2016

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Recommended Citation

Harding, Juliana M. and Mann, Roger L., "Habitat Disturbance Combined With Life History Traits Facilitate Establishment Of Rapana Venosa In The Chesapeake Bay" (2016). *VIMS Articles*. 308.
https://scholarworks.wm.edu/vimsarticles/308

Journal of Shellfish Research, Vol. 35, No. 4, 885–910, 2016.

HABITAT DISTURBANCE COMBINED WITH LIFE HISTORY TRAITS FACILITATE ESTABLISHMENT OF *RAPANA VENOSA* IN THE CHESAPEAKE BAY

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ABSTRACT The veined rapa whelk (*Rapana venosa*) invasion of the Chesapeake Bay in the United States was first observed in 1998. Chesapeake Bay rapa whelk population demographics, age-at-length relationships, and invasion progression (temporal, spatial) from 1998 to 2009 are described. Between June 1998 and November 2009, 27,624 rapa whelks, ranging from 11- to 195-mm shell length (SL), were collected from the lower Bay. Using a Von Bertalanffy age-at-length model ($R^2 = 0.99$), the 195-mm-SL whelk collected in 2007 was 26 y old, making 1981 the estimated year of first introduction. Age-frequency distributions for Ocean View, Hampton Bar, and the lower James River showed increased whelk numbers per age class and consistent representation of Age 2–3 through Age 7–8 whelks throughout the time series indicating recruitment and establishment. Whelk range expansion into James River oyster habitats began in 2004 and continued through 2009. Whelks occupy shallow areas during warmer months, move into deeper habitats during cooler months, and annually reinvade shallow areas as temperatures warm seasonally. Channels act as salinity refugia and conduits between foraging habitats. Salinity tolerances allow rapa whelk use of epifaunal habitats bounded by the 10–12 isohalines formerly used by native oyster drills [*Urosalpinx cinerea* (Say, 1822); *Eupleura caudata* (Say, 1822)] as juveniles and infaunal habitats with salinities of 15–25 that do not overlap with native whelks (*Busycotypus canaliculatus*, *Busycon carica*) as adults. Establishment was facilitated by local disturbance of native species distributions by Tropical Storm Agnes (1972).

KEY WORDS: veined rapa whelk, *Rapana venosa*, Chesapeake Bay, invasion, muricid, age growth

INTRODUCTION

Establishment of an invasive species in a receptor habitat is facilitated by a combination of life history traits that promote rapid propagation and distribution of both progeny and mature individuals, physiological tolerances that are suited to receptor environmental conditions at relevant temporal scales (diurnal, seasonal, annual), and ecological characters that allow invaders to compete with local species for space and food resources (Elton 1958, Bufford & Daehler 2011). Within the receptor communities, interspecific and species–habitat relationships across temporal and spatial scales are vulnerable to natural (e.g., weather and climate effects) and anthropogenic (e.g., natural resource harvest, shoreline development, dredging) disturbances in both isolation and combination. Disturbance has the potential to "reset" ecological interactions as well as environmental conditions across spatial scales providing opportunities for invasions. Invaders are common in disturbed habitats (Herbold & Moyle 1986, Hobbs 1989, Williamson 1996, Shea & Chesson 2002, Bugnot et al. 2016), particularly in estuaries (Carlton 1989, Ruiz et al. 1997, Ruiz et al. 2000, Preisler et al. 2009).

The Chesapeake Bay is a geologically young, dynamic ecosystem with a recent history of extensive disturbance from the terrestrial watershed (e.g., deforestation for agriculture, shoreline modification, and urbanization, major port development; Sprague et al. 2006) to estuarine water column eutrophication (Cooper & Brush 1993, Zimmerman & Canuel 2002) and benthic ecology (e.g., oyster population declines with loss of associated complex habitat and associated trophic changes; Baird & Ulanowicz 1989, Ulanowicz & Tuttle 1992, Coleman & Bratton 2003, Mann 2006). The Bay is also home to major international ports, insuring a continuing influx of hull fouling and ballast water–associated invaders (Carlton & Geller 1993, Carlton & Hodder 1995, Cohen & Carlton 1998, Carlton 1999, Mann & Harding 2000, Fofonoff et al. 2003, Mann 2006, Albert et al. 2013, Ruiz et al. 2013). The veined rapa whelk [*Rapana venosa* (Valenciennes, 1846)] invasion into the Chesapeake Bay via ballast water introduction, from discovery in 1998 through 2009 (Harding & Mann 1999), is described herein.

The rapa whelk is a predatory muricid gastropod, which is native to the Sea of Japan and Korean coastal waters (Tsi et al. 1983). It was introduced to the Black Sea post-World War II (Drapkin 1963, Chukchin 1984, Zolotarev 1996) and subsequently spread to the Aegean, Adriatic, and Mediterranean Seas (Mann et al. 2004) as well as the Rio de la Plata (Pastorino et al. 2000, Giberto et al. 2006) and the North Sea (Vink et al. 2005). Rapa whelk life history includes several noteworthy differences with native Chesapeake muricids (summarized by Harding et al. 2007a) including pelagic larvae, a life span exceeding 15 y, maximum shell lengths (SL) greater than 180 mm with the potential to reach a size refuge from predation at 60–80 mm SL (Harding 2003), and annual individual fecundities of at least 1 million offspring (Harding et al. 2007a, 2008). These life history traits promote successful colonization postintroduction. Additionally, rapa whelks enjoy apparent immunity from the castrating effects of tributyltin-induced imposex (Mann et al. 2006, Harding et al. 2013, Harding et al. 2016).

Rapa whelks were introduced to the Chesapeake Bay by ballast water transport of veliger larvae from the Black Sea (Mann & Harding 2000, Chandler et al. 2008). Beyond the presence of an additional muricid gastropod in the lower Bay to compete with the native oyster drills (*Urosalpinx cinerea*, *Eupleura caudata*), rapa whelks are cause for concern ecologically because

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DOI: 10.2983/035.035.0417

their prey field and foraging habitats change ontogenetically (Harding 2003, Harding et al. 2007b). Rapa whelk ontogenetic changes in resource use do not have an analog in the aboriginal Chesapeake fauna. Rapa whelk life history transitions encompass a sequence of food and space resources and accompanying competitive interactions and facilitate escape or relief strategies based on whelk SL. Black Sea nearshore benthic bivalve guild decimation by rapa whelks within 20 y postintroduction (Drapkin 1963) fundamentally altered local food webs much like zebra mussels [*Dreissena polymorpha* (Pallas, 1771)] have transformed ecosystem dynamics in the Laurentian Great Lakes (Cuehl & Anguillar 2013). Chesapeake Bay rapa whelks co-occur spatially with native oyster [*Crassostrea virginica* (Gmelin, 1791)]; northern quahogs [*Mercenaria mercenaria* (Linnaeus, 1758)]; blue crab [*Callinectes sapidus* (Rathbun, 1896)]; oyster drills, and whelk [*Busycotypus canaliculatus* (Linnaeus, 1758); *Busycon carica* (Gmelin, 1791)] populations during their life cycles thus insuring competition for resources. At decadal scales, competition between invasive species and native fauna dictates establishment and the invader's range.

Chesapeake Bay rapa whelk population dynamics and distribution between 1998 and 2009 are described. Whelk collections were made in collaboration with commercial fishermen demonstrating the power of an expanded collection network of trained individuals as partners when an invasive species is susceptible to commercial fishing gear and a predator on targeted commercial species. The objectives were to document (1) Chesapeake Bay *Rapana venosa* population demographics and age-at-length relationships and (2) the temporal and spatial invasion progression from 1998 to 2009 as influenced by extant environmental conditions. The hypothesis that rapa whelk distribution is bounded by a lower salinity threshold of 12–15 (Golikov 1967, Tsi et al. 1983, Rubinshtein & Hiznjak 1988, Mann & Harding 2000), similar to the historic distribution of *Urosalpinx cinerea* and *Eupleura caudata* (salinity minimum of 9–12, Zachary & Haven 1973, with preference for salinities greater than 15; Menzel & Nichey 1958), is evaluated.

MATERIALS AND METHODS

Sources of Wild Whelk Samples

The Virginia Institute of Marine Science (VIMS) bounty program for *Rapana venosa* accepted whelks that were found in the Virginia portion of the Chesapeake Bay (Tables 1 and 2, Fig. 1) from September 1998 through September 2009. Whelks were usually collected as bycatch in the commercial blue crab, northern quahog, and/or eastern oyster fisheries. The collection location, date, status (live, dead with tissue, shell only), and SL (maximum distance from the top of the spire to the bottom of the columella, mm) were recorded at the time of donation. The collection site substrate type was also reported for many whelks. The first rapa whelk collections were made in June 1998 by VIMS Trawl Survey staff near the Monitor–Merrimac Bridge–Tunnel (MMBT, Fig. 1, Harding & Mann 1999).

Collection locations were grouped according to tributary or region (Tables 1 and 2, Fig. 1). Each region was considered as a unique unit, but whelks are mobile and it is possible for whelks to move between regions as planktonic larvae, benthic juveniles, and/or adults. The degree of larval connectivity between regions is related to physical oceanography (Wood & Hargis 1971, Mann 1988, Mann & Harding 2000) as well as larval whelk biology and settlement behavior (Mann & Harding 2003, Harding 2006). Juvenile and adult whelk movement remains poorly understood although migration between adjacent regions occurs.

Several assumptions were made to consider all bounty donations as a group rather than on a fishery-by-fishery basis. First, although whelk "catchability" varied with gear (crab pot, crab dredge, patent tong, oyster dredge/scrape), catchability remained relatively the same across years because the same fisheries contributed each year, that is, no whelk size class was potentially omitted from sampling within a year. The contributing fisheries covered the same spatial area each year regardless of whelks (by-catch). Relative increases (trends) in whelk abundance from a basin over time were due to an increase in regional whelk abundance (numbers) rather than a change in fishery effort. Finally, there was/is a lag between whelk recruitment to the benthos and whelk recruitment to fishing gear. All fishing gear selectively caught whelks with SL greater than 50–70 mm. Relatively low incidence of whelks smaller than approximately 50 mm SL does not mean that they were not present. Relatively rare encounters with whelks less than 50 mm SL almost certainly means that smaller whelks were consistently undersampled by the available sampling methods. A second, less likely, possibility is that smaller whelks had migrated from the specific habitat area(s) where the fisheries were active during fishing. Rapa whelks begin using infaunal rather than epifaunal habitats for at least a portion of the time at approximately 50 mm SL as their prey preferences and relative vulnerability to predators changes with changing SL (Harding 2003).

