities throughout the world. Here, we evaluated available data on the role of NIS in marine and estuarine communities and their interactions with other anthropogenic stressors, using an intensive analysis of the Chesapeake Bay region as a case study. First, we reviewed the reported ecological impacts of 196 species that occur in tidal waters of the bay, including species that are known invaders as well as some that are cryptogenic (i.e., of uncertain origin). Second, we compared the impacts reported in and out of the bay region for the same 54 species of plants and fish from this group that regularly occur in the region's tidal waters. Third, we assessed the evidence for interaction in the distribution or performance of these 54 plant and fish species within the bay and other stressors. Of the 196 known and possible NIS, 39 (20%) were thought to have some significant impact on a resident population, community, habitat, or process within the bay region. However, quantitative data on impacts were found for only 12 of the 39, representing 31% of this group and 6% of all 196 species surveyed. The patterns of reported impacts in the bay for plants and fish were nearly identical: 29% were reported to have significant impacts, but quantitative impact data existed for only 7% (4/54) of these species. In contrast, 74% of the same species were reported to have significant impacts outside of the bay, and some quantitative impact data were found for 44% (24/54) of them. Although it appears that 20% of the plant and fish species in our analysis may have significant impacts in the bay region based upon impacts measured elsewhere, we suggest that studies outside the region cannot reliably predict such impacts. We surmise that quantitative impact measures for individual bays or estuaries generally exist for <5% of the NIS present, and many of these measures are not particularly informative. Despite the increasing knowledge of marine invasions at many sites, it is evident that we understand little about the full extent and variety of the impacts they create—singly and cumulatively. Given the multiple anthropogenic stressors that overlap with NIS in estuaries, we predict NIS–stressor interactions play an important role in the pattern and impact of invasions.

Non-indigenous species (NIS) are increasingly conspicuous in marine, and especially estuarine, communities as their number and impacts continue to accumulate. Marine NIS are reported for most geographic regions of the world, and the total number of these species known for some sites or regions underscores the scale and potential ecological significance of these invasions (e.g., Por 1978; Pollard and Hutchings 1990; Hutchings 1992; Boudouresque et al. 1994; Cohen and Carlton 1996; Eno 1996). For example, as many as 230 NIS have been documented for a single estuary, and about 400 NIS are known to be established in marine and estuarine habitats of the continental U.S. (Cohen and Carlton

1998; Ruiz et al. 1997). These are only minimum estimates for the extent of NIS invasions, since many NIS will never be recognized as such (Carlton 1996a; Geller 1996). Furthermore, contemporary surveys of NIS are very incomplete, and the rate of new invasions seems to be increasing for many of the best-studied sites (Mills et al. 1993; Ruiz et al. in press; Cohen and Carlton 1998).

It is evident that NIS invasions are a significant stressor and force of change in marine communities. Various recent studies have measured effects associated with invasions by plants, fish, crabs, snails, clams, mussels, bryozoans, and nudibranchs (e.g., Race 1982; Brenchley and Carlton 1983; Bertness 1984; Partridge 1987; Allmon and Sebens 1988; Goss-Custard and Moser 1988; Posey 1988; Lambert et al. 1992; Posey et al. 1993; Roberts et al. 1995; Cloern 1996; Grosholz et al. in press). Although these studies provide illustrative examples of some quantified impacts, many additional invaders are believed to have significant impacts based on a broad range of qualitative to quantitative criteria (e.g., see Mills et al. 1993, 1996; Cohen and Carlton 1996; Ruiz et al. in press). Analyses of invasion impacts (as above) have not, however, produced a framework with which to characterize and evaluate impact type, data quality, magnitude of impacts, or spatial and temporal extent of impacts. As a result, the evidence and nature of NIS impacts for particular sites are often unclear.

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Interactions between NIS and other anthropogenic stressors may greatly influence colonization and distribution patterns as well as the effects of marine invaders. Estuaries, bays, and other sheltered coastal regions are frequent sites of marine invasions, probably as a result of the relatively high rate of human-mediated transfer compared to exposed coastal habitats. These sheltered coastal regions experience a broad spectrum of anthropogenic disturbances or stressors that overlap and interact with invasion processes. Estuaries are often centers of human activities that release chemical pollutants (e.g., heavy metals, hydrocarbons, chlorine, nutrients), modify thermal environment and habitat characteristics, deplete fishery stocks, increase sedimentation, and increase anoxia (e.g., Kennish 1992; Cooper and Brush 1991, 1993; Rothschild et al. 1994; Cornwell et al. 1996; Nixon 1997). These and other stressors may have a strong influence on invasions, modifying opportunities to invade as well as the subsequent effects. For example, numerous studies demonstrate that physical disturbances allow colonization and persistence by locally rare species (*see* Sousa 1984; Pickett and White 1985). Furthermore, episodic or chronic disturbance is thought to facilitate invasion by NIS (e.g., Crawley 1986; Fox and Fox 1986; Moyle 1986; Mills et al. 1993; Carlton 1996b), resulting especially from reduced competition or predation (e.g., Robinson and Dickerson 1984; Case 1990, 1996; Baltz and Moyle 1993). Anthropogenic change can provide or cancel a requisite condition for invasion, but many complex interactions may also exist in which anthropogenic stressors influence the probability of establishment and the characteristics of invasions.

In this paper, we review and characterize the ecological impacts reported for NIS in Chesapeake Bay and evaluate evidence for the interaction of NIS with other stressors in the bay and elsewhere. More specifically, we have classified the quality of existing data for impacts according to impact type (e.g., competition, predation, bioturbation) and information type (e.g., qualitative to various quantitative measures). Because significant spatial variation may occur for both impact type and magnitude (e.g., Grosholz and Ruiz 1996), we have analyzed data from Chesapeake Bay and other regions separately to be explicit about geographic sources of information. Although we discuss the magnitude of some impacts, we did not attempt to classify impact magnitude (including both spatial scale and severity), which is the topic of a separate paper (Ruiz et al. in prep.). Finally, we have reviewed the present state of knowledge about interactions between NIS and other stressors, using examples from Chesapeake Bay and elsewhere.

Methods

Data sources and classifications—We used existing data to evaluate the known role of NIS invasions as stressors in Chesapeake Bay. We compiled information for 196 species that may have invaded the Chesapeake region in the past four centuries, based upon published literature as well as unpublished reports, dissertations, long-term data, and observations (Ruiz et al. in press). The resulting database includes species that occur within tidal waters of the Chesapeake Bay region, including the outer coast from Assateague, Maryland, to the border of North Carolina. We classified these species according to residence and invasion status. Residence status distinguishes regular residents from occasional ones (i.e. those species that are usually found outside of our boundaries, such as some freshwater fish and terrestrial plants, but which occasionally occur within the tidal waters or littoral zone of the bay). Invasion status characterizes the degree of certainty that a species is non-indigenous. Each species was assigned to one of three categories: definite, probable, or possible. Strong evidence suggests that the definite and probable species were introduced to the region by human activities. In contrast, the status of many other species as native or introduced remains ambiguous. Here, these species were classified as possible invaders (i.e., cryptogenic species as defined by Carlton 1996a).

There are hundreds of cryptogenic species in the bay (Fononoff et al. unpubl. data), but we have included only a small fraction of these for which the best data exist. For example, the emergent plant *Typha angustifolia* (narrow-leaved cattail) and invasive populations of *Phragmites australis* (common reed) are widely thought to be non-indigenous to North America, although some uncertainty exists (Marks et al. 1994; Stuckey and Salamon 1987; Stuckey 1993; *also* Fononoff et al. unpubl.). Species that are classified as possible invaders are clearly designated as such (C—cryptogenic) in our tables.

Analysis of NIS invasions as stressors—We analyzed the role of NIS as stressors in two ways, using the database described above. First, we placed all species into one of three categories for ecological impact: probable impact, possible impact, and impact not evaluated. Assignment was based solely on whether an impact within tidal waters of the bay was reported as probable or possible in the literature. For those species with a reported probable impact, we further classified the impact by impact type and information type (*see below*). Second, using a subset of these data, we compared the impacts reported within and outside of the bay region. For species of vascular plants (hereafter plants) and fish in our database, we classified the reported impacts of all 54 regular residents by impact type and information type, distinguishing results within vs. outside of the region. Occasional residents were excluded from the second analysis, as they were not reported to have significant impacts in the tidal waters of the bay (*see results*).

We selected plants and fish for the most comprehensive analysis of impacts (as above), since they contributed the most species to the database and it was not manageable to perform this fine-grained analysis for all 196 species. Furthermore, the quantity and quality of information available for these two taxa are relatively high, beginning with surveys and observations from the early 1800s and including many ecological studies during the past decades to century. Furthermore, invasions by plants and fish are often reported to have significant impacts in invaded communities (e.g., Smith 1907; Taylor et al. 1984; Posey 1988; Carter and Rybicki 1994). Plants and fish perhaps offer exceptional opportunities to measure or observe impacts, compared to many planktonic and benthic invertebrates, because of their con-

spicuous size and the feasibility of manipulative experiments (e.g., Carpenter and Kitchell 1988; Power 1990). We therefore surmise that analysis of fish and plants provides a view of the best available impact data for Chesapeake Bay and elsewhere and includes taxa that are among the most likely to have significant, detectable impacts.

For both analyses, we included available information on categorical abundance (e.g., rare, common, abundant) in each source region, as indicated in the literature. This was used to test for relationships between abundance and impact. Although densities were preferable, they were often not available, and comparisons of absolute densities across taxa (e.g., fish, plants, etc.) are perhaps of little value.

Impact type—For each species selected as above, we assigned the reported ecological impact(s) to one of nine different categories or impact types: competition, habitat change, food-prey, predation, herbivory, hybridization, parasitism, toxicity or bioturbation. We defined ecological impacts as significant and measurable changes in the abundance or distribution of resident species or habitats. Therefore, interactions that were not shown or considered to significantly affect resident populations or communities, ecological processes, or habitats were omitted as impacts. For example, a number of introduced plant and fish species are known to hybridize with native species in Chesapeake Bay (e.g., *T. angustifolia*, *Mentha* spp., *Lycopus europaeus*, *Lepomis* spp., and *Morone saxatilis* × *chrysops*), but the frequency of these hybrids seems to be low (Harrell et al. 1993; Harvill et al. 1992; Jenkins and Burkhead 1993), suggesting that the effects of genetic introgression on abundance are negligible. Furthermore, diet analyses that indicated an introduced predator ate resident species was not considered sufficient evidence of significant impacts without further assessment of population-level effects on the prey population.

Our analyses of impacts distinguishes explicitly the source region of information. The first analysis includes only impacts reported within the bay, and the second analysis identifies impact information as either Chesapeake Bay or “other” for direct comparison.

We have not attempted to characterize information on the magnitude, areal extent, and temporal variation of impacts. With few exceptions, there simply were insufficient data to analyze these attributes. Instead, we have provided information on magnitude and temporal variation where available.

Information type—To clearly indicate empirical data that underlie the impact(s) described for each species, we classified the method used to measure or assess each impact type. These methods included seven categories of information type, which range from qualitative observations to various quantitative measures: 0—no information; 1—qualitative observations, observed change on some temporal or spatial scale that corresponds with an invasion (but without quantitative measure); 2—presence-absence comparisons, quantified differences between invaded and non-invaded areas in space or time; 3—quantitative correlations, quantified relationship(s) between invader density and impact; 4—mechanistic, autecological measures, estimated impact based

upon quantified rate process; 5—controlled experiments, laboratory or field experiments that employ controls to quantify impact; 6—before-after-control-impact or BACI measures, any one of a series of designs that may deploy multiple control sites, and possibly including time-series approaches, to estimate impact at one or more sites (e.g., Underwood 1994; Stewart-Oaten 1996).

Thus, for each species and impact type, we indicated the existing information types. Where multiple information types existed, all were indicated; if no information was available for a particular impact type, we entered a zero.

The methods yielding these information types differ in the inferences that can be drawn from them. Each method provides insights into the dynamics of invasions and can be used to test hypotheses about patterns and effects. However, the methods differ in their capacity to discern cause-effect relationships among the many changes or events that correspond in space and time with an invasion. The stringency of criteria that must be met, and our confidence in the likelihood of causal relationships, increases generally in descending order among methods 1 through 5 or 6 (above). The quality of information is most limited for the first three methods, as they are usually not designed a priori to measure invasion impacts and have no control treatment(s) to discount the role of other independent variables. This limitation is of particular concern given the number of confounding factors that may covary with observed changes, especially in estuarine environments where invasions are frequent and conditions are highly variable. The last three methods are usually designed to explicitly test for specific impacts. Although still lacking a control treatment, mechanistic measures estimate rate functions that underlie potential impacts (e.g., measurement of feeding rates or functional responses, diet characteristics, and seasonal abundance of predators to estimate an impact). The final two methods employ control sites or treatments to account for changes due to natural (or non-invasion-related) variation, providing the strongest inference about impacts. (See Diamond 1986; see also Schmitt and Osenberg 1996 and chapters therein.)

Although our classification of most methods was clear-cut, there were some additional criteria. For competition, qualitative evidence included listing as weeds (plants) or invasive species, or occurrence of significant overlap on food and habitat use, indicated either verbally or by numerical indices. Experimental demonstration of impacts was considered to require realistic population densities in a reasonably natural setting. As a result, experiments showing only that species A ate species B in a laboratory setting were considered to be qualitative evidence. Most data on impacts of introduced fish came not from invaded areas but rather from areas within their native ranges (Mississippi and Great Lakes Basin) and were classified as data from outside the Chesapeake region.

Interaction of invasions with other stressors—To evaluate interactions between NIS and other anthropogenic stressors, we used two approaches. We analyzed all information for species in our database (as above) for reported interactions with other stressors. Almost all available information consisted of qualitative observations of association between NIS

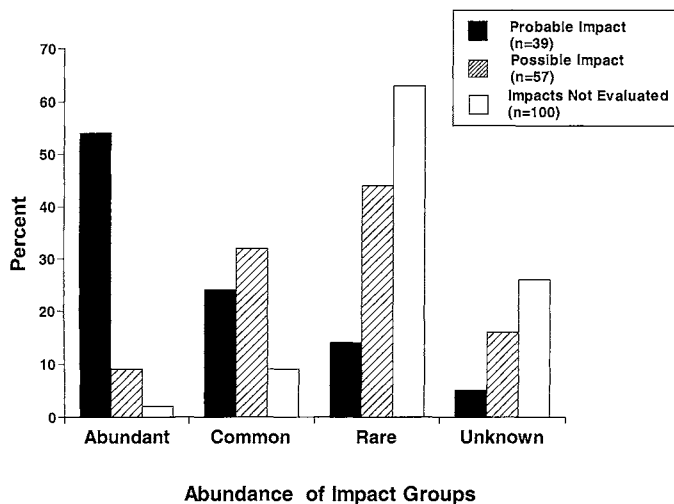


Fig. 1. Relative abundance of introduced species in Chesapeake Bay according to impact status. Classification was based on literature reports of probable or possible ecological impacts in the bay. Species lacking such reports were classified as impact not evaluated. (Note: Some cryptogenic species are included in this analysis; explanation given in text.)

and various disturbances. To present this information, we categorized reported associations for the plants and fish (in our second analysis, as above) as follows: *N*—no information; *U*—relatively undisturbed; *A*—agricultural; *C*—urban-suburban (near lawns, roadsides, developed waterfront); *E*—eutrophication; *I*—wetland modifications; *S*—physically disturbed substrata. In addition, we reviewed the few cases with additional support for interactions between NIS and other stressors in the bay region.

Results

Overall patterns of invasions as stressors in Chesapeake Bay—Of the 196 known and possible NIS in our analysis, 39 species (20%) were thought to have some significant ecological impact in the Chesapeake Bay region (Fig. 1, Table 1). For most of them (51% of the total 196), we found no information on potential ecological impacts in the region; another 29% were considered to have a possible impact, for which little evidence existed. The perceived impacts of these 196 species, as reported in the literature, were associated with abundance. Specifically, more of the 39 species with probable impacts were considered abundant in Chesapeake Bay than were all of the other species combined (Fig. 1; $21/39$ vs. $7/157$; $\chi^2 = 68.33$, $P < 0.001$).

For the 39 species considered to have probable impacts, the reported frequencies of impact types among species were: competition—69%; habitat change—38%; food-prey—44%; predation—15%; herbivory—21%; hybridization—8%; parasitism—8%; toxicity—0%; bioturbation—3%. Two species, the rat (*Rattus norvegicus*) and mute swan (*Cygnus olor*), were believed to have probable impacts in the region based on observations elsewhere, but no specific information was provided on impact type; thus, these species

were characterized with zeros in each impact type and are not included in the frequencies above.

Although it appears that these NIS may have significant impacts in Chesapeake Bay, there were relatively few quantitative data with which to evaluate the reported impacts of NIS in the bay (Table 1, Fig. 2). Our analysis found that data of information type 2 or greater (in any impact type) existed for only 31% of those 39 species classified as having probable impacts. Most of the quantitative data were correlative or presence-absence comparisons. Six of the 39 species (15%) were classified as cryptogenic, so their invasion status is presently unconfirmed. Thus, even including those cryptogenic species in our database, quantitative data to test for impacts was found for 6% of the 196 we surveyed.

Plants and fish represented the largest taxonomic groups, 23% and 18% of those species considered to have probable impacts (Fig. 3). No other taxonomic group (i.e., phyla, or class of vertebrates) contributed more than 10% to the total. Below, we review the evidence of impacts for a few species, both to provide examples where impacts may be most severe and to illustrate some of the limitations in existing data. We do not include plants and fish here, as these are examined intensively later.

The impacts of introduced pathogens seem to have resulted in significant, widespread, and complex changes throughout the bay. The two protistan pathogens *Haplosporidium nelsoni* and *Perkinsus marinus*, classified respectively as a probable and a possible introduction, have been a significant factor in the decline in abundance of the oyster *Crassostrea virginica* (e.g., Andrews 1979; Kennedy 1996; see Lauckner 1983; Sindermann 1990). In Chesapeake Bay, oyster abundance has declined >90% in the past century. These two pathogens have been a primary, and often dominant, source of mortality for oysters in the bay and elsewhere in the mid-Atlantic region since the 1950s. This relationship is clear, based upon detailed studies of pathology and field surveys of the prevalence and intensity of infection. The dynamics of host and pathogen populations suggest that these pathogens now limit the oyster population of the bay, although other factors may interact with them (see below). Furthermore, the demise of oysters has apparently resulted in many indirect effects through reduction of the physical structure of oysters as habitat and the significant role of oysters in both benthic and planktonic food webs.

In contrast, despite its high prevalence and severe effects on individual hosts, ecological impacts of the parasitic barnacle *Loxothylacus panopaei* remain surprisingly unclear. This parasite was introduced from the U.S. Gulf Coast in the 1960s and has spread throughout much of Chesapeake Bay, where it infects and castrates multiple species of mud crabs. The prevalence of this parasite can exceed 70% for local populations, resulting in reproductive death for the infected individuals (Van Engel et al. 1966; Grosholz and Ruiz 1995; Hines et al. 1997). Nonetheless, it is not clear whether this high level of individual mortality has a significant effect on the host population. Of the crabs with high prevalences, *Rhithropanopeus harrissii* remains one of the most abundant crabs in the bay. There are some refuge habitats for these crabs where *L. panopaei* is not found (see below), and the relationships between reproductive stock and larval recruit-

Table 1. Ecological impacts reported among all taxa in Chesapeake Bay. For each species considered to have a significant impact in the bay, the evidence of impacts (information type) is indicated numerically for each impact type: A—competition; B—habitat change; C—food-prey; D—predation; E—herbivory; F—hybridization; G—parasitism; H—bioturbation. Impact summary indicates of the highest numerical score for information type across all impact types by species. Reported abundance is shown by category (rare, common, abundant). Species marked “C” are considered cryptogenic (i.e., possibly introduced) in the bay. Information types: 0—no information; 1—qualitative observations; 2—presence-absence comparison; 3—quantitative correlation; 4—inference from mechanistic, autecological study; 5—controlled experiments; 6—BACI, before-after control vs. invaded comparisons.