Whelk Culture at Ambient Conditions

Larval rapa whelks were cultured from egg masses at ambient Chesapeake Bay conditions between July and September 2005. After settlement, these juvenile whelks were cultured in ambient flow-through conditions through maturity with subsequent growth until September 2007. Whelks always had access to two or three prey items [e.g., oysters, mussels *Geukensia demissa* (Dillwyn, 1817); *Modiolus* sp. (Lamarck, 1799); *Mytilus* sp. (Linnaeus, 1758), northern quahogs] per individual and were thus not food limited. Monthly cultured whelk SL measurements combined with egg capsule deposition observations provide a guide for establishing maturity (onset of egg mass deposition) as well as age-at-length relationships for Chesapeake Bay rapa whelks less than 100 mm SL.

Data Analyses

All rapa whelks including empty shells, shells occupied by hermit crabs, and shells for which lengths could not accurately be measured have been included in the descriptions of whelk presence/absence by basin and year. A total of 27,624 rapa whelks were collected between June 1998 and November 2009 (Tables 1 and 2). Of these, 85% (23,375) were whelks that were either live or recently deceased (tissue still present in the shell) when collected (Table 3).

Wild Whelk Demographic Analyses

Demographic analyses include only whelks with tissue (live or recently deceased, hereafter referred to as live whelks) for

TABLE 1.

Summary of lower Chesapeake Bay *Rapana venosa* collection locations (Fig. 1), year of first collection, and observed SL range.

Tributary or region (abbreviation)	Description	Year of first collection	Total *n*	Min SL	Max SL
Atlantic Ocean	Within sight of land east and either north or south of Cape Henry and Cape Charles	2000	5	101	140
Eastern Shore	Tributaries entering on the Bay's eastern shoreline	2000	5	95	118
Chesapeake Bay mainstem	Chesapeake Bay between Cape Henry and Windmill Pt at the Rappahannock River mouth	1998	305	71	185
Lynnhaven Inlet		1999	59	94	150
OV	Inshore of the Thimble Shoals and Norfolk Channels along the Southern Bay shoreline extending from Lynnhaven Inlet to the HRBT	1998	7,241	49	195
Little Creek		1998	77	116	140
James River (JRship, HB, zones 1, 2, and 3)	JR includes the JR from Chesapeake Bay to DWS. JR regions include (1) HB (in between the HRBT and the MMBT at NNP), (2) the "lower" JRship parallel to Newport News Shipyard and coal terminals (between the SR 258 bridge and MMBT), and (3) the "upper" JR (between the SR 258 bridge and DWS near Mulberry Pt	1998	16,482	11	183
Lafayette River	Tributary draining into HB; south of Norfolk Naval base	1998	412	67	156
Elizabeth River	Tributary draining into HB	2001	376	41	159
Buckroe Beach	Buckroe Beach is on the western Bay shoreline inshore of the Thimble Shoals channel, immediately north of the JR	1998	309	58	165
Grandview	Grandview is on the western Bay shoreline inshore of the Thimble Shoals channel north of Buckroe Beach but south of the Back River mouth. Buckroe Beach and Grandview are separated by the mouth of Salt Pond	2001	19	53	171
Back River		1999	59	93	162
Poquoson River		2001	9	96	153
York River		1998	89	76	160
Mobjack Bay		2001	176	76	169
Rappahannock River		1998	2	130	142
Chesapeake Bay: Windmill Pt to Smith Pt	This area includes Virginia waters around Tangier Island and Pocomoke Sound and up to the Potomac River mouth	2000	3	125	146
Unknown	Specimens for which the collection location was unclear	NA	3,114	49	168
	Total number of rapa whelks collected		27,622		

Total *n*, the total number of whelks collected by region from 1998 to 2009; min SL, the region-specific minimum recorded shell length (mm); max SL, the region-specific maximum recorded shell length (mm); NA, not applicable; HRBT, Hampton Roads Bridge Tunnel; JR, James River; Pt, point; NNP, Newport News Pt. Regions where enough whelks were collected to use in demographic analyses have been assigned abbreviations. Year- and region-specific whelk collections are described in Table 2.

which an accurate SL could be recorded. Empty rapa whelk shells or rapa whelk shells occupied by hermit crabs [usually *Clibinarius vittatus* (Bosc, 1802); Harding & Mann 1999) were not included because the longevity of a rapa whelk shell postmortem is unknown. Inclusion of these whelk shells in the demographic analyses would potentially introduce error by considering whelks from previous years. Live whelks with damaged shells were also not included in demographic analyses because their SL could not be estimated accurately.

Annually, most live whelks (63.5%) were collected between January 1 and May 31 (Table 4). Whelk shell growth was assumed to be less than 5 mm in total between January 1 and May 31 because whelks grown at VIMS less than 70 mm SL did not begin seasonal shell deposition until late March or April (Fig. 2) and would not likely have increased SL by more than approximately 2 mm prior to May 31. Thus, only whelks collected between January 1 and May 31 were used in demographic analyses to ensure that whelks in similar growth conditions were compared.

The majority of live whelks were collected from Ocean View (OV), Hampton Bar (HB; between the Hampton Roads Bridge Tunnel and the MMBT), and James River non-oyster bar habitats between the MMBT and the SR-258 bridge [James River shipyard (JRship); Tables 1, 2, and 5, Fig. 1]. The collection methods used at OV, HB, and JRship did not sample the anthropogenic hard substrates (pilings, seawalls, tunnels, rip-rap). These regional data sets had enough whelks to analyze the demographic data using 5-mm-SL classes (Tables 1, 2, and 5).

Kolmogorov–Smirnov two sample tests (Sokal & Rohlf 1981) were used to test for differences in whelk SL demographics (5-mm-length classes) between OV, HB, and JRship within years. With one exception (described below), collections within these region and year combinations had sample sizes of more than 40 live whelks per 5-mm-length class and thus the large sample formulation for the Kolmogorov–Smirnov test statistic (*D*; Sokal & Rohlf 1981, Eq. 13.5, p. 445) was used. Whelk length demographics from OV, HB, and JRship (January–May)

TABLE 2.

Total number of rapa whelks collected by year including all types (live, dead, shell only, shell with hermit crab) and all months.

Region	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Total
Atlantic Ocean			1		1	1				1		1	**5**
Eastern Shore			2			2	1						**5**
Chesapeake Bay mainstem	4		3	5	6	60	28	17	21	129	32		**305**
Lynnhaven Inlet		2	11					3		3	40		**59**
OV	125	81	193	683	536	699	947	456	611	901	943	1,066	**7,241**
Little Creek	1	2	25	18	19	5					3	4	**77**
James R													
HB	12	158	22	859	842	368	764	501	619	599	650	1,724	**7,118**
JRship	60	155	132	114	399	146	402	2,757	1,016	265	467	757	**6,670**
Zone 1													
Nansemond R	1			56	17		431	576	109		1	337	**1,528**
Nansemond Ridge (NR)				1			8	64					**73**
High Shoal (HS)								8			2		**10**
Cruiser's Shoal (CS)							11	13	11				**35**
Dog Shoal (DS)								9					**9**
Brown Shoal (BS)					13			98	12		43	46	**212**
Thomas Rock (TR)							5	1,187	405	69	143	331	**2,140**
Miles Watch House (MW)									81				**81**
Gum Rock (GR)								50	3		25		**78**
White Shoal (WhS)						2		15	1	3			**21**
Warwick R								15				31	**46**
Zone 2													
Days Point (DP)												15	**15**
Wreck Shoal (WS)								4					**4**
Zone 3													
Burwell's Bay*												2	**2**
Pt of Shoals (PS)									3				**3**
DWS												11	**11**
Lafayette R	7	14	31	2	74	15	39	61		22	39	108	**412**
Elizabeth R				12	2	98		30	15	54		165	**376**
Buckroe Beach	31	3		57	46	24	25	27	40	40	7	9	**309**
Grandview				2	1	3		2	2		9		**19**
Back R		1		15	1	12	8	2	3	3	3	11	**59**
Poquoson R					3		2				2	2	**9**
York R	1	5	6	6	9	26		8		4	16	8	**89**
Mobjack Bay				14	125	4	1	1	2	10	17	2	**176**
Rappahannock R	1											1	**2**
Ches Bay: Windmill Pt to Smith Pt			2					1					**3**
Unknown	8	0	112	74	23	368	400	486	234	629	515	265	**3,114**
Total whelks	**251**	**421**	**540**	**1,917**	**2,104**	**1,831**	**3,048**	**4,943**	**2,672**	**2,660**	**2,744**	**4,491**	**27,622**

R, river; Pt, point. James River oyster substrate collections (italicized) were assigned to salinity zones using Haven and Fritz (1985).

* Burwell's Bay extends from Mulberry Pt to approximately Wreck Shoal (Fig. 1) and is useful only as a general designation versus a specific location.

were not significantly different from each other within each year between 1999 and 2009 (Table 6) with the exception of OV–JRship habitats for 2007 ($n = 88$, low JRship sample size). Thus, the length data from these three regions were pooled and compared across years with Kolmogorov–Smirnov two sample tests and used to describe the wild whelk age-at-length relationship in the next section.

Rapa Whelk Age-at-Length Relationship

Rapa whelk age-at-length estimations based on wild whelk collections for whelks up to 170 mm SL were made using the cohort analysis method described by Bhattacharya (1967). Wild whelk age-at-length estimates from these cohort analyses were offset to reflect an estimated hatch date of July 1 and an estimated collection date of March 15. The estimated hatch date is midway through the observed Chesapeake Bay spawning season (Harding et al. 2007a, 2008). The estimated collection date is midway between January 1 and May 31. The offset (9.5 mo/12 mo or 0.792 y) reflects the fact that whelks had not yet completed a full year of growth relative to their hatch date when collected.