Species	Impact summary	A	B	C	D	E	F	G	H	Abundance	References*
Phylum Haplosporidia											
<i>Haplosporidium nelsoni</i>	4	2	1	0	0	0	0	4	0	abundant	1, 2, 3, 4, 5, 6
Phylum Apicomplexa											
<i>Perkinsus marinus</i> (C)	4	2	1	0	0	0	0	4	0	abundant	6, 7, 8, 9, 10, 11
Phylum Angiospermophyta											
<i>Alternanthera philoxeroides</i>	1	1	0	0	0	0	0	0	0	rare	12, 13
<i>Hydrilla verticillata</i>	5	1	5	2	0	0	0	0	0	abundant	14, 15, 16, 17, 18, 19, 20, 21, 22
<i>Iris pseudacorus</i>	3	3	1	1	0	0	0	0	0	common	23
<i>Lythrum salicaria</i>	1	1	0	1	0	0	0	0	0	common	24, 25
<i>Murdannia keisak</i>	1	1	0	1	0	0	0	0	0	abundant	13, 26
<i>Myriophyllum spicatum</i>	3	1	1	3	0	0	0	0	0	abundant	16, 19, 20, 22, 27, 28, 29, 30
<i>Phragmites australis</i> (C)	3	3	1	1	0	0	0	0	0	abundant	31, 32, 33, 34
<i>Trapa natans</i>	1	1	1	1	0	0	0	0	0	rare (now)	16, 20, 30, 35
<i>Typha angustifolia</i> (C)	1	1	0	1	0	0	1	0	0	abundant	31, 33, 36
Phylum Cnidaria											
<i>Cordylophora caspia</i>	5	5	5	1	1	0	0	0	0	abundant	37, 38, 39
<i>Garveia franciscana</i>	1	1	1	1	0	0	0	0	0	abundant	40, 41, 42
<i>Nematostella vectensis</i> (C)	5	0	0	1	5	0	0	0	0	unknown	43
Phylum Bryozoa											
<i>Victorella pavidia</i> (C)	1	1	1	1	0	0	0	0	0	abundant	39, 41, 42, 44
Phylum Mollusca											
<i>Bithynia tentaculata</i>	1	1	0	1	0	0	0	0	0	common	45
<i>Corbicula fluminea</i>	4	2	2	2	0	4	0	0	0	abundant	20, 26, 46, 47, 48, 49
<i>Ischadium recurvum</i> (C)	1	1	0	0	0	0	0	0	0	abundant	50, 51, 52
<i>Rangia cuneata</i>	1	0	1	1	0	0	0	0	0	abundant	53, 54, 55
Phylum Crustacea											
<i>Loxothylacus panopaei</i>	1	0	0	0	0	0	0	1	0	abundant	56, 57, 58
<i>Orconectes virilis</i>	1	1	0	0	0	0	0	0	0	abundant	59, 60, 61
Phylum Hexapoda, Class Insecta											
<i>Galerucella calmariensis</i>	1	0	0	0	0	1	0	0	0	rare	25
<i>Galerucella pusilla</i>	1	0	0	0	0	1	0	0	0	rare	25
<i>Hylobius transversovittatus</i>	1	0	0	0	0	1	0	0	0	rare	25
Phylum Chordata, Class Ascidiacea											
<i>Botryllus schlosseri</i>	1	1	0	1	0	0	0	0	0	common	62
Phylum Chordata, Class Osteichthyes											
<i>Cyprinus carpio</i>	1	0	0	0	0	1	0	0	1	abundant	30, 63, 64, 65
<i>Dorosoma petenense</i>	1	0	0	1	0	0	0	0	0	common	65
<i>Ictalurus punctatus</i>	1	1	0	0	1	0	0	0	0	common	65, 66, 67
<i>Lepomis macrochirus</i>	1	1	0	0	1	0	0	0	0	abundant	65, 67, 68, 69
<i>Micropterus dolomieu</i>	1	1	0	0	1	0	0	0	0	rare	65, 70, 71, 72
<i>Micropterus salmoides</i>	1	1	0	0	1	0	0	0	0	common	15, 63, 65, 73
<i>Morone saxatilis</i> × <i>chrysops</i>	1	0	0	0	0	0	1†	0	0	rare	74

Table 1. Continued.

Species	Impact summary	A	B	C	D	E	F	G	H	Abundance	References*
Phylum Chordata, Class Aves											
<i>Anas platyrhynchos</i>	1	1	0	0	0	0	1	0	0	abundant	26, 75, 76, 77, 78
<i>Branta canadensis</i>	1	1	1	0	0	0	0	0	0	common	78, 79, 80
<i>Cygnus olor</i>	0	0	0	0	0	0	0	0	0	common	78
Phylum chordata, Class Mammalia											
<i>Cervus nippon</i>	3	3	0	0	0	1	0	0	0	abundant	81, 82
<i>Equus caballus</i>	5	0	2	0	0	5	0	0	0	rare	82, 83
<i>Myocastor coypus</i>	5	1	5	0	0	5	0	0	0	abundant	36, 84, 85, 86
<i>Rattus norvegicus</i>	0	0	0	0	0	0	0	0	0	abundant	80, 87, 88

* 1—Wood and Andrews 162; 2—Ford and Tripp 1996; 3—Andrews 1982; 4—Andrews 1984; 5—Barber et al. 1988; 6—Kennedy 1996; 7—Andrews and Hewatt 1957; 8—Andrews 1967; 9—Burrenson and Ragone Calvo 1996; 10—Kennedy et al. 1995; 11—Paynter 1996; 12—Massey 1957; 13—Va. Dep. of Conservation and Recreation <http://www.hort.vt.edu.vnps.invasive.html>; 14—Carter and Rybicki 1986; 15—Killgore et al. 1989; 16—Hurley 1990; 17—Carter and Rybicki 1994; 18—Posey et al. 1993; 19—Thorp et al. 1997; 20—Perry and Deller 1996; 21—Rybicki et al. 1997; 22—Wigand et al. 1997; 23—Thomas 1980; 24—Guerrero abstr.; 25—Swearingen pers. comm.; 26—Perry 1981; 27—Bean et al. 1973; 28—Bayley et al. 1978; 29—Bayley et al. 1968; 30—Stevenson and Confer 1978; 31—Brown and Brown 1984; 32—Marks et al. 1994; 33—Havens et al. 1997; 34—Allstock et al. abstr.; 35—U.S. Army Corps of Engineers 1977; 36—Willner et al. 1979; 37—Bibbins 1892; 38—Von Holle and Ruiz abstr.; 39—Von Holle unpubl. data; 40—Cory 1967; 41—Abbe 1987; 42—Thompson 1993; 43—Posey and Hines 1991; 44—Ruiz et al. unpubl. data; 45—Hamilton 1979; 46—Cohen et al. 1984; 47—Clarke 1986; 48—Diaz 1994; 49—Phelps 1994; 50—Beaven 1947; 51—Andrews unpubl.; 52—Shaw 1967; 53—Cain 1972; 54—Ebersole and Kennedy 1994; 55—Everett unpubl. data; 56—Daugherty 1969; 57—Grosholz and Ruiz 1995; 58—Hines et al. 1997; 59—Schwartz et al. 1963; 60—Odell and Grimm 1966; 61—Norden pers. comm; 62—Otsuka and Dauer 1982; 63—Hildebrand and Schroeder 1928; 64—Chamberlain 1948; 65—Jenkins and Burkhead 1993; 66—Menzel 1943; 67—McGovern and Olney 1988; 68—Flemer and Woolcott 1966; 69—Johnson and Dropkin 1992; 70—Smith 1907; 71—Ferguson 1877; 72—Pavol and Davis 1982; 73—Fewlass 1980; 74—Harrell et al. 1993; 75—Stewart and Robbins 1958; 76—Johnsgard and DiSilvestro 1976; 77—Krementz et al. 1992; 78—Robbins and Blom 1996; 79—Checklist Committee 1979; 80—White 1989; 81—Feldhamer and Armstrong 1993; 82—Keiper 1990; 83—Walthers and Rebach abstr.; 84—Reshetiloff 1994; 85—Haramis and Colona <http://www.pwrc.usgvs.gov.haramis2shtm>; 86—Haramis pers. comm.; 87—Bailey 1946; 88—Paradiso 1969.

† A probable reduction in importance due to recent changes in hybrid releases.

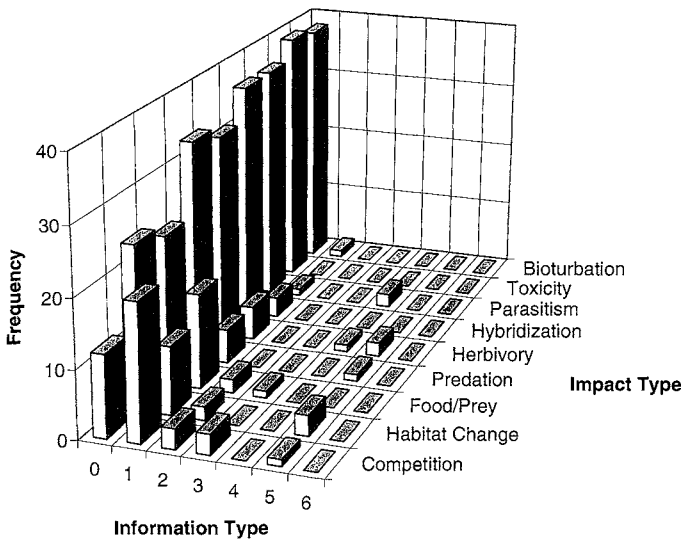


Fig. 2. Ecological impacts reported in Chesapeake Bay for those species considered to have significant effects (i.e., the 39 species classified as having a probable impact in Fig. 1). Shown is frequency of information types that underlie reported effects by impact type. Information types: 0—no information; 1—qualitative observations; 2—presence-absence comparison; 3—quantitative correlation; 4—inference from mechanistic, autecological study; 5—controlled experiments; 6—BACI, before-after control vs. invaded comparisons. (Additional explanation given in Table 1 and text.)

ment have not been assessed. If there is a strong stock-recruitment correlation, it would support population-level effects of *L. panopaei*; if this relationship is weak, parasitism may have little effect on the host population (see Kuris and Lafferty 1992; Lafferty and Kuris 1996).

For many of the free-living species in Table 1 with some quantitative data, the evidence for significant impacts on some spatial scale is relatively strong. Based on estimates of biomass and filtration rates, it was suggested that the Asian clam *Corbicula fluminea* could clear all phytoplankton from one stretch of the Potomac River every 3–4 d (Cohen et al. 1984). The arrival of these clams, which can represent 90% or more of the bivalve biomass at some Chesapeake localities, has also been associated with a variety of changes in water clarity, aquatic vegetation, benthic community composition, and sediment characteristics. Experimental exclusion of feral horses (*Equus caballus*) and nutria (*Myocaster coypus*) has resulted in a significant increase of plant biomass in marshes, relative to control sites (Keiper 1990; Haramis and Colona <http://www.pwrc.usgs.gov.haram2shtm>; Haramis pers. comm.). In addition, experimental inoculation of substrates with the hydroid *Cordylophora caspia* significantly altered the abundances of multiple invertebrate species compared to control substrates (Von Holle and Ruiz unpubl. data).

An unusual case for evaluating impacts existed for the anemone *Nematostella vectensis*. Controlled field experiments found a significant reduction in the density of spionid polychaetes in the presence of this anemone, and laboratory observations demonstrated predation by the anemone on spionid larvae (Posey and Hines 1991). However, further

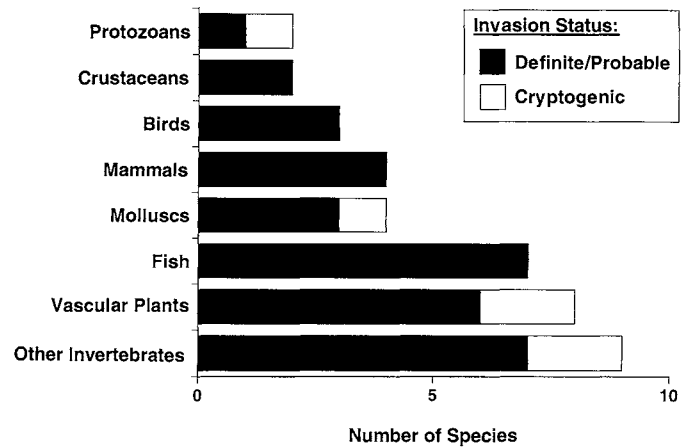


Fig. 3. Taxonomic distribution of introduced species considered to have significant ecological impact in Chesapeake Bay (i.e., the 39 species classified as having a probable impact in Fig. 1). The contribution of cryptogenic species to the total is indicated by unshaded portion of each bar.

experiments demonstrated that grass shrimp are significant predators on *N. vectensis* and can significantly reduce the abundance of this anemone, which seems to be abundant rarely in Chesapeake Bay. Thus, despite a complex experimental analysis which demonstrates possible impacts, such impacts may not occur in the field.