The adjusted age-specific SL estimates were used to describe Chesapeake Bay wild rapa whelk population age-at-length relationships using the Von Bertalanffy (Von Bertalanffy 1938) growth model (Eq. 1). The Von Bertalanffy model has been used to describe age-at-length relationships in other gastropods that attain maximum SL in excess of 100 mm [e.g., *Lobatus*

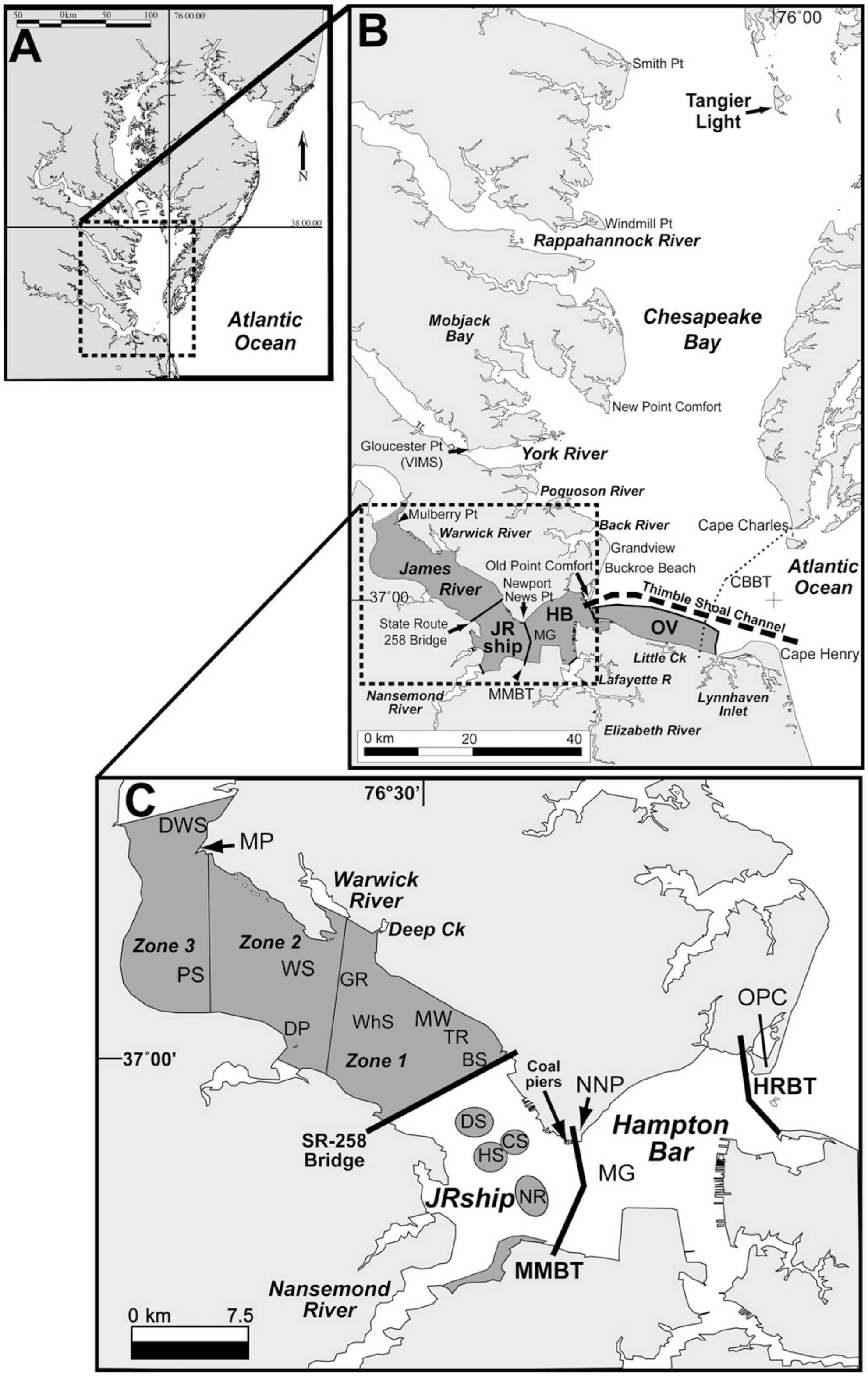

Figure 1. The U.S. mid-Atlantic coast with focus on the Chesapeake Bay rapa whelk range. Regions discussed in text and Tables 1 and 2 are identified. The three James River salinity zones are indicated (dark grey). Zone 1 includes oyster substrate within the JRship region and at the Nansemond River mouth as discussed in text. Abbreviations follow Tables 1 and 2.

TABLE 3.

Proportion of all rapa whelks by year and month that were live or recently deceased at collection (= live + dead with tissue).

					Month						
Year	January	February	March	April	May	June	July	August	September	October	November	December
1998	NW	NW	NW	NW	NW	1.00	NW	0.56	0.75	0.79	0.90	0.98
1999	0.95	0.86	0.67	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.94
2000	1.00	0.91	0.82	0.98	0.95	0.89	1.00	1.00	NW	1.00	0.94	1.00
2001	0.57	0.03	NW	0.99	0.99	0.93	0.93	0.88	0.86	0.89	1.00	0.81
2002	0.68	0.72	0.82	0.99	0.95	0.88	0.84	0.62	0.51	0.69	0.83	0.82
2003	0.80	0.94	0.65	0.92	0.97	0.89	0.32	0.93	0.50	0.80	0.86	0.70
2004	0.57	0.67	0.63	0.96	0.96	0.98	0.99	1.00	1.00	1.00	0.93	0.85
2005	0.53	0.33	0.42	0.78	0.90	0.77	0.83	0.72	0.82	0.57	0.77	0.33
2006	0.36	0.48	0.64	0.92	0.87	0.76	0.65	0.67	1.00	0.42	0.63	NW
2007	0.81	0.52	0.67	0.87	0.98	0.84	0.76	1.00	0.58	0.30	0.86	0.93
2008	0.52	0.70	0.88	0.95	0.84	0.91	0.87	0.75	NW	0.71	0.91	0.58
2009	0.44	0.92	0.64	0.95	0.89	0.93	0.79	0.77	0.90	NW	1.00	NW

NW, no whelks donated.

(=*Strombas*) *gigas* (Linneaus, 1758), Appledorn 1988; *Busycon carica*, Eversole et al. 2008; *Busycotypus canaliculatus*, Peemoeller & Stevens 2013], as well as numerous fish species. It assumes an initial SL of zero, reduction in SL growth rates with age, and attainment of a maximum terminal size (L_{inf}).

$$L_t = L_{\text{inf}}\left[1-e^{-K(t-t_0)}\right] \qquad (1)$$

where L_t is SL at age t, L_{inf} is the maximum asymptotic SL, K is the coefficient that describes the maximum growth rate to attain L_{inf} and t_0 is the age when SL is zero or an approximation of hatching time.

Twenty-six whelks between 170 and 196 mm SL were collected during the time series. The cohort analysis techniques of Bhattacharya (1967) require continuous and consecutive populations of length bins to estimate age-at-length. These larger SL classes did not satisfy this requirement (Fig. 3). Application of the Von Bertalanffy model to adjusted age-specific SL estimates for whelks less than 170 mm SL resulted in a maximum SL prediction (L_{inf}) of 173 mm (Table 7), more than 20 mm less than the actual largest Chesapeake Bay rapa whelk collected. To include the larger whelks in the age-at-length estimate and more accurately parameterize the maximum attainable size (L_{inf}), annual growth rates were estimated for SL bins 170–174.9 (3 mm/y), and 175–179.5 mm as well as 180–184.9, 185–189.9, and 190–195 mm (2 mm/y for each) and whelks were assigned to an age class after the appropriate seasonal adjustment described above. These growth rate estimates are based on reductions in annual shell growth each year after Age 12–13 indicated by the Von Bertalanffy fit for only whelks less than 170 mm SL (Table 7, Fig. 4).

Cultured rapa whelk age–length data (Fig. 2) were used to validate predicted age-at-length relationships for wild whelks less than 100 mm SL (Fig. 4) and provide information on length-at-maturity. Age-specific analysis of variance (ANOVA) were used to test for differences in SL-at-age between cultured and wild whelks. Shell lengths satisfied assumptions of homogeneity of variance and normality without

TABLE 4.

Number of live (= live whelks + dead whelks with tissue) rapa whelks by year and month across all locations and habitat types.

						Month							
Year	January	February	March	April	May	June	July	August	September	October	November	December	Total
1998	NW	NW	NW	NW	NW	2	NW	4	3	22	9	195	**235**
1999	39	101	6	52	139	4	24	2	6	4	4	15	**396**
2000	8	50	167	57	118	34	23	3	NW	2	15	9	**486**
2001	4	1	NW	623	851	228	51	30	6	8	12	25	**1,839**
2002	56	64	94	915	323	211	121	8	48	9	30	9	**1,888**
2003	16	15	22	144	911	147	129	37	2	4	6	32	**1,465**
2004	8	42	127	758	816	543	347	59	8	73	27	41	**2,849**
2005	29	56	99	295	949	857	554	232	18	163	336	69	**3,657**
2006	64	94	316	535	310	313	227	38	1	5	24	NW	**1,927**
2007	42	11	112	583	738	349	223	25	67	24	48	13	**2,235**
2008	22	39	162	1,435	302	102	177	114	NW	42	30	14	**2,439**
2009	8	22	23	995	1,077	843	801	162	27	NW	1	NW	**3,959**
Total	**296**	**495**	**1,128**	**6,392**	**6,534**	**3,633**	**2,677**	**714**	**186**	**356**	**542**	**422**	**23,375**

NW, no whelks collected.

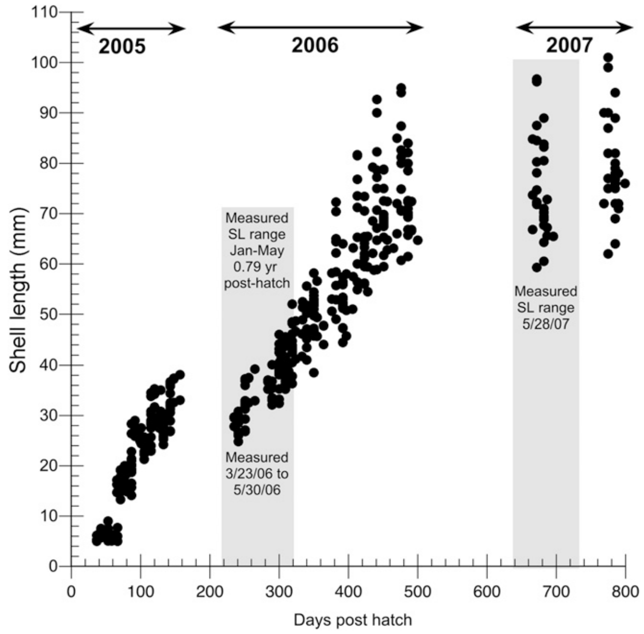

Figure 2. Age-at-length relationship for rapa whelks cultured under known growth conditions at the VIMS from hatch through settlement, maturity, and subsequent growth until September 2007.

transformation. Fisher's test was used for a post hoc multiple comparison.