Although impact information is limited to qualitative data (i.e., information type 1) for over half of the 39 species in Table 1, additional quantitative impact data exist for some of these species outside of the Chesapeake region. Examples include the clam *Rangia cuneata*, the ascidian *Botryllus schlosseri*, the crayfish *Orconectes virilis*, the swan *C. olor*, the sika deer *Cervus nippon*, as well as the three insects (*Galerucella californiensis*, *Galerucella pusilla*, and *Hylobius transversovittatus*) that were released intentionally as bio-control agents to control the introduced plant *Lythrum salicaria*. These data certainly provide insights into potential interactions of species in the Chesapeake region. However, we did not want to infer impacts based on research elsewhere, and the effect of adding such data is examined below.

Finally, there is evidence of hybridization for multiple species in Table 1 (see also below), but the significance of such hybridization to native populations was difficult to assess. Hybrid bass (*M. saxatilis* × *chrysops*) that are known to back-cross with native *M. saxatilis* have been intentionally released. Concerns about the impact of these introduced hybrids on the genetic stock of *M. saxatilis* resulted in cessation of such stockings (Harrell et al. 1993; Harrell pers. comm.). In addition, the mallard duck (*Anas platyrhynchos*) population is thought to be descendent largely from released non-native stock; these birds are known to hybridize with black ducks (*Anas rubripes*). The extent of this hybridization and its impact on the latter species is uncertain (Johnsgard and DiSilvestro 1976; Ankney et al. 1987; McCauley et al. 1998).

Plant and fish invasions as stressors in Chesapeake Bay—Among the 54 species of plants and fish in our database that

were considered regular residents of Chesapeake Bay, 29% were thought to have had some significant impact in the bay region, including 26% of plants and 37% of fish (Tables 2, 3). Nine of the 54 species (17%) were classified as probable or possible invaders. Including all 54 species, the frequency of specific impact types were reported as: competition—26% of plants and 21% of fish; predation—21% of fish; toxicity—3% of plants; herbivory—5% of fish; bioturbation—5% of fish; habitat change—14% of plants and 0% of fish; hybridization—0% of plants and 5% of fish; prey-food resources—22% of plants and 15% of fish. Multiple impact types were reported for many species of plants and fish. The absence of reported impacts for species in Tables 2 and 3 resulted primarily from the lack of studies designed to test for impacts rather than absence of detectable impacts in existing studies.

Quantitative data that evaluated potential impacts within the Chesapeake region were found for only four of these fish and plant species, representing 25% of the 16 species considered to have significant impacts or 7% of all 54 species (Tables 2, 3, Fig. 4A,C). Those four species with some quantitative impact data were all plants: *Hydrilla verticillata*, *Iris pseudacorus*, *Myriophyllum spicatum*, and *P. australis*. Two, *H. verticillata* and *M. spicatum*, are submersed aquatic plants that have received a great deal of attention in Chesapeake Bay and elsewhere. Both have been relatively abundant, forming dense mats that seem to have affected local chemical and physical habitat characteristics, fish and invertebrate communities, other plant populations, and local food resources for waterfowl and fish. A combination of presence-absence studies, correlations, and controlled experiments for these species strongly supports the hypothesis that these invasions caused observed changes, both in Chesapeake Bay and outside the region (see Table 2); it is noteworthy that the only BACI study of impacts among all 54 species is for *M. spicatum*, although outside the Chesapeake region (Keast 1984). Both of these submersed species were the target of control programs (through mechanical removal or mowing) to reduce biomass that interfered with boat and recreational use. Interestingly, the abundance of *M. spicatum* has declined significantly from its peak abundances in the early 1960s, removing the need for control and presumably limiting its current impacts (Hurley 1990).

The other two species with quantitative impact data are both emergent plants, and their importance as invaders is less clear than the submersed plants. The emergent plant *I. pseudacorus* has been common to rare in most of the bay, but locally abundant in only one area of the tidal Potomac. There, its abundance was inversely correlated with that of native plant species (Thomas 1980). This species was also thought to adversely affect food supply for waterfowl, muskrats, and nutria because it contains toxic glycosides that can cause gastroenteritis in livestock (Thomas 1980; Sutherland 1990), but experimental evidence of effects on food webs in Potomac marshes is lacking. In contrast to *I. pseudacorus*, the other emergent plant *P. australis* (a cryptogenic species) has become widespread and abundant throughout much of the bay, where it is thought to out-compete resident plant species and modify the physical habitat characteristics as well as animal abundances. Use of herbicide and fire to remove *P. australis* resulted in increased diversity and abun-

dance of other plants relative to untreated plots. However, we have classified these data as correlational, because the measured changes were in response to a non-specific disturbance that included extirpation of all plant species and perhaps other changes associated with the respective treatments. Further qualitative observations suggest that mammal and bird diversity is relatively low surrounding *P. australis* in Chesapeake Bay (Marks et al. 1994). Thus, although it appears that both emergent plants have had impacts in the region, such impacts are not well documented. Unlike the submersed plants above, the magnitude or spatial scale of known impacts for *I. pseudacorus* is relatively small. Although *P. australis* is a frequent dominant in marshes around the bay, where it likely has many significant effects, its invasion status remains unresolved (i.e., cryptogenic; Table 2).

Two other plant species seem to have had significant but unmeasured impacts in Chesapeake Bay (see Table 2 and references therein). One of these (*T. angustifolia*, an emergent plant) is a possible invader to the region, and the other (*Trapa natans*, a floating plant) is a definite invader (Stuckey and Salamon 1987; Carter and Rybicki 1994; Marks et al. 1994). Like *P. australis* (above), *T. angustifolia* has become abundant in the bay, where it forms dense stands that appear to out-compete other plants, impede water flow, increase sedimentation, and change sediment chemistry. Although some correlational data from outside the Chesapeake region are consistent with competitive dominance by *T. angustifolia* over native species, it has not been assessed within the bay (Grace and Wetzel 1982; Roman et al. 1984; Grace and Harrison 1986; Grime et al. 1988). The floating species, *T. natans*, was once abundant in the bay and seemed to out-compete native plants. In addition, the increased abundance of this species in the 1930s was thought to have a negative impact locally on fish and regionally on waterfowl abundance in the bay (Perry and Deller 1996). These effects were not measured quantitatively. Following an eradication program that extended into the 1960s, *T. natans* has been relatively rare (Hurley 1990).

Despite the perceived impacts of introduced fish species in the bay, especially as competitors and predators (Table 3), none of these impacts has actually been assessed quantitatively (i.e., using information type >1, Fig. 4A). Observed declines and even local extinctions of native fish populations in the bay have been attributed, fully or partially, to the invading fish (e.g., Jenkins and Burkhead 1993). In the late 1800s, the smallmouth bass, *Micropterus dolomieu*, was largely blamed for declines of shad, herring, minnows, and suckers in the Potomac River (Ferguson 1877). The introduction of *M. dolomieu* and other predatory species has been considered a factor in local extinctions of two small species of benthic fish, *Percopsis omiscomaycus* (or trout perch, formerly abundant but now extinct in the upper Potomac and Susquehanna Rivers) and *Percina caprodes* (or log-perch, extinct in the Potomac but still present in the Susquehanna). Since 1870, 10 large (>60-cm max length) piscivorous fish species have been established in the tidal freshwater of Chesapeake Bay; many of these may be important predators of native fish populations, based on diet information (Tables 3, 4). Some introduced fish also seem to have a relatively large degree of diet overlap with native species in the bay. For

Table 2. Comparison of ecological impacts reported among vascular plants within and outside of Chesapeake Bay. For each species the evidence of impacts (information type) is indicated numerically for each impact type within vs. outside (“other”) of the bay. A summary of the highest numerical score for information type across all impact types is also indicated by species. Reported abundance is shown by category (rare, common, abundant). Reported association with disturbance is indicated by disturbance type for each species. Species marked “C” are considered cryptogenic (i.e., possibly introduced) in the bay. Information and impact (with the addition of I—toxicity) types as in Table 1. Disturbance types: *N*—no information; *U*—relatively undisturbed; *A*—agricultural; *C*—urban-suburban; *E*—eutrophication (nutrients, turbidity, etc.); *I*—impoundment or wetland modification (damming, ditching, diking); *S*—soil disturbance (dry ballast, ore piles, “disturbed sands”).

Species	Impact location	Impact summary	A	B	C	F	I	Disturbance	Abundance	References*
<i>Alternanthera philoxeroides</i>	Chesapeake	1	1	0	0	0	0	A	rare	1, 2
	Other	4	1, 4	1	0	0	0	A, E, I	abundant	3, 4, 5
<i>Althaea officinalis</i>	Chesapeake	0	0	0	0	0	0	U	rare	6
	Other	0	0	0	0	0	0	U	rare	
<i>Amorpha fruticosa</i>	Chesapeake	0	0	0	0	0	0	U	common	6
	Other	0	0	0	0	0	0	U	common	
<i>Atriplex prostrata</i> (C)	Chesapeake	0	0	0	0	0	0	U, C, S	common	6, 7
	Other	0	0	0	0	0	0	U, C, S	common	7, 8, 9, 10, 11
<i>Bassia hirsuta</i>	Chesapeake	0	0	0	0	0	0	U	rare	6
	Other	0	0	0	0	0	0	U	rare	6, 12
<i>Cakile maritima</i>	Chesapeake	0	0	0	0	0	0	U, S	rare	6, 7
	Other	5	5	0	0	0	0	U, S	rare	13, 14
<i>Carex distans</i>	Chesapeake	0	0	0	0	0	0	U	no info	15
	Other	0	0	0	0	0	0	S	no info	16
<i>Carex divisa</i>	Chesapeake	0	0	0	0	0	0	U	rare	6
	Other	0	0	0	0	0	0	U	rare	17
<i>Carex extensa</i>	Chesapeake	0	0	0	0	0	0	U	rare	6
	Other	0	0	0	0	0	0	U	rare	17
<i>Cyperus difformis</i>	Chesapeake	0	0	0	0	0	0	U	rare	18
	Other	1	1	0	0	0	0	U, A	abundant	19
<i>Egeria densa</i>	Chesapeake	0	0	0	0	0	0	I	rare	6, 20
	Other	4	1, 4	1	1	0	0	I	abundant	21, 22
<i>Heliotropium curassavicum</i> (C)	Chesapeake	0	0	0	0	0	0	U, S	rare	7, 18
	Other	1	1	0	0	0	0	U, A, S	common	10
<i>Hydrilla verticillata</i>	Chesapeake	5	1	1, 2, 5	1, 2	0	0	E	abundant	23, 24, 25, 26, 27, 28, 29, 30, 31, 32
	Other	4	1, 4	1, 3	1, 3	0	0	E, I	abundant	22, 33, 34, 35, 36
<i>Iris pseudacorus</i>	Chesapeake	3	1, 3	1	1	0	1	I	common	37
	Other	1	1	0	1	0	1	I, S	common	16, 38
<i>Kyllinga gracillima</i>	Chesapeake	0	0	0	0	0	0	U, C	common	6, 18
	Other	1	1	0	0	0	0	U, A, C, I	common	39, 40
<i>Ludwigia peploides</i>	Chesapeake	0	0	0	0	0	0	U, C	rare	6, 18
	Other	1	1	0	0	0	0	E, S	abundant	41, 42, 43
<i>Lycopus europaeus</i>	Chesapeake	0	0	0	0	0	0	C	rare	6, 18
	Other	0	0	0	0	0	0	U, C, S	common	44
<i>Lythrum salicaria</i>	Chesapeake	1	1	0	1	0	0	U, A, C, I, S	rare	7, 45, 46
	Other	5	1, 5	1	1, 3	1	0	U, A, C, I, S	abundant	47, 48, 49, 50, 51, 52
<i>Mentha aquatica</i>	Chesapeake	0	0	0	0	0	0	U	rare	6, 18
	Other	0	0	0	0	0	0	S	rare	16
<i>Mentha spicata</i>	Chesapeake	0	0	0	0	0	0	C	rare	6, 18
	Other	1	1	0	0	0	0	C	rare	53
<i>Mentha xpipertia</i>	Chesapeake	0	0	0	0	0	0	C	rare	6, 18
	Other	1	1	0	0	0	0	C	rare	53