The resulting Von Bertalanffy growth model ($R^2 = 0.99$ based on measurements of 13,749 individual whelks; Table 7, Fig. 4) was used to predict annual age-frequency distributions for the combined OV–HB–JRship region. Shell lengths were converted to ages for individual whelks using Eq. 2 (Bartoo & Parker 1983) and the Von Bertalanffy model coefficients calculated above.

$$t = t_0 + \ln\left[\frac{\left(1 - \frac{L_t}{L_{\text{inf}}}\right)}{-k}\right] \tag{2}$$

The resulting age-frequency distributions from 1999 to 2009 were compared between years with Kolmogorov–Smirnov two sample tests.

TABLE 5.

Rapa whelks from OV, HB, and JRship as a proportion of the total live whelks caught from January through May from 1999 to 2009.

Year	January	February	March	April	May
1999	1.00	0.99	1.00	0.92	0.97
2000	0.75	0.96	1.00	0.63	0.12
2001	1.00	1.00	NW	0.92	0.89
2002	1.00	1.00	0.96	0.80	0.90
2003	0.94	1.00	0.50	0.98	0.70
2004	0.88	0.93	0.87	0.81	0.65
2005	1.00	0.84	0.78	0.84	0.53
2006	0.94	0.74	0.64	0.82	0.57
2007	0.40	0.73	0.95	0.61	0.68
2008	0.95	0.36	0.73	0.83	0.66
2009	1.00	0.77	1.00	0.91	0.90

NW, no whelks collected.

TABLE 6.

Summary of two sample Kolmogorov–Smirnov tests between OV, HB, and JRship across years.

Year	OV–HB	OV–JRship	HB–JRship
1999	ND	ND	ND
2000	ND	ND	ND
2001	ND	ND	ND
2002	ND	ND	ND
2003	ND	ND	ND
2004	ND	ND	ND
2005	ND	ND	ND
2006	ND	ND	ND
2007	ND	*	ND
2008	ND	ND	ND
2009	ND	ND	ND

1998 was not included because there were no whelks collected from January to May.
* Demographics that were significantly different at alpha = 0.05; ND, demographics that were not significantly different at alpha = 0.05.

Spatial Invasion Trends

James River: Newport News Point to SR-258 Bridge (JRship)

The James River reach between Newport News Point and the SR-258 bridge (JRship, Fig. 1) encompasses soft bottom habitats used by infaunal bivalves such as northern quahogs (Mann et al. 2005) as well as habitats that are primarily oyster shell and/or living oysters (Haven et al. 1978, Mann et al. 2005, 2009b). Rapa whelk SL collected from oyster and nonoyster habitats within this region were compared to evaluate potential habitat use differences with length. Whelk length data satisfied neither homogeneity of variance nor normality regardless of the transformation (natural logarithm, logarithm, reciprocal, square root). Thus two Kruskal–Wallis tests were used to evaluate the effects of year and substrate type on observed rapa whelk SL. Years 1999 and 2000 were not included because the number of whelks collected from shell substrates in these years was 0 and 3, respectively.

Elizabeth and Lafayette Rivers

The Elizabeth and Lafayette Rivers join the HB region of the lower James River (Fig. 1). The Lafayette River has a narrow channel of approximately 3 m depth, whereas the Elizabeth River channel is maintained at 6–7 m depth to support the commercial and federal facilities that line the river banks. Both tributaries have substrate and food (oysters, northern quahogs) resources for rapa whelks. These tributary-specific demographic trends describe the time series of range expansion from the lower James River. Relatively low whelk numbers from the Lafayette (total $n = 91$) and Elizabeth River ($n = 287$) from January to May precluded river-specific SL demographic analyses using two sample Kolmogorov–Smirnov tests; however, a box-whisker plot for Lafayette and Elizabeth River whelk SL during 2005 and 2009 (when more than five whelks were collected from both tributaries) shows overlap between the tributary-specific SL frequency distributions (Fig. 5). Thus, SL frequency distributions from these tributaries were pooled for presentation and analyses. Two sample Kolmogorov–Smirnov tests were used to compare SL frequency distributions for 2002, 2003, 2005, 2007, and 2009 when more than 40 whelks were

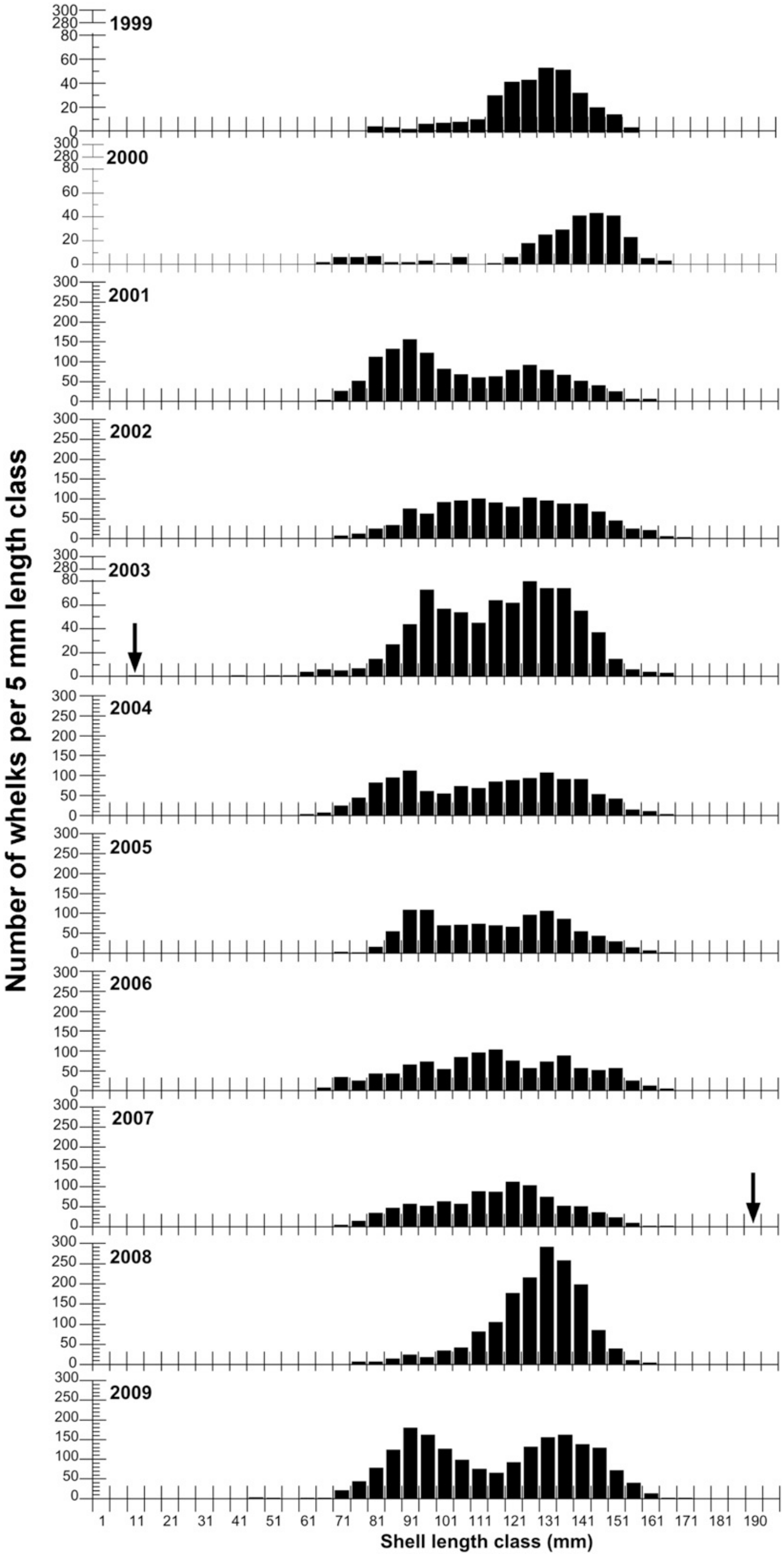

Figure 3. Shell length frequency distribution for live whelks collected at OV, HB, and JRship from January to May between 1999 and 2009. Vertical arrows distinguish the minimum (11 mm) and maximum (195 mm) SL observed.

collected. Age-frequency distributions for the combination of Lafayette and Elizabeth River whelk collections each year from 2002 through 2009 were also evaluated with two sample Kolmogorov–Smirnov tests.

James River Oyster and Shell Substrates (Zones 1, 2, 3)

The increase in whelks observed on oyster substrates in the lower James River after 2004 reflects known whelk range expansions (Harding & Mann 2005) into the James River oyster

TABLE 7.

Summary of Von Bertalanffy models used to estimate Chesapeake Bay *Rapana venosa* age-at-SL.

Metric	Bhattacharya (1967) estimates only	Bhattacharya (1967) and growth estimates for whelks >170 mm SL*
Minimum SL used for estimate	31	31
Maximum SL used for estimate	165	195
n data pairs	63	82
n whelks contributing	13,724	13,749
R^2	0.98	0.99
L_{inf} (standard error)	173.32 (4.65)	188.34 (1.76)
K value (standard error)	0.2013 (0.0154)	0.1608 (0.0057)
t_0 value (error)	–0.8477 (0.1370)	–1.2031 (0.1103)

* Annual growth rates were estimated for SL bins 170–174.9 (3 mm/y) and 175–179.5 mm as well as 180–184.9, 185–189.9, and 190–194.9 mm (2 mm/y for each), and whelks were assigned to an age class based on reductions in annual shell growth each year after Age 12–13 indicated by the Von Bertalanffy fit for only whelks less than 170 mm SL.

habitats above Newport News Point (Tables 1 and 2, Fig. 1). Based on oyster distribution (Mann et al. 2009a, 2009b) and salinity (Haven & Fritz 1985), James River whelk collections from oyster and shell substrate were categorized into zone 1 (between Wreck Shoal and Newport News Point/MMBT, including the lower Nansemond River and the Warwick River), zone 2 (between Point of Shoals and Wreck Shoal, including Wreck Shoal), and zone 3 [above Point of Shoals to Deep Water Shoal]. Only zone 1 had enough whelks (>5 whelks per year per 5-mm-SL bin) in consecutive years to apply Kolmogorov–Smirnov tests to evaluate demographic changes over time related to upriver range expansions. Two sample Kolmogorov–Smirnov tests were used to describe potential changes in zone 1 length-frequency distributions from 2004 to 2009.

The observed SL demographics for whelks collected in zone 1 on oysters from 2004 to 2009 were recast as annual age demographics using Eq. 2 and the Von Bertalanffy parameters described above. The resulting age demographics were then compared using two-sample Kolmogorov–Smirnov tests.