Table 2. Continued.

Species	Impact location	Impact summary	A	B	C	F	I	Disturbance	Abundance	References*
<i>Murdannia keisak</i>	Chesapeake	1	1	0	1	0	0	<i>U</i>	abundant	6, 18, 54, 55
	Other	1	1	0	1	0	0	<i>U</i>	abundant	56, 57
<i>Myriophyllum aquaticum</i>	Chesapeake	0	0	0	0	0	0	<i>U</i>	rare	58
	Other	1	1	1	1	0	0	<i>U, I</i>	abundant	59
<i>Myriophyllum spicatum</i>	Chesapeake	3	1	1	1, 2, 3	0	0	<i>U, E</i>	abundant	25, 31, 60, 61, 62, 63
	Other	6	1, 4	1, 2, 4, 6	1, 3, 5	0	0	<i>U, E</i>	abundant	22, 62, 63, 64, 65, 66, 67, 68
<i>Najas minor</i>	Chesapeake	0	0	0	0	0	0	<i>U, E</i>	common	6, 18, 25
	Other	1	1	0	1	0	0	<i>U, E</i>	common	69, 70
<i>Parapholis incurva</i>	Chesapeake	0	0	0	0	0	0	<i>U, S</i>	rare	7, 18
	Other	0	0	0	0	0	0	<i>U, S</i>	common	16, 71
<i>Phragmites australis</i> (C)	Chesapeake	3	3	1	1	0	0	<i>U, A, C, E, I, S</i>	abundant	6, 7, 18, 72, 73, 74, 75, 76
	Other	3	1, 3	1	1	0	0	<i>U, A, C, E, I, S</i>	abundant	9, 16, 73, 77, 78, 79
<i>Polygonum hydropiper</i> (C)	Chesapeake	0	0	0	0	0	0	<i>U, A, C</i>	common	6, 18, 54, 80
	Other	1	1	0	0	0	1	<i>U, A, C</i>	common	43, 53
<i>Polygonum lapathifolium</i> (C)	Chesapeake	0	0	0	0	0	0	<i>U, A, C</i>	common	6, 7, 18, 54, 80
	Other	5	1, 5	0	0	0	0	<i>U, A, C</i>	common	53
<i>Potamogeton crispus</i>	Chesapeake	0	0	0	0	0	0	<i>U, E</i>	common	6, 25
	Other	1	1	1	1	0	0	<i>U, E</i>	common	81
<i>Ranunculus sceleratus</i> (C)	Chesapeake	0	0	0	0	0	0	<i>A, C, S</i>	rare	6, 7, 18
	Other	3	1, 3	0	1	0	1	<i>A, C, E, S</i>	common	9, 53
<i>Spergularia salina</i> (C)	Chesapeake	0	0	0	0	0	0	<i>U, S</i>	common	6, 18
	Other	0	0	0	0	0	0	<i>U, S</i>	common	6, 18, 82, 83
<i>Suaeda maritima</i> (C)	Chesapeake	0	0	0	0	0	0	<i>U, S</i>	rare	6, 18
	Other	0	0	0	0	0	0	<i>U, S</i>	rare	10, 84
<i>Trapa natans</i>	Chesapeake	1	1	1	1	0	0	<i>E</i>	rare (once abundant)	20, 25, 31, 60
	Other	1	1	0	1	0	0	<i>E</i>	abundant	85, 86, 87
<i>Typha angustifolia</i> (C)	Chesapeake	1	1	0	1	0	0	<i>U, A, C, S</i>	abundant	6, 7, 18, 74, 75
	Other	4	1, 3, 4	1	1	1	0	<i>U, A, C, S</i>	abundant	88, 89, 90, 91

* 1—Massey 1957; 2—Va. Dep. of Conservation and Recreation <http://www.hort.vt.edu.vnps.invasive.html>; 3—Penfound 1940; 4—Julien and Broadbent 1980; 5—Coulson 1977; 6—Brown and Brown 1984; 7—Reed 1964; 8—Bassett and Munro 1987; 9—Grime et al. 1988; 10—Smith 1867; 11—Brown 1879; 12—Collins and Blackwell 1979; 13—Boyd and Barbour 1993; 14—Rodman 1986; 15—Hotchkiss 1951; 16—Torrey Bot. Club 1888; 17—Gleason and Cronquist 1991; 18—Harvill et al. 1992; 19—Holm et al. 1977; 20—U.S. Army Corps of Engineers 1977; 21—Cook and Ürmi-König 1984; 22—Barko and Smart 1981; 23—Carter and Rybicki 1986; 24—Carter and Rybicki 1994; 25—Hurley 1990; 26—Posey et al. 1993; 27—Thorp et al. 1997; 28—Wigand et al. 1997; 29—Killgore et al. 1989; 30—Serafy et al. 1994; 31—Perry and Deller 1996; 32—Hench et al. 1994; 33—Cook and Luond 1982; 34—Langeland 1996; 35—Esler 1989; 36—Esler 1990; 37—Thomas 1980; 38—Sutherland 1990; 39—Ferren and Schuyler 1980; 40—Bryson and Carter 1994; 41—Dutaire 1986; 42—Rejmankova 1992; 43—U.S. Agric. Res. Serv. 1970; 44—Andrus and Stuckey 1981; 45—Swarth 1996; 46—Guerrero abstr.; 47—Thompson et al. 1987; 48—Gaudet and Keddy 1988; 49—Edwards et al. 1995; 50—Anderson 1995; 51—Strefeler et al. 1996; 52—Grout et al. 1997; 53—Muenscher 1980; 54—Perry 1981; 55—Riefner and Hill 1983; 56—Dunn and Sharitz 1991; 57—Hotchkiss 1940; 58—Sutton 1985; 59—McCann et al. <http://aquatl.ifas.ufl.edu/mctitle.html>; 60—Stevenson and Confer 1978; 61—Bayley et al. 1978; 62—Bean et al. 1973; 63—Bayley et al. 1968; 64—Aiken et al. 1979; 65—Smith and Barko 1990; 66—Menzie 1979; 67—Engel 1995; 68—Keast 1984; 69—Meriläinen 1968; 70—Wentz and Stuckey 1971; 71—Callaway et al. 1990; 72—Williamson 1974; 73—Marks et al. 1994; 74—Willner et al. 1979; 75—Havens et al. 1997; 76—Allstock et al. abstr.; 77—Haslam 1972; 78—Roman et al. 1984; 79—Fell et al. 1998; 80—Williams 1993; 81—Catling and Dobson 1985; 82—Rossbach 1940; 83—Hill 1986; 84—Stuckey 1983; 85—Groth et al. 1996; 86—Tsuchiya and Iwakuma 1993; 87—Mills et al. 1993; 88—Stuckey and Salamon 1987; 89—Grace and Harrison 1986; 90—Grace and Wetzel 1982; 91—Hotchkiss and Dozier 1949.

Table 3. As Table 2, but among introduced fish species within and outside Chesapeake Bay.