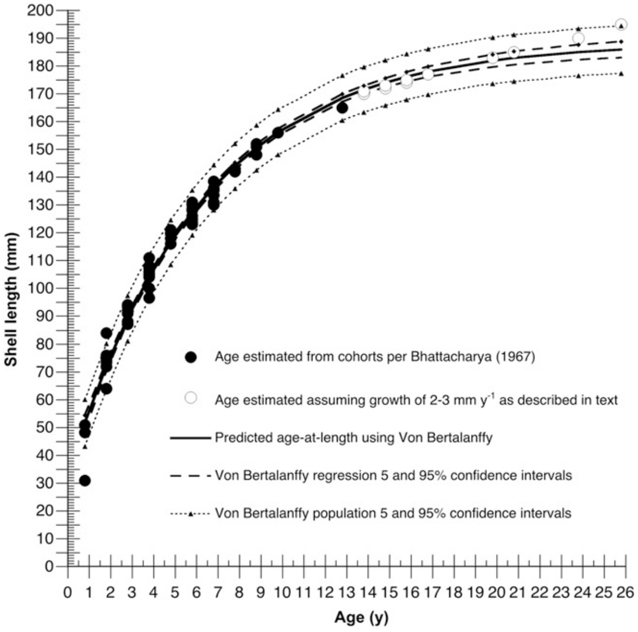

Figure 4. Chesapeake Bay rapa whelk age-at-length relationship with the fitted Von Bertalanffy growth curve including regression and population 5 and 95% confidence intervals. Regression coefficients, error terms, and coefficient of determination are provided in Table 7.

Influence of Environmental Conditions

Average daily water temperatures from the VIMS at Gloucester Point on the York River were used to calculate average monthly and quarterly water temperatures. Mann et al. (2009a) demonstrated that Wreck Shoal (James River, zone 1; Fig. 1) water temperatures are similar to those recorded at Gloucester Point. Average daily salinities at 3 m depth for Wreck Shoal were estimated using USGS discharge data (http://waterdata.usgs.gov/va/nwis/uv/?site_no=02037500, station 02037500) per Mann et al. (2009a) and summarized at monthly and quarterly intervals.

Average daily water temperature data measured at Middle Ground Light (MG on Fig. 1; Harding et al. 2013) were compared with measured VIMS water temperatures from 729 dates in 2007 through 2009 when both monitoring stations were active at both sites using a linear regression ($y = 0.35 + 0.96 \times x$; $R^2 = 0.995$). A slope of 1 indicates that water temperatures are the same at both sites. York River water temperatures were used for monthly, quarterly, and decadal (1979 to 2009) residual descriptions at Middle Ground because the resulting slope (0.96) indicated that water temperatures at Middle Ground are approximately equal to those observed at VIMS.

Average daily salinity at Middle Ground Light was compared with average daily VIMS salinity with a linear regression using average daily salinity measured for 526 dates in 2007 to 2009 when both monitoring stations were active. The resulting regression ($y = 0.09 + 1.00^* x$; $R^2 = 0.85$) accounted for 85% of the variation observed in salinity between sites. Because the slope of the line (1.00) indicated a 1:1 relationship between salinity at these sites, VIMS salinity was used to describe monthly, quarterly, and decadal residual values from the 20 y (1989 to 2009) monthly and quarterly averages for OV, HB, JRship, and the Elizabeth and Lafayette Rivers. These salinity estimates were used in Pearson correlations evaluating salinity influences on whelk collections that are described below.

A linear regression was applied to daily salinity estimates at 3 m for Wreck Shoal and average daily Middle Ground Light salinity from March 2007 through December 2009 ($y = 13.83 + 0.47 \times x$; $R^2 = 0.47$). Wreck Shoal salinity estimates were used

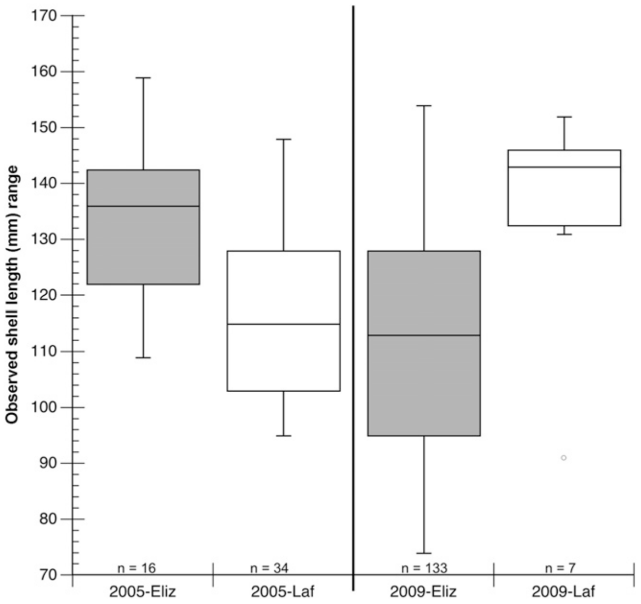

Figure 5. Box–Whisker plot presenting the observed rapa whelk SL ranges in the Elizabeth (Eliz, grey) and Lafayette (Laf, white) Rivers during 2005 and 2009 when whelks were collected in both rivers. *n*, the number of whelks within a river and year. The single horizontal line within each box indicates the median. The upper and lower box boundaries show the 25th and 75th percentile. The "whiskers" or vertical lines show the data range (maxima, minima).

only to describe salinity in zone 1, adjacent to Wreck Shoal, rather than all sites within the James River because this regression accounts for only 47% of the salinity variation observed between Wreck Shoal and Middle Ground. Monthly and quarterly average salinity estimates as well as deviations from the 30 y (1979 to 2009) monthly and quarterly averages were made.

Pearson correlations were made between average monthly (January, February, March, April, and May), quarterly (January–March and April–June) water temperature or salinity and the number of whelks collected from January to May in the same year within each geographic area (OV–HB–JRship, Elizabeth and Lafayette Rivers, and James River zone 1). Pearson correlations were also made between observed conditions in December and the fourth quarter (October–December) immediately preceding the January–May whelk collections for each geographic region.

RESULTS

A total of 27,624 rapa whelks ranging in SL from 11 to 195 mm were collected in the Chesapeake Bay between June 1998 and November 2009 (Tables 1 and 2). Whelks were present in every major western Chesapeake Bay region south of Windmill Point by November 2009 (Table 1, Fig. 1). The observed benthic whelk distribution generally follows the distribution of the 15 isohalines at approximately10 m across seasons (Stroup & Lynn 1963, Rennie & Neilson 1994, Mann & Harding 2000, 2003). Rapa whelk range expansion from the lower James River [adjacent to the coal terminals at Newport News Point (Harding & Mann 1999, 2005, Mann & Harding 2000)] into oyster habitats between Newport News Point and Mulberry Point (Fig. 1) including the Nansemond and Warwick Rivers was facilitated by local physical oceanography (local gyres, two-layer partially mixed estuary) centered at Newport News Point (Wood & Hargis 1971, Mann 1988, Mann & Harding 2000).

Whelk presence in the Elizabeth and Lafayette Rivers and oyster habitats between Newport News Point and Mulberry Point (Fig. 1) including the Nansemond and Warwick Rivers increased from 1999 to 2009 (Table 2). Between 2004 and 2009, the James River rapa whelk range expanded to Deep Water Shoal, the most up-estuary location for commercially fished oyster bars (Tables 1 and 2, Fig. 1). Thus, by September 2009, the James River rapa whelk range encompassed the entire spatial footprint for extant commercial northern quahog and oyster populations (Mann et al. 2005, Mann et al. 2009a).

The largest whelks (170–195 mm SL) were consistently found near the Chesapeake Bay mouth and off OV in the vicinity of the Chesapeake Bay Bridge Tunnel and islands (Table 1, Fig. 1). This region includes the shipping deballasting zones just up-estuary of Cape Henry and adjacent to the Thimble Shoals Channel.

Of the whelks received through the bounty program, 85% (23,375) were either alive or recently deceased (tissue still present in the shell) when reported (Table 3). As described above, demographic analyses focused on whelk collections between January 1 and May 31 (63.5% of all annual collections) from the combined OV, HB, and JRship locations (Table 4) to ensure valid comparisons across years and large sample sizes.

SL Demographic Trends

The observed whelk demographics for OV, HB, and JRship showed consistent representation across the 81- to 161-mm SL range and a general increase in whelks per length class with time (Fig. 3). With the exception of 2007, observed whelk length frequencies in these regions were similar within a year (Table 6). During 2007, whelks less than 116 mm SL were not observed among the 88 whelks (total) collected from JRship.

The incidence of whelks less than 81 mm SL was always relatively low but did increase with time between 1999 and 2009 (Fig. 3). Small whelks typically were collected as epifauna on larger whelks, notably the 11- and 41-mm SL whelks in 2003, the 25-, 31-, 35- and 46-mm SL whelks in 2005 and the 36- and 46-mm SL whelks in 2009 (Fig. 3). Whelks greater than 170 mm SL were rarely reported (25/23,375 or 0.1%). Whelks greater than approximately 170 mm SL are too large to fit within the funnels of a standard commercial crab pot. These large whelks were/are vulnerable to collection only when a patent tong (for oyster or northern quahog harvest) or dredge (for oyster, blue crab, channel whelk, or knobbed whelk harvest) deployment was directly coincidental or when whelks remained attached to a crab pot exterior when the pot was pulled. The latter primarily applied to large females that were cementing egg capsules to the crab pot mesh.

Whelk demographics observed across OV, HB, and JRship changed significantly between 1999 and 2009 (Table 8). Whelk demographics in 2000 were different from those in all other years. This is probably due to both relatively low representation across length classes but particularly limited representation of whelks less than approximately 120 mm SL compared with other years (Fig. 3). The 2008 demographics were significantly different from all other years except 1999 (Table 8, Fig. 3) and

TABLE 8.

Summary of two sample Kolmogorov–Smirnov tests on SL frequency distributions for rapa whelks collected between January 1 and May 31 from the combined OV, HB, JRship regions during 1999 to 2009.

Year	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
1999	ND	*	ND	ND	*	*	*	*	ND	*
2000		*	*	*	*	*	*	*	*	*
2001			*	*	ND	*	*	*	*	ND
2002				ND	ND	ND	ND	ND	*	ND
2003					ND	ND	ND	ND	*	ND
2004						ND	ND	ND	*	ND
2005							ND	ND	*	ND
2006								ND	*	*
2007									*	*
2008										*

No whelks were collected from January to May 1998.
* Demographics that were significantly different at alpha = 0.05; ND, demographics that were not significantly different at alpha = 0.05.

were characterized by a unimodal distribution or single peak across the 121- to 145-mmlength classes rather than the broad, relatively flat distribution observed from 2002 to 2006 for the approximately 76- to 160-mmlength range (Fig. 3). Bimodal length distributions were observed in 2001, 2004, and 2009 (Fig. 3). Within these years, only 2001 was significantly different from other years in multiple years (6 out of 8 y examined; Table 8). The first distribution peak, centered at 91–95 mm SL, was consistent across these years (Fig. 3). The second demographic peak shifted with time from a center of approximately126–130 (2001) to 131–135 mm (2004), and then 136–141 mm SL (2009).

Wild Whelk Age-at-Length Relationship

The combined OV–HB–JRship SL demographic was used for estimates of age-at-length per Bhattacharya (1967) for cohorts between 71 and 171 mm SL. The fitted Von Bertalanffy growth curve ($n = 82$ data pairs based on 13,749 individual whelk measurements) using cohorts and growth estimates based on cohort growth predicted 99% of the SL variation with age (Table 7, Fig. 4). The resulting regression and population 5 and 95% confidence intervals encompassed the range of data pairs from cohort analyses (Fig. 4). The maximum predicted SL (L_{inf}, 188 mm) includes all but 2 of the 23,375 live whelks collected between 1999 and 2009. The lengths of these two very large whelks fall within (190 mm SL) or on (195 mm SL) the boundaries of the regression population 95% confidence limits (Fig. 4).

Whelks cultured at ambient conditions in the lower York River (VIMS) between July 2005 and September 2007 reached SL of 35.2–52.0 mm ($n = 32$ whelks) by 0.86 y post-hatch (May 2006, Fig. 2). These 2005-hatched cultured whelks reached SL of 59.3–96.7 mm ($n = 31$ whelks) by May 28, 2007, 1.86 y post-hatch (Fig. 2). These age–length data for whelks cultured at ambient environmental conditions are in agreement with the lengths predicted by the Von Bertalanffy model for 0.86 (53.2 mm) and 1.86 y (73.3 mm; Fig. 4). Cultured and wild whelks had similar SL at Age 1 (ANOVA, df = 1, $F = 2.92$, $P = 0.09$) and Age 2 (ANOVA, df = 1, $F = 0.02$, $P = 0.88$).

The Von Bertalanffy age estimates were combined with collection year for whelks larger than 169 mm SL to estimate the year of first introduction to the Chesapeake Bay (Table 9). These data identify 1981 as the earliest year that rapa whelk veligers were introduced to the Bay with survival through metamorphosis and recruitment. This estimate is 17 y before the first confirmed reports of adult whelks (June 1998; Harding & Mann 1999). Whelks greater than 169 mm SL were typically collected from relatively deep regions (Table 9, Fig. 1) where northern quahogs occur at densities of more than 9–20/m^2 (Mann et al. 2005).

The Chesapeake Bay Von Bertalanffy age-at-length relationship was applied to individual whelk SL resulting in combined OV–HB–JRship whelk age-frequency distributions from 1999 to 2009 (Fig. 6). Whelks younger than Age 2 and older than Age 10 were rarely collected (Fig. 6). Nine and 10 y-old whelks were present in every year from 1999 to 2009. The relative abundance of these older age classes remained static until 2009 when the number of Age 9 whelks increased by approximately 50% from 2008 (52 versus 107 in 2009). This increase may be due to the progression of the 1998 year class that was evident in 2001 (Age 3) reaching Age 9 (Fig. 5). Limited numbers of 11- to 15-y-old whelks were consistently represented through the time series (Fig. 6). Representation within individual age classes increased during the time series, whereas the observed age class range remained generally unchanged. In general, most (49/55 pairs) of the annual age-frequency distributions were significantly different from each other (Table 10) indicating a dynamic population with both active recruitment to the younger age classes and emigration from fished habitats, mortality, or both in age classes older than approximately 10–11 y.

Rapa whelk age distributions from OV–HB–JRship in 1999, 2000, and 2008 had few whelks less than Age 5 represented. The 2001 age distribution was strongly skewed toward Age 3 individuals (1998 year class; 414 of 1334 whelks; 31%) and significantly different from the age distribution in any other year (Table 10). 2001 was also notable because it was the first year in which age classes from Age 1–12 were represented simultaneously with six age classes containing more than 100 whelks each. Five to six age classes between Age 2–3 and 7–8 were always represented by 100 whelks annually between 2001 and 2008. By 2009, five age classes had at least 200 whelks. Although the 2009 age distribution was also dominated by Age 3 individuals (446 of 1,927; 23%), Age 6 and Age 7 were also well represented (249 whelks in these age classes; 13%).

Whelk recruitment was strong in 1998 and 2001, and the resulting cohorts were still evident in the population demographic 7–8 y post-recruitment (Figs. 3 and 6); 1990 appears to also have been a good year for recruitment as that cohort was still disproportionately represented in the 2000 demographic (Figs. 3 and 6). The 1990 year class produced 3 of the 25 oldest whelks observed between 1999 and 2009 (Table 9). The 1989 year class also resulted in three of the 25 oldest whelks, whereas the 1986 year class contributed four of the largest whelks (Table 9). The 2009 age demographic for the combined OV–HB–JRship region suggests that the 2006 year class was also a strong year class but it remains to be seen how long or if this recruitment signal will persist in the population.

Spatial Invasion Trends

James River: Newport News Point to SR-258 Bridge (JRship)

The James River reach between the SR-258 bridge and Newport News Point (and the MMBT, JRship; Fig. 1) is a transition zone between the upper and lower estuaries. Remnants of the

TABLE 9.

Estimated natal year and year of first introduction to Chesapeake Bay via veligers for rapa whelks less than 170-mm SL.

Collection year	SL (mm) at collection	Estimated age at collection (y)	Estimated natal year	Collection location
2007	195	25.79	1981	OV
2002	183	19.79	1982	HB
2008	190	23.79	1984	OV
2000	173	14.79	1985	HB
2001	175	15.79	1985	HB
2000	170	13.79	1986	OV
2002	174	15.79	1986	OV
2002	175	15.79	1986	OV
2007	185	20.79	1986	Bay mouth near CBBT
2001	171	13.79	1987	HB
2001	171	13.79	1987	HB
2002	173	14.79	1987	HB
2002	170	13.79	1988	OV
2002	171	13.79	1988	HB
2003	171	13.79	1989	HB
2003	171	13.79	1989	Buckroe Beach
2005	174	15.79	1989	OV
2004	170	13.79	1990	OV
2006	174	15.79	1990	Bay mouth near CBBT
2007	177	16.79	1990	Bay mouth near CBBT
2005	170	13.79	1991	HB
2007	172	14.79	1992	Bay mouth near CBBT
2008	173	14.79	1993	JRship
2009	171	13.79	1995	JRship
2009	171	13.79	1995	HB

Natal year estimates are based on collection information for large whelks combined with the Chesapeake Bay *Rapana venosa* age-at-length relationship (Table 7, Fig. 4).

historic oyster reef system (Haven et al. 1978, Hargis 1999, Woods et al. 2005) persist in the relatively shallow regions just south and west of the deep main channel that parallels the heavily developed eastern shoreline (Mann et al. 2009b). The public oyster grounds (Nansemond Ridge, Cruisers Shoal, High Shoal, and Dog Shoal) are relatively shallow (<6 m) and receive oyster recruitment annually (Fig. 1; Haven & Fritz 1985, Mann 1988, Southworth et al. 2009, 2010, 2011). These oyster beds are also adjacent to privately leased bottom in the nearshore subtidal waters along the southern shoreline that extend into the Nansemond River mouth, which annually supports additional oysters.

Although live oyster and oyster shell substrate are largely absent in the modern Hampton Roads region, these substrate types are still present above the SR-258 bridge (Fig. 1). Whelks from oyster substrates below the SR-258 bridge were considered with zone 1. Whelks from non-shell substrate within this reach were considered with the OV–HB–JRsh region. Although reported collection depths for both habitat types span the range from 1.5 to 19.8 m, the mean depth for whelk collections associated with shell substrate was 8.1 m, whereas the mean depth for non-shell whelk collections was 10.1 m. The standard deviation for both habitat collection depths was 5.48 m.

Although the whelk SL range observed from non-shell substrate (50–168 mm SL) overlapped the whelk length range from oyster habitats (47–171 mm SL), rapa whelks collected from oysters or oyster shell substrate were significantly larger than whelks collected from non-shell habitats (Kruskal–Wallis, $H = 61.89$, $P < 0.01$) with a 16 mm difference in mean SL between habitat types. The observed length difference with habitat type may relate to predation vulnerability as well as foraging strategies. Whelks on oyster substrates are epifaunal, at least when feeding. Whelks on non-shell substrates are typically infaunal and burrowing affords them a potential predation refuge. It should be noted that rapa whelks follow a diel activity pattern whereby they are more active at night (Harding, unpublished data). It is likely that infaunal whelks, particularly those that have not reached a size refuge from predation, move into different habitats at night and then resume infaunal residency by day. Bombace et al. (1994) described nocturnal migration onto artificial reefs by Mediterranean rapa whelks from adjacent infaunal habitats. Rapa whelks larger than 30–40 mm SL transition from drilling their bivalve prey to other predation strategies (Harding et al. 2007b). At larger lengths, rapa whelks and other large whelks open infaunal or epifaunal bivalves through a combination of mechanical and chemical methods that rely on the whelk foot being suitably sized to grasp the prey item (Carriker 1951, Wells 1958, Ansell & Morton 1987). Larger whelks are more capable of opening larger oysters than smaller whelks.