Species	Impact location	Impact summary	A	B	C	D	E	F	H	Distur- bance	Abundance	References*
<i>Carassius auratus</i>	Chesapeake	0	0	0	0	0	0	0	0	U, C, E	common	1
	Other	5	0	0	1	0	5	1	5	U, C, E	abundant	1, 2, 3, 4
<i>Ctenopharyngodon idella</i>	Chesapeake	0	0	0	0	0	0	0	0	U, C, I	rare	1
	Other	5	0	1	1	0	1, 5	0	0	U, C, I	abundant	5, 6, 7, 8, 9
<i>Cyprinus carpio</i>	Chesapeake	1	0	0	0	0	1	0	1	U, C, E, I	abundant	1, 10, 11
	Other	5	1	1, 5	0	1	1, 5	1	3	U, C, E, I	abundant	3, 4, 7, 12, 13, 14, 15
<i>Dorosoma petenense</i>	Chesapeake	1	0	0	1	0	0	0	0	U, I	common	1
	Other	5	5	5	1	1, 5	0	0	0	U, C, E, I	common	16, 17, 18
<i>Ictalurus furcatus</i>	Chesapeake	0	0	0	0	0	0	0	0	U, I	rare (incr.)†	1
	Other	2	0	0	1, 2	1	0	0	0	U, I	common	19, 20
<i>Ictalurus punctatus</i>	Chesapeake	1	1	0	0	1	0	0	0	U, I	common	1, 21, 22
	Other	2	2	0	1	1, 2	1	0	0	U, I	common	12, 19, 23, 24
<i>Lepomis cyanellus</i>	Chesapeake	0	0	0	0	0	0	0	0	U	common	1, 25
	Other	5	1, 5	1	1	1	0	0	0	U, E, I	common	26, 27, 28, 29
<i>Lepomis gulosus</i>	Chesapeake	0	0	0	0	0	0	0	0	U	rare	1, 25, 30
	Other	1	1	1	0	0	0	0	0	U	common	12, 26
<i>Lepomis macrochirus</i>	Chesapeake	1	1	0	0	1	0	0	0	U, C, E, I	abundant	1, 30, 31, 32
	Other	5	1, 2, 3, 5	1	1, 2	1, 2, 5	0	1	0	U, C, E, I	abundant	12, 26, 27, 28, 33, 34, 35, 36, 37, 38, 39, 40, 41
<i>Lepomis megalotis</i>	Chesapeake	0	0	0	0	0	0	0	0	U	rare	1, 25
	Other	1	1	1	0	1	0	0	0	U	common	12, 42, 43
<i>Lepomis microlophus</i>	Chesapeake	0	0	0	0	0	0	0	0	U, I	rare	1, 25
	Other	5	1, 4	1	1	1, 5	0	0	0	U, I	common	12, 26, 44, 45, 46
<i>Micropterus dolomieu</i>	Chesapeake	1	1	0	0	1	0	0	0	U	rare	1, 25, 47, 48, 49, 50
	Other	4	1, 3	1	0	1, 4	0	0	0	U, I	common	4, 26, 51, 52, 53, 54, 55
<i>Micropterus salmoides</i>	Chesapeake	1	1	0	0	1	0	0	0	U, I	common	1, 11, 25, 47, 56, 57
	Other	5	1, 5	5	0	1, 3, 5	0	0	0	U, I	common	4, 26, 51, 52, 53, 54, 55, 58, 59, 60, 61
<i>Morone saxatilis</i> × <i>americana</i>	Chesapeake	0	0	0	0	0	0	0	0	N	rare	62, 63
	Other	0	0	0	0	0	0	0	0	N	rare	
<i>Morone saxatilis</i> × <i>chrysops</i>	Chesapeake	1	0	0	0	0	0	1††	0	U, I	rare	53, 62
	Other	1	1	0	0	1	0	1	0	U, I	common	64, 65, 66
<i>Pomoxis annularis</i>	Chesapeake	0	0	0	0	0	0	0	0	U, I	rare	1
	Other	5	1, 3, 5	0	1, 3	1	0	0	0	U, I	abundant	16, 17, 26, 67
<i>Pomoxis nigromaculatus</i>	Chesapeake	0	0	0	0	0	0	0	0	U, I	common	1, 68, 69
	Other	2	2	0	1	1	0	0	0	U, I	abundant	18, 26, 70
<i>Pylodictis olivaris</i>	Chesapeake	0	0	0	0	0	0	0	0	U	rare	1
	Other	2	0	0	0	1, 2	0	0	0	U, I	common	20, 58, 71, 72, 73
<i>Stizostedion vitreum</i>	Chesapeake	0	0	0	0	0	0	0	0	U	rare	1, 25
	Other	4	1, 2	0	0	1, 4	0	0	0	U, I	common	26, 59, 74

* 1—Jenkins and Burkhead 1993; 2—Richardson et al. 1995; 3—Cole 1905; 4—Page and Burr 1991; 5—Pierce 1983; 6—Shireman and Smith 1983; 7—Taylor et al. 1984; 8—McKnight and Hepp 1995; 9—Raibley et al. 1995; 10—Hildebrand and Schroeder 1928; 11—Stevenson and Confer 1978; 12—McCrary 1990; 13—Crivelli 1983; 14—King et al. 1997; 15—Robertson et al. 1997; 16—Guest et al. 1990; 17—Crowl and Boxrucker 1988; 18—Jackson and Bryant 1993; 19—Carlander 1969; 20—Guier et al. 1981; 21—Menzel 1943; 22—McGovern and Olney 1988; 23—Townsend and Winterbourn 1992; 24—Krummrich and Heidinger 1973; 25—Musick 1972; 26—Carlander 1977; 27—Kirby 1982; 28—Werner and Hall 1976; 29—Lemly 1985; 30—Flemer and Woolcott 1966; 31—Johnson and Dropkin 1992; 32—Weaver and Garman 1994; 33—Fox 1994; 34—Mittelbach 1984; 35—Mittelbach 1988; 36—Olson abstr.; 37—Osenberg et al. 1994; 38—Pazkowski 1986; 39—Hubbs 1955; 40—Lazaro 1987; 41—Lazaro et al. 1992; 42—Laughlin and Werner 1980; 43—Cooner and Bayne 1982; 44—Wainwright 1996; 45—Martin et al. 1992; 46—Fisher Huckins 1997; 47—Smith 1907; 48—Pavol and Davis 1982; 49—Ferguson 1877; 50—Sanderson 1958; 51—Savitz 1981; 52—Winemiller and Taylor 1987; 53—Gilliland and Clady 1981; 54—Garvey et al. 1994; 55—Hambright 1994; 56—Killgore et al. 1989; 57—Fewlass 1980; 58—Fla. Caribbean Sci. Center <http://www.nfrcg.gov/nas>; 59—Poe et al. 1994; 60—Matthews et al. 1992; 61—Post et al. 1997; 62—Harrell et al. 1993; 63—Kerby and Joseph 1979; 64—Gleason 1982; 65—Avisé and Van den Ayle 1984; 66—Forshage et al. 1986; 67—Cichra et al. 1981; 68—Lippson and Moran 1974; 69—Smith 1971; 70—Schiavone 1985; 71—Ashley and Buff 1987; 72—Thomas 1993; 73—Stein and Flack 1996; 74—Schlagenhaft and Murphy 1985.

† Abundance is reported to be increasing.

†† A probable reduction in importance due to recent changes in hybrid releases.

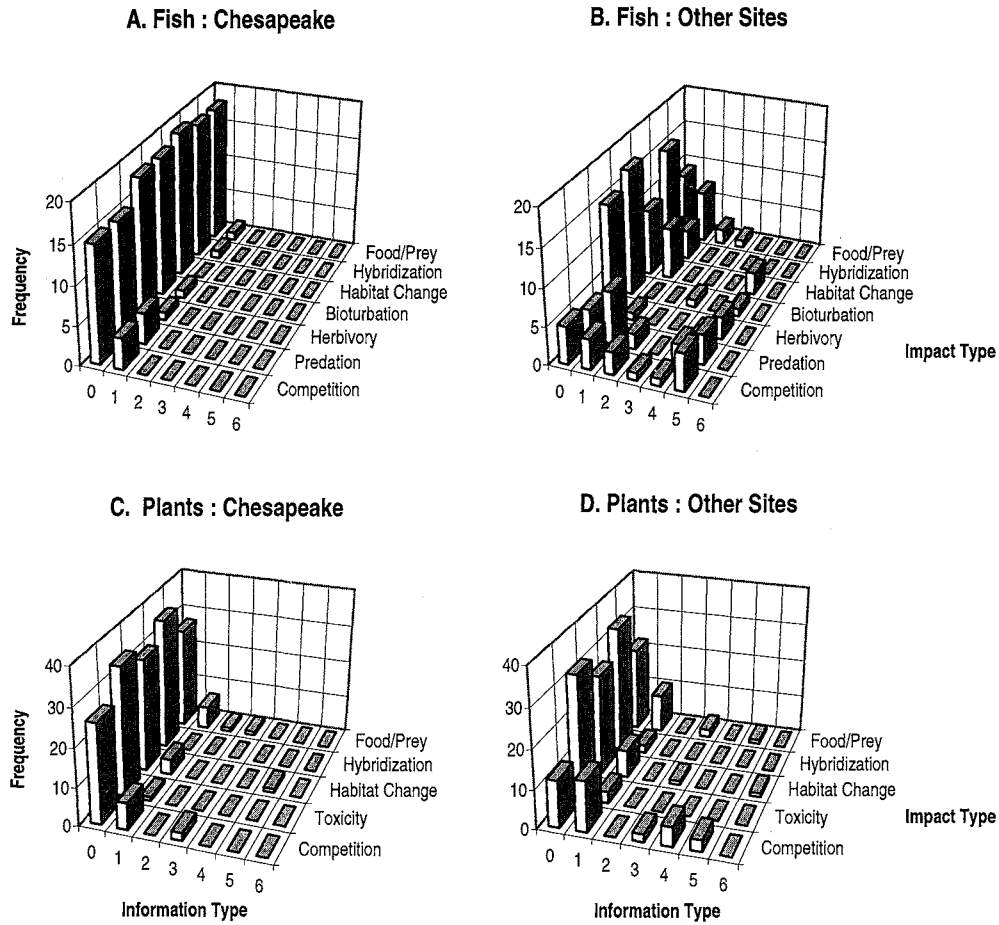


Fig. 4. Comparison of ecological impacts reported within vs. outside the Chesapeake Bay region for the same species of plants and fish. Shown are the frequencies of information types that underlie reported effects by impact type for 19 species of fish and 35 species of plants that have been introduced to the bay. (Additional detail given in Tables 2 and 3 and the text.) Information types explained in Fig. 2 legend.

example, based on work by Flemer and Woolcott (1966), dietary overlap between *Lepomis macrochirus* and other sunfish was as high as 0.38 (based on the formula of Pianka 1975, where complete overlap is 1.0).

Numerous experimental studies outside of the Chesapeake region, especially for the sunfish (*Lepomis* spp.), demonstrate the significant impact of these same species on invertebrate and fish populations, plant densities, and community dynamics (e.g., Mittelbach 1988; Osenberg et al. 1994; Table 2 and references therein). It therefore seems likely that significant impacts have resulted from some fish invasions in the Chesapeake region, particularly for those species that have been abundant and that have documented impacts elsewhere (see below). As yet, none of these impacts has been confirmed in the bay, where observed changes may also have resulted from any combination of anthropogenic changes such as overfishing, dam construction and habitat alteration, and pollution (e.g., Hildebrand and Schroeder 1928; Jenkins and Burkhead 1993; Dill and Cordone 1997).

Twice as many of these same species of plants and fish are thought to have caused significant impacts outside (74%) compared to within (29%) the region, including impacts

mentioned for 62% of the plants and 95% of the fish (Tables 2, 3). The frequency of specific impact types outside the region were: competition—66% of plants and 74% of fish; predation—79% of fish; herbivory—21% of fish; bioturbation—11% of fish; toxicity—9% of plants; habitat change—26% of plants and 47% of fish; hybridization—6% of plants and 21% of fish; prey-food resources—37% of plants and 53% of fish.

There is some quantitative information on impacts for 44% of the 54 plant and fish species outside of the bay, in contrast to only 7% in the bay (Tables 2, 3, Fig. 4). This represents a significant difference in quantitative information between the two source regions (4/54 vs. 24/54; $\chi^2 = 21.78$, $df = 1$, $P < 0.001$), resulting mostly from an increase in presence-absence comparisons and controlled experiments outside of the Chesapeake region.

Nearly twice as many of the 54 species are known to be common or abundant outside of the region (81%) than within it (43%), representing a significant difference in maximum reported abundances (Fig. 5; $\chi^2 = 16.23$, $df = 2$, $P < 0.005$). Although not all common or abundant species have reported impacts, it is most often these species for which impacts are

Table 4. Maximum total lengths of native and introduced fish >60 cm found in tidal waters of Chesapeake Bay and tributaries (Page and Burr 1991).