Elizabeth and Lafayette Rivers

The whelks collected in the Elizabeth and Lafayette Rivers from 2000 through 2009 ranged from 41 (Age 0) to 159 mm SL (Age 10; Figs. 7 and 8). Whelk abundance was lower in these tributaries than in the OV–HB–JRship region in all years (Table 2). No whelks were reported from either river in 1999 or 2001, whereas only two whelks were reported between January and

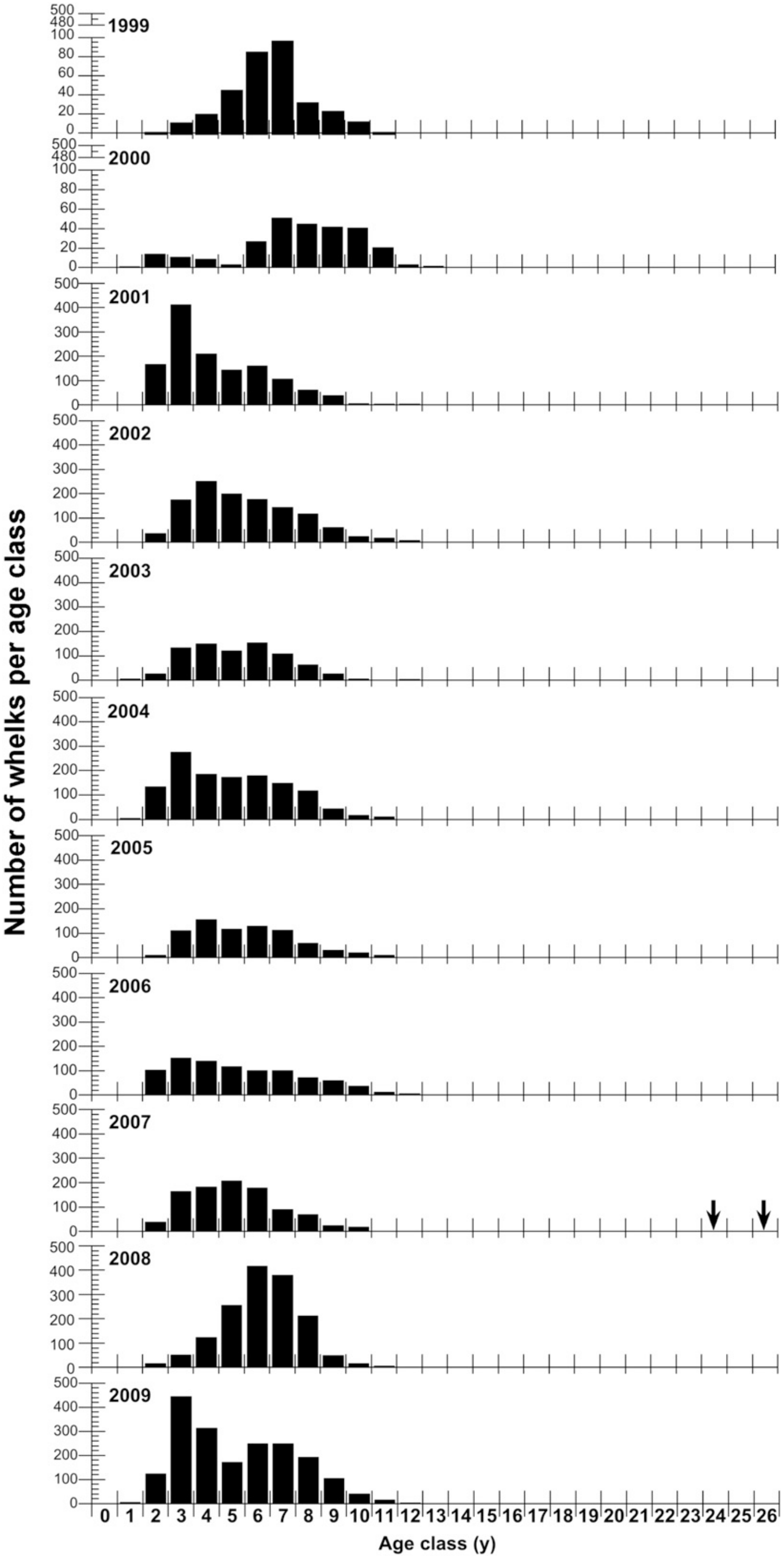

Figure 6. Age-frequency distribution for live rapa whelks collected at OV, HB, and JRship between 1999 and 2009 from January to May. Vertical arrows distinguish the two oldest whelks (24 and 26 y, both in 2007).

May 2000. The apparent ''alternation'' of whelk collections in these rivers in 2003, 2004, and 2006 through 2008 as well as the demographic gaps between Age 2–3 and Age 7–8 in 2006, 2007, 2008 probably have more to do with the opportunistic nature of the bounty program combined with commercial fisherman behavior than whelk biology. Ninety-two percent of whelk donations from these rivers ($n = 696$) across all years and months came from the blue crab pot fishery. The timing of blue

TABLE 10.

Summary of two sample Kolmogorov–Smirnov tests on age-frequency distributions for whelks collected between January 1 and May 31 from the combined OV, HB, and JRship regions from 1999 to 2009.

Year	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
1999	*	*	*	*	*	*	*	*	ND	*
2000		*	*	*	*	*	*	*	*	*
2001			*	*	*	*	*	*	*	*
2002				ND	*	*	*	ND	*	*
2003					*	*	*	ND	*	*
2004						*	*	*	*	ND
2005							*	*	*	ND
2006								*	*	*
2007									*	*
2008										*

No whelks were collected from January to May 1998.
* Demographics that were significantly different at alpha = 0.05; ND, demographics that were not significantly different at alpha = 0.05.

crab migration from Hampton Roads into and out of the Elizabeth and Lafayette Rivers depends on the speed at which the water warms in the spring and cools in the fall, respectively. A fisherman's decision on where to set pots relates to the level of success at the current pot deployment location(s) as well as landing and vessel logistics. Biological and logistical factors determine when (or if) crab pots will be placed in these rivers and these factors vary within a year as well as across years. It is likely that some rapa whelks used these rivers in each year between 2002 and 2009 and simply did not overlap with gear that was fishing between January 1 and May 31.

There were no differences in rapa whelk SL or age demographics in the Lafayette and Elizabeth Rivers between 2003 and 2009 (Table 11, Fig. 5). Most whelks in these tributaries were 3–8 y old (Fig. 8). Two and 3 y old whelks were not observed in the Lafayette and Elizabeth Rivers during 2002 even though these age classes were relatively abundant in the OV–HB–JRship region during 2002 (Fig. 6). Age 9–10 whelks were observed in 2005 and then from 2007 through 2009. The gradual increase in observed Age 9–10 whelks matches the increase in relative abundance of these age classes observed in the OV–HB–JRship region that probably serves as a source for the Elizabeth and Lafayette River whelks. In 2009, the strength of the 2006 year class, indicated by higher relative abundance of Age 3 whelks, also observed in the OV–HB–JRship region was evident in the Elizabeth and Lafayette River demographics (Figs. 6 and 8).

James River Oyster and Shell Substrates (Zones 1, 2, 3)

Rapa whelks were absent from zones 1 through 3 from 1998 through 2000 with the exception of a single whelk collected from the Nansemond River in 1998 (Table 2). From 2001 to 2003, 73 of the 87 whelks collected across years were from the lower Nansemond River, whose location adjacent to HB and the deeper non-oyster reef habitats of the JRship region as well as resident oyster populations made it a logical dispersal region for whelks from these areas (Table 2). This trend continued in 2004 when more whelks (total $n = 431$) were collected from the lower Nansemond River than from the JRship region (total $n = 402$; Table 2). Although whelks were collected from three other zone 1 locations during 2004, none of these collections included more than 11 whelks (Table 2). The collection of 44 whelks from James River zone 1 sites above the SR-258 bridge between December 2004 and February 2005 prompted Harding and Mann's (2005) description of this range expansion. The number of zone 1 collections continued to increase through spring and summer 2005, particularly when fishermen used small dredges on private leased oyster grounds within the region, ultimately yielding a total of 2,035 whelks for the year (Table 2). Zone 1 whelk catch declined during 2006, relative to 2005, although both Thomas Rock and the Nansemond River still produced hundreds of whelks (Table 2). Relative abundance remained low in 2007 and 2008 but zone 1 whelk catch increased in 2009, with most of the 745 whelks being collected from oyster habitats in the Nansemond River and Thomas Rock (Table 2).

Whelk occupancy of zone 2 was first reported on the north side of the shipping channel in 2005 (Wreck Shoal; Fig. 1). Whelks were not observed in zone 2 again until 2009 when they were found on the south side of the shipping channel at Day's Point (DP; Table 2, Fig. 1). Whelks were only collected from zone 3 in 2006 ($n = 3$; Point of Shoals, PS; Table 2, Fig. 1) and 2009 ($n = 11$; Deep Water Shoal, DWS; Table 2, Fig. 1).

Zone 1 collections from January through May included whelks ranging from 46 to 175 mm SL with most SL and age classes represented in 2002 as well as from 2004 through 2006 and again in 2009 (Figs. 9 and 10). Rapa whelks were completely absent from zone 1 from 1998 to 2000 and only collected from June through September in 2001 (Table 2). Whelks from Age 1 (2004) to 14 (2009) were observed including representatives from Age 9 and older in every year when whelks were observed. The James River zone 1 demographics changed significantly between years until 2007 to 2009 (Table 12). Although no whelks were collected from zone 1 from January to May 2003, the numbers of whelks, particularly in the Age 2 and Age 3 classes, were relatively high in 2004 compared with previous years (Fig. 10). This trend for strong recruitment increased in 2005 but recruitment declined from 2006 through 2008. Relative abundance also declined in each year after 2005 with the lowest whelk numbers since 2001 ($n = 6$) observed in 2007 ($n = 32$). Whelk numbers were relatively low in 2009 ($n = 39$) but Age 2 and Age 3 whelks were observed in 2009 after a 2 y absence as part of a demographic in which most size or age classes were represented (Figs. 9 and 10).