Species	Common name	Max length (cm)
Native Fish		
<i>Ameiurus catus</i>	White catfish	62
<i>Amia calva</i>	Bowfin	109
<i>Anguilla rostrata</i>	American eel	152
<i>Esox niger</i>	Chain pickerel	99
<i>Lepisosteus osseus</i>	Longnose gar	183
<i>Morone saxatilis</i>	Striped bass	200
<i>Petromyzon marinus</i>	Sea lamprey	120
Introduced Fish		
<i>Esox lucius</i>	Northern pike	133
<i>Esox masquinongy</i>	Muskellunge	183
<i>Esox masquinongy</i> × <i>lucius</i>	“Tiger muskie”	158
<i>Ictalurus furcatus</i>	Blue catfish	165
<i>Ictalurus punctatus</i>	Channel catfish	127
<i>Micropterus dolomieu</i>	Smallmouth bass	69
<i>Micropterus salmoides</i>	Largemouth bass	97
<i>Morone saxatilis</i> × <i>chrysops</i>	“Palmetto bass”	82
<i>Pylodictis olivaris</i>	Flathead catfish	155
<i>Stizostedion vitreum</i>	Walleye	91

reported and for which quantitative data exist (Tables 2, 3; see also Fig. 1). Thus, as the area included in our analysis expands from Chesapeake Bay to include the entire range of each species, both the maximum reported abundance and the reported impacts increase.

Interaction of invasions with other stressors in Chesapeake Bay—More than half of the 54 plant and fish species in our analysis were associated with some form of anthropogenic disturbance in the bay, including 66% of plants and 58% of fish (Tables 2, 3). In most cases, the reported associations were based solely on qualitative observation, suggesting distribution or abundance of the invader was correlated with some human-mediated physical or chemical disturbance. For example, disturbance is thought to facilitate invasion of marshes by the emergent plants *P. australis* and *Typha* spp. A recent survey of 15 constructed wetlands in Virginia found that 80% were colonized by these species and predicted that these sites would be overrun by both species within 40 yr (Havens et al. 1997). Although the invasion of these sites is clear and the pattern of invasion was quantified, the effect of disturbance (the construction of these wetlands) on “invasibility” is uncertain in the absence of control sites or some measure of disturbance magnitude as an independent variable.

For some species, there are also quantitative measures that correspond to temporal or spatial patterns of habitat change. Often this has involved additional wetland modifications, such as reservoir construction, which drastically alter flow regime and other habitat characteristics that seem to favor an invader. However, as above, we found no studies that either quantified a change or stressor (e.g., magnitude and frequency of pollution, eutrophication, hypoxia) and ex-

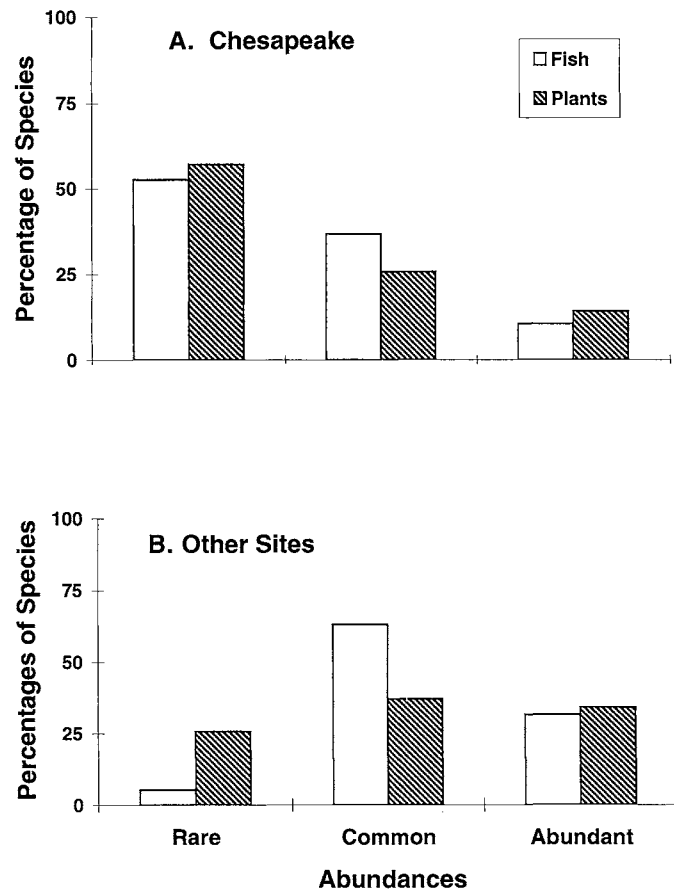


Fig. 5. Comparison of abundance within and outside Chesapeake Bay for the same species of plants ($n = 35$) and fish ($n = 19$) that have been introduced to the bay. The relative abundances of species in each group are indicated as percentage rare, common, or abundant. (Further description given in Tables 2 and 3 and the text.)

PLICITLY tested for correlation with the distribution or effects of invaders among sites or that used manipulative experiments or control sites to compare a response of invaders in the presence and absence of a stressor within the region.

A higher percentage of these same species was associated with disturbed habitat for both plants (79%) and fish (77%) outside of the Chesapeake Bay region compared to within it. As above, most of the data consisted of qualitative observations. Additionally, some quantitative measures demonstrated that a few invaders were most abundant in areas with human-modified flow regimes (e.g., Moyle 1986; Meffe 1991; Poe et al. 1994; Weaver and Garman 1994). However, despite further qualitative evidence of such associations across the geographic ranges of these species (Tables 2, 3), we were unable to identify additional quantitative or experimental measures of the interaction among NIS invasions and the many other stressors in estuaries.

Similar to fish and plants, interesting observations were reported for other taxa concerning possible interactions among NIS and other stressors in the bay, but they have not been quantified. The most intriguing interactions were reported for the two oyster pathogens, *P. marinus* and *H. nel-*

soni. The dynamics and effects of both pathogens in local oyster populations are influenced by temperature and salinity (e.g., Lauckner 1983; Cook et al. 1998). Furthermore, it appears that the effect of *P. marinus* on infected oysters is increased by pollutants (e.g., Chu and Hale 1994). Anthropogenic changes that influence these local conditions may therefore affect this host–pathogen interaction and the subsequent community-level effects (as above). However, the significance of such interactive effects, and those of other potential stressors (e.g., sediment and nutrient loading; Kennedy 1996) on this host–pathogen dynamic, remains untested.

Discussion

Invasions as stressors in Chesapeake Bay—NIS invasions are important stressors in the Chesapeake Bay region, but the effects of most invaders remain unexplored. On some level, every established NIS has an effect through its interactions with the invaded community and surrounding environment. However, few studies have attempted to measure potential impacts of NIS in the Chesapeake region, let alone estimate the magnitude and complex interactions involved in such impacts. In our analysis, 20% of all 196 species were thought to have significant impacts, and this percentage was slightly higher (29%) for the 54 species of plants and fish that were regular residents. Yet, quantitative data to test for any impact type within the bay existed for only 12 species, representing 6% of all species or 7% of the plants and fish. Furthermore, data for some of these species were restricted to correlations in space or time, confounding cause-effect relationships with other covariates (as discussed above).

Further consideration of existing data for plants and fish suggests that the ecological effects of NIS in Chesapeake Bay are much greater than can be shown at present. In addition to the four species (*H. verticillata*, *I. pseudacorus*, *M. spicatum*, and *P. australis*) with some quantitative impact data, 12 of the other 50 species are thought to have significant impacts on population or community processes in the region. A convincing case can be made for some species that are reported to be abundant and that have been associated with observed changes in the bay, especially when associated changes have been quantified outside of the Chesapeake region. This latter group includes two plant species (*T. natans*, and *T. angustifolia*) and five fish species (*Cyprinus carpio*, *Ictalurus punctatus*, *L. macrochirus*, *M. dolomieu*, and *Micropterus salmoides*). The inference is perhaps strongest for the two species of plants, which have been very abundant. Both plants occur in dense stands that seemed to reduce the abundance of native vegetation. Further qualitative observations outside of the region suggested such changes in native vegetation were coincident with invasions. Importantly, these observations did not seem to be confounded with other major changes reported at the site of invasions. The five fish species have also been very abundant and are thought to be responsible for either predation or food-based competition that contributed to declines in abundance of native fish species. However, the case for invasion impacts of these fish is confounded by many other anthro-

pogenic stressors that may play a role in declining fish populations (e.g., Hildebrand and Schroeder 1928; Horwitz 1986).

Combining these quantitative and qualitative data, it appears that impacts in Chesapeake Bay may be significant for 20% of the 54 plant and fish species examined (17% of the plants and 26% of the fish). These impact rates for the bay are twice that hypothesized for invasions generally (Williamson and Fitter 1996). Furthermore, it is important to recognize that existing data for the bay provide only a minimum estimate of invasion impacts. First, we have not included a large number of cryptogenic species in our analysis. Second, most of the plant and fish species, as well as 51% of all 196 species, considered in our analysis have yet to be studied from this perspective. Even where studied, the scope of investigation is quite limited. For example, an invading plant species could result in direct displacement of native plants, changes in surrounding benthic and pelagic animal communities, changes in sediment deposition and characteristics, and shifts in chemical processes such as nutrient cycling (e.g., Adam 1990; Grout et al. 1997; Wigand et al. 1997). Fish invasions can also result in diverse population and community effects, including trophic cascades (e.g., Carpenter 1988; Power 1990, 1992; Osenberg et al. 1994). Most of these possibilities, as well as potential indirect effects, remain virtually unexplored for every invasion in Chesapeake Bay. In addition, there has been no attempt to consider the cumulative impact of invading species. For example, impacts are often considered for only large or abundant (i.e., conspicuous) species, but even the less abundant species may cause significant change when considered as a group. For Chesapeake Bay, 30 species of non-indigenous plants and fish alone are considered rare but may contribute collectively to important changes.

Although some of the invaders are known to have significant direct and indirect effects outside of the Chesapeake region, we did not accept this as sufficient evidence for effects within the region. Such studies certainly demonstrate the potential for similar impacts. Where qualitative observations within the region indicated relatively high abundance of an invader and associated changes consistent with impacts measured outside the region, we consider such impacts likely. However, when the abundance of an invading population is considered rare in the Chesapeake region but common elsewhere, we are skeptical that impacts in one region are predictive of those in another. For example, the flathead catfish *Pylodictis olivaris* is common in several rivers along the southeast Atlantic coast, where its invasion is correlated with drastic declines of native catfish *Amieurus* spp. and other fish species (Guier et al. 1981; Ashley and Buff 1987; Thomas 1993; Stein and Flack 1996). Experiments with the long-ear sunfish *Lepomis microlophus* in Tennessee suggest its predation has a significant direct impact on invertebrate prey populations with indirect effects on vegetation (Martin et al. 1992). However, both of these organisms are currently rare in the Chesapeake region, and there is no reason to believe that impacts observed at relatively high densities also occur at lower densities.

We predict that significant spatial and temporal variation of impact magnitudes (and types) exists for most NIS in our

analysis, resulting primarily from underlying patterns of density. This is perhaps best illustrated for the 54 species of plants and fish in our analysis (Tables 2, 3, Fig. 5). Although some species may not have any significant effects at even their highest observed densities, most (74%) are thought to have an impact at some location within their range (*see results*). In contrast, only 29% of these same species are thought to have impacts in the Chesapeake region. Maximum reported abundances parallel this pattern, with 81% of species indicated as common-to-abundant outside the region compared to 43% within it. We suggest that these general patterns of abundance and impacts may be causally linked. More specifically, the probability of encountering a relatively high density population for each species increases with increasing geographic extent of our analysis. If impacts for these species are often density-dependent, it would result in an increase in the frequency or magnitude of impacts as the geographic area of analysis expands.

It is noteworthy that density dependence can interact with local conditions to modify the type and magnitude of impacts among sites. Changes in water temperature or current, turbidity, sediment characteristics, or prey species may all influence the relationship between impact and density (e.g., Lipcius and Hines 1986). For example, the submerged plant, *H. verticillata*, is considered to have severe adverse effects on many fish populations in Florida, where it often fills entire bodies of water with dense growth, limiting movement of predatory species and promoting anoxia (Langeland 1996; McCann et al. <http://aquatl.ifas.ufl.edu/mctitle.html>). However, in the Chesapeake region, where its growth is limited by turbidity and winter cold, the *Hydrilla* invasion seems to have resulted in increased populations of largemouth bass (*M. salmoides*), and other predatory fish, by providing a refuge for high densities of small fish (Killgore et al. 1989; Phelps 1994; Serafy et al. 1994). Another submerged plant, *M. spicatum*, has shown a historical pattern of strong temporal variation in impacts, with explosive growth during early colonization and severe accompanying effects on native biota (shading, restriction of water flow, reduction of food quality, etc.), followed by sharp declines and stabilization of populations at less dominant densities (Bean et al. 1973; Stevenson and Confer 1978; Smith and Barko 1990; Engel 1995; Carter and Rybicki 1994). Thus, this potential for impact variation, even when controlling for density, highlights the need for caution in extending results of invasion impacts in space or time.

Invasions as stressors in other marine communities—Although our analysis of NIS is limited to Chesapeake Bay, we believe the results are general for marine and estuarine communities. More specifically, it appears that Chesapeake Bay is not unusual in the number and frequency of quantitative studies on invasion impacts. For example, Cohen and Carlton (1996) indicate that few quantitative data exist to measure population or community impacts in San Francisco Bay, and we estimate that quantitative impact measures have been made for fewer than 5% of the 230 known NIS that they report. Of the approximately 100 marine NIS known from Australia (Thresher and Martin ICES CM 1995/O4; Hewitt pers. comm.), we are aware of quantitative impact

data for only three (*Asterias amurensus*, *Carcinus maenas*, *Sabella spallanzanii*); of these data, none has yet been published.

Despite current limitations in the amount of data available to assess the scope and diversity of invasion impacts, it is evident that NIS are significant stressors in many marine communities. As in Chesapeake Bay, there is now a small percentage of case studies among the hundreds of known NIS that underscores the probable magnitude of effects. For example, a combination of studies on the Asian clam *Potamocorbula amurensis* in San Francisco Bay provides perhaps the best documentation of impacts for a marine invasion to date (e.g., Nichols et al. 1990; Alpine and Cloern 1992; Kimmerer et al. 1994; Cloern 1996 and references therein). Following establishment of the invading clam population at densities $>10,000\text{ m}^{-2}$, long-term data indicated shifts in the broadscale abundance of benthic and planktonic organisms. Most remarkably, the usual spring phytoplankton bloom is no longer evident following the invasion of this clam, which has many potential consequences for indirect and cascading effects. In addition, quantitative experiments and correlative data on impacts of the European green crab *C. maenas* in California and Massachusetts, as well as Tasmania, have demonstrated remarkable concordance for impacts on prey population among sites (Ruiz et al. unpubl. data). Finally, experimental studies of numerous marine plants and algal species demonstrate strong effects on community structure in the western U.S., New Zealand, the Mediterranean Sea, and elsewhere (e.g., Partridge 1987; Posey 1988; Adam 1990; Viejo 1997).

Our analysis was not intended to discount the value of qualitative data and observation in understanding invasion processes, but instead to clearly characterize the data available on NIS impacts. This study demonstrates that many fewer impacts are measured than is generally perceived. This disparity is not unique to marine invasions and certainly exists for freshwater and terrestrial invasions as well. For example, the non-indigenous *L. salicaria* (purple loosestrife) is widely believed to out-compete native plants and disrupt food webs in freshwater wetlands of North America, but a review of 71 articles concerning this species indicates that the evidence is lacking or contradictory, calling for quantitative data (Anderson 1995; *see also* Edwards et al. 1995 for recent field experiments). In addition, Mills et al. (1996, 1997) indicated that few quantitative studies have measured perceived impacts for the 113 NIS they documented in the nontidal freshwater drainage of the Hudson River, New York. It would be worthwhile to identify these disparities in terrestrial, freshwater, and marine systems alike. Such analyses could help direct future research on understanding and comparing NIS impacts among systems, as well as provide a basis for management decisions and priorities involving hundreds of NIS.

A considerable body of knowledge is now emerging about the extent and patterns of invasion in marine systems, but many more quantitative studies on the ecology of NIS are needed to estimate the full scope and significance of this important stressor. Although various quantitative measures are possible, each has inherent strengths and limitations (e.g., Diamond 1986; Schmitt and Osenberg 1996; Lodge et al.

1998). These trade-offs need to be evaluated for any study, as does the strength and scale of the inference. The use of multiple methods on different scales is the most desirable approach for measuring NIS impacts. Such a strategy helps overcome limitations associated with any one method and provides independent tests of impact hypotheses. We recommend that reports of NIS impacts include explicit information about the characteristics measured that include impact type, impact magnitude, information type (or method), and the spatial and temporal scale of analysis. Since spatial and temporal variation may be significant for both impact type and magnitude (e.g., Elton 1958; Thompson et al. 1987; Andow et al. 1990; Smith and Barko 1990; *see above*), such information would provide the resolution and accuracy of impact measures needed to compare measures among sites, times, or taxa.

Interaction of invasions with other stressors—Non-indigenous species interact with a broad spectrum of other anthropogenic stressors, but the consequences of these interactions remain virtually unexplored. This topic has not been studied in Chesapeake Bay or many other estuaries throughout the world where anthropogenic stressors such as chemical pollutants, overfishing, and hypoxia are notorious (e.g., Cooper and Brush 1991, 1993; Kennish 1992).

Despite considerable discussion about the role of disturbance in estuarine invasions, empirical data were not evident. Some theoretical and empirical support for disturbance-mediated invasion exists for terrestrial and freshwater communities (e.g., Robinson and Dickerson 1984; Crawley 1986; Hobbs 1989; Case 1990, 1996). Conversely, invaders can alter disturbance regimes such as fire and erosion, having diverse effects in terrestrial systems (Mack and D'Antonio 1998). For Chesapeake Bay and other marine systems, the existing data on such interactions are qualitative and correlative. The association of non-native fish in California with sites of modified water flow seems to be the exception, which may result from creation of preferred habitat instead of the disturbance itself (Moyle 1986; Baltz and Moyle 1993; *see results*).

There are some interesting data concerning the potential role of local and/or global warming on NIS invasions and impacts. First, it appears that the elevated thermal environments surrounding powerplants have been essential to sustain some invading marine species, providing a refuge from the relative cold of surrounding waters at some times (Naylor 1965; Hoagland and Turner 1980; Paine 1993). Some species are so restricted in their tolerance that this modified thermal environment is required to survive. However, in other cases, invaders may be only partially dependent on this thermal environment—perhaps only during winter. Thus, the thermal effluent may provide a refuge during inhospitable seasons, allowing a species to colonize and possibly impact other regions when severe conditions abate. There is also the possibility that NIS may adapt to local conditions, allowing them to expand beyond their original environmental constraints (e.g., *C. fluminea*, Kreiser and Mitton 1995). Second, changes in temperature regionally may greatly influence the geographic range, abundance, and impact of NIS. For example, the abundance of European green crabs fluctuates

considerably among years along both sides of the North Atlantic, resulting apparently from die-offs during years with severe winters (e.g., Welch 1968; Elnor 1981; Berrill 1982; Beukema 1991). Furthermore, the impact of this predator on its molluscan prey is thought to fluctuate in parallel. Similarly, the effect of oyster pathogens (as above), as well as many other ecological interactions, may be highly temperature-dependent. Thus, changes in sea surface temperature due to global warming or regional events, such as El Niño Southern Oscillation, may have profound effects on NIS as stressors.

Another example of interaction with anthropogenic stressors involves the eutrophication of estuaries. Increased nutrient loading and sediment runoff has perhaps favored invasion of Chesapeake Bay by exotic submerged plants (*Hydrilla*, *Myriophyllum*, *Trapa*) whose growth habits and physiology make them competitive at low light levels (Barko and Smart 1981; Carter and Rybicki 1994). Eutrophication also seems to have favored some invasive emergent plants, such as *P. australis* and *T. angustifolia* (Grace and Harrison 1986; Marks et al. 1994), but may have increased the susceptibility of oysters to pathogens (Kennedy 1996; *see results*). In addition, nutrient loading can influence noxious phytoplankton blooms, which have been increasing in frequency and geographic distribution (Smayda 1990; Hallegraeff 1993). These blooms can cause direct kills of fish, birds, and mammals, as well as indirect die-offs due to various mechanisms (hypoxia, reduced food quality, light limitation). The increase of phytoplankton blooms results in part from recent invasions by NIS. This has been confirmed for a few species of toxic dinoflagellates in Australia that caused fishery closures (Hallegraeff et al. 1988; Hallegraeff and Bolch 1992), although the broader range of ecological effects for these particular species have not been documented. Thus, eutrophication may allow both native and exotic phytoplankton, as well as various vascular plants (as above), to achieve a threshold of abundance which permits them to become significant stressors.

Although the role of stressors in invasion processes remain unresolved, we believe this topic represents an important aspect of marine invasion ecology that may well explain many patterns of NIS distribution and impact. Indeed, given the multiple stressors that increasingly dominate many estuarine processes, we predict that interactions between invasions and other stressors are frequent and significant. Clearly there is much to explore in this area. Previous studies on population and community responses to various stressors should be examined, as these undoubtedly include data on NIS and their dynamics. These studies may also provide a useful template for designing future correlative and experimental tests of NIS–stressor interactions. Considering the constellation of probable interactions between stressors and invasions, a major challenge of invasion ecology is to build upon the few existing data in this area.

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