Influence of Environmental Conditions on Whelk Recruitment

Average monthly water temperature ranged from 2.45°C (January 2005) to 29.15°C (August 2005), as is typical for these regions of the lower Chesapeake Bay (Mann et al. 2009a). Seven out of 11 y during the time series experienced January–March temperatures that were above the 1979 to 2009 average (Table 13, Fig. 11). In most cases, temperatures during April, May, and June were also above average relative to the 30 y average except for 2003 and 2005, which were below average. The number of whelks observed from January to May from 1999 to 2009 was not correlated with monthly or quarterly water temperatures during the same year of collection, or water temperatures experienced in December or October–December of the previous year (Tables 14 and 15) with one exception. There was a significant correlation between second Quarter (January–March) water

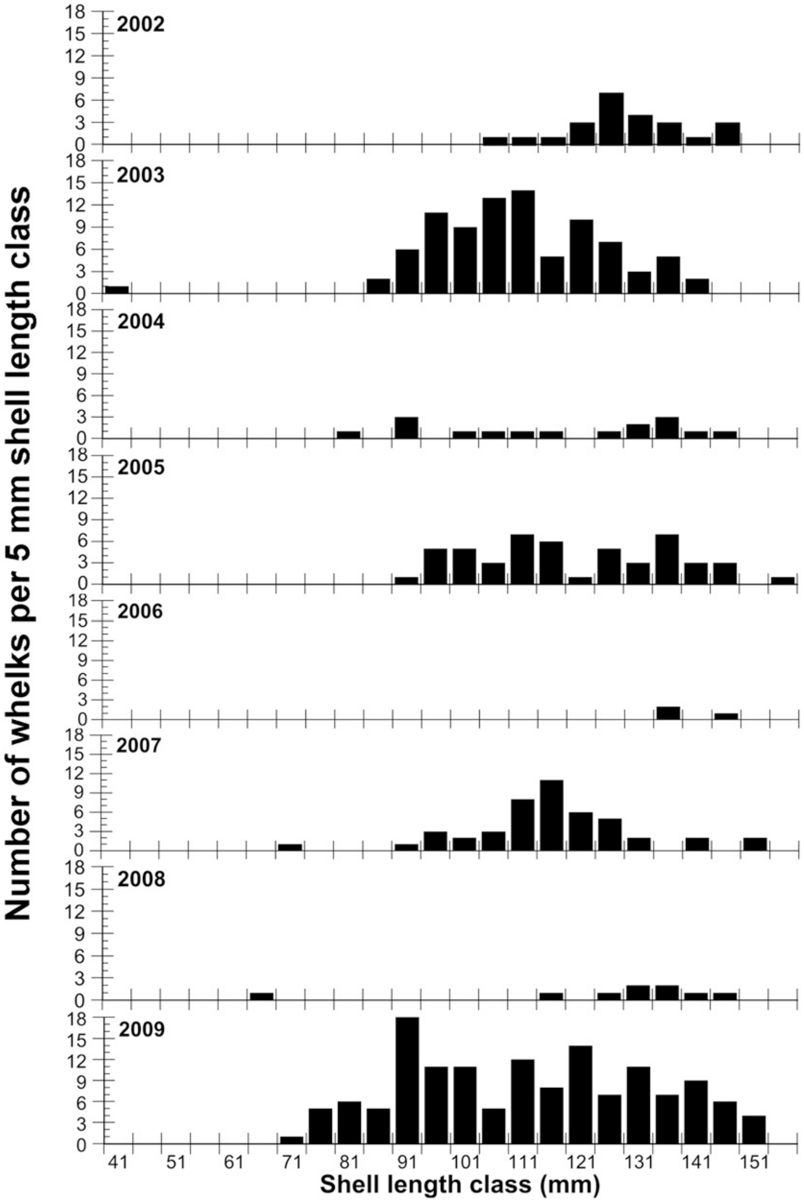

Figure 7. Shell length demographics for the combined Elizabeth and Lafayette Rivers from 2002 to 2009 presented by 5-mm SL class. The smallest SL within a size class is used to refer to that group. Whelk collections from these tributaries in 1998 to 2001 were not numerous enough to consider for demographic analyses.

temperatures and the number of whelks observed in the Elizabeth and Lafayette Rivers (Table 15) with fewer whelks observed during colder years.

The observed annual and decadal Chesapeake Bay temperature ranges were within the reported thermal range for rapa whelk native habitats (Tsi et al. 1983, Chung & Kim 1997, Chung et al. 1993) as well as other estuaries where rapa whelks have successfully invaded (Black Sea: Mann & Harding 2000; Rio de la Plata: Giberto et al. 2006). Benthic whelks are mobile and will remain within appropriate temperature boundaries, much like mid-Atlantic Bight shelf molluscan distributions are set seasonally by the isotherm distributions (Franz & Merrill 1980). If shallow habitats get too warm or cold, whelks will leave them seasonally to occupy deeper more stable habitats. As mentioned above, the seasonal trends observed in the Elizabeth and Lafayette Rivers likely result from thermally modulated seasonal migrations.

Although temperature sets the upper and lower boundaries for survival, it also dictates thresholds for fundamental biological processes directly related to establishment of an introduced species in the receptor habitat. Water temperatures of 10–12°C mark the seasonal onset of feeding in rapa whelks (Harding, unpublished data) as with the native oyster drills (Federighi 1931, Andrews 1956). Rapa whelk egg capsule deposition begins at 18°C (Chung et al. 2002, Harding et al. 2007a, 2008) and ceases after temperatures exceed 28°C (Harding et al. 2007a, 2008). The temperature parameters associated with reproduction describe spawning season duration, which may be a key factor in the resulting year class strength and observed interannual variation in year class persistence observed

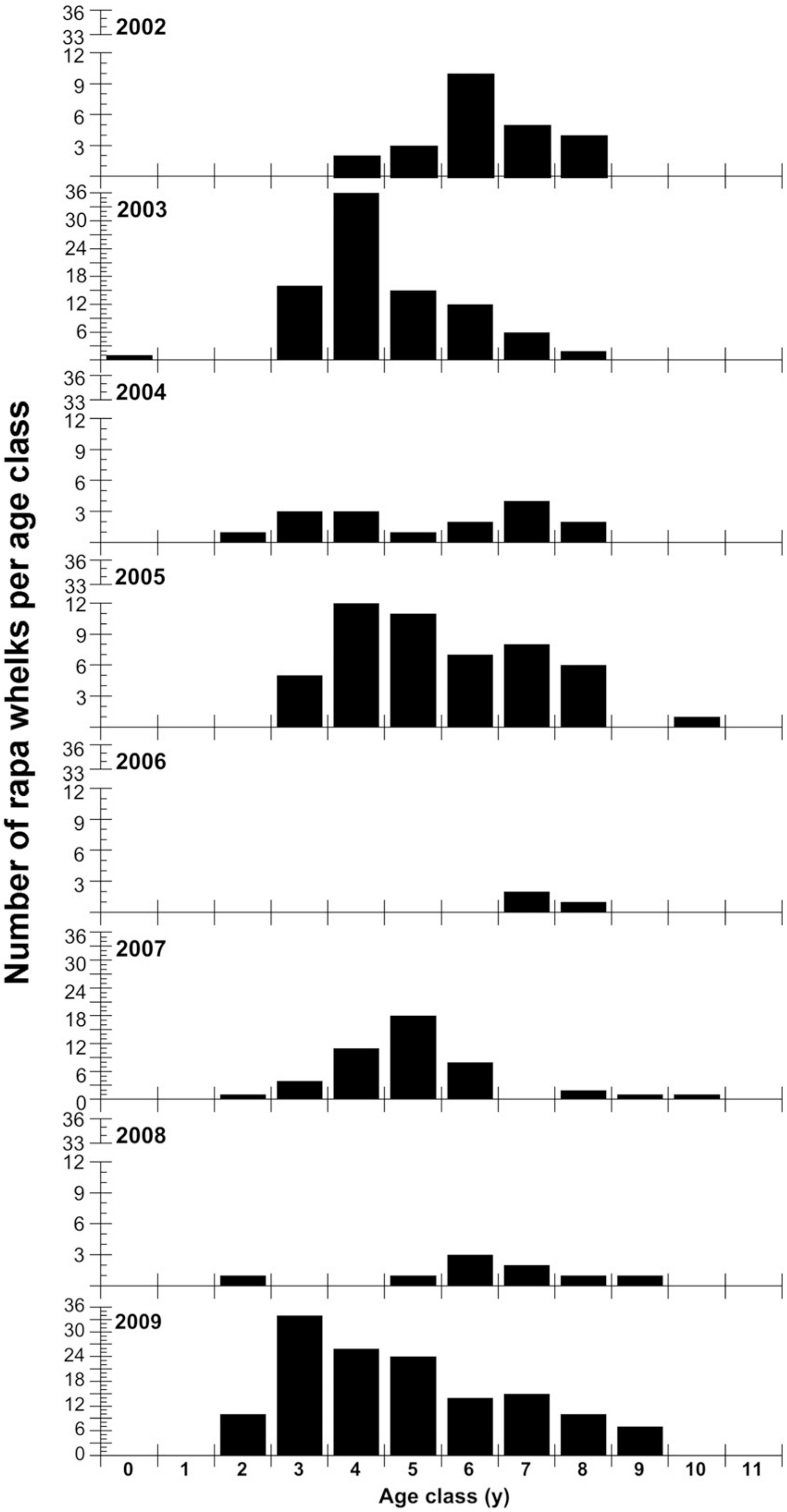

Figure 8. Age-frequency distribution for Elizabeth and Lafayette River rapa whelks from 2002 through 2009.

in whelk demographics because of the obvious implications for increased propagule pressure. For example, the 2001 year class presents a strong age demographic signal for all three regions examined. The spawning season duration can be calculated by the difference between the week of the year when water temperatures reach 18°C and when they exceed 27–28°C. The 2001 egg-laying season lasted for at least 13 wk as compared with the 8–11 wk spawning seasons predicted by water temperatures in 7 of the

TABLE 11.

Summary of two sample Kolmogorov–Smirnov tests on the SL and age frequency distributions for whelks collected between January 1 and May 31 from the combined Elizabeth and Lafayette Rivers during 2003, 2005, 2007, and 2009.

SL		2005	2007	2009
	2003	ND	ND	ND
	2005		ND	ND
	2007			ND
Age		**2005**	**2007**	**2009**
	2003	ND	ND	ND
	2005		ND	ND
	2007			ND

ND, demographics that were not significantly different at alpha = 0.05.

11 y from 1998 through 2008 (Table 16). The predicted spawning season was also longer in 2000, 2003, and 2009 (13, 14, and 13 wk, respectively). The 2000 year class signal was likely confounded by a cooler than average fall (Fig. 11) following a very wet summer (see below, Figs. 12 and 13). The 2003 year class encountered a relatively cooler (Fig. 11) and much wetter than average summer and fall (see below, Figs. 12 and 13) including rains from Hurricane Isabel in September 2003 which may have locally reduced salinity below survival thresholds for as long as several days. No information is available on the success or failure of the 2009 year class.

Salinity followed a general seasonal trend with lower values observed from February through July or August followed by increasing salinity from August through January (Table 13, Figs. 12 and 13). This pattern is commensurate with spring and early summer rainfall followed by seasonally high evaporation and low precipitation associated with late summer, fall, and winter. The number of whelks observed from January to May from 1999 through 2009 was not correlated with monthly or quarterly salinity during the same year of collection, or salinity in December or October–December of the previous year (Tables 14 and 15).

While the (seasonal) wet/dry pattern influences habitats at OV and throughout the James River rapa whelk range, average monthly salinity below the James River SR–258 bridge typically does not fall below 15, although 2003 was an exceptionally wet year with monthly salinity of 12–14 observed (Fig. 12). Annual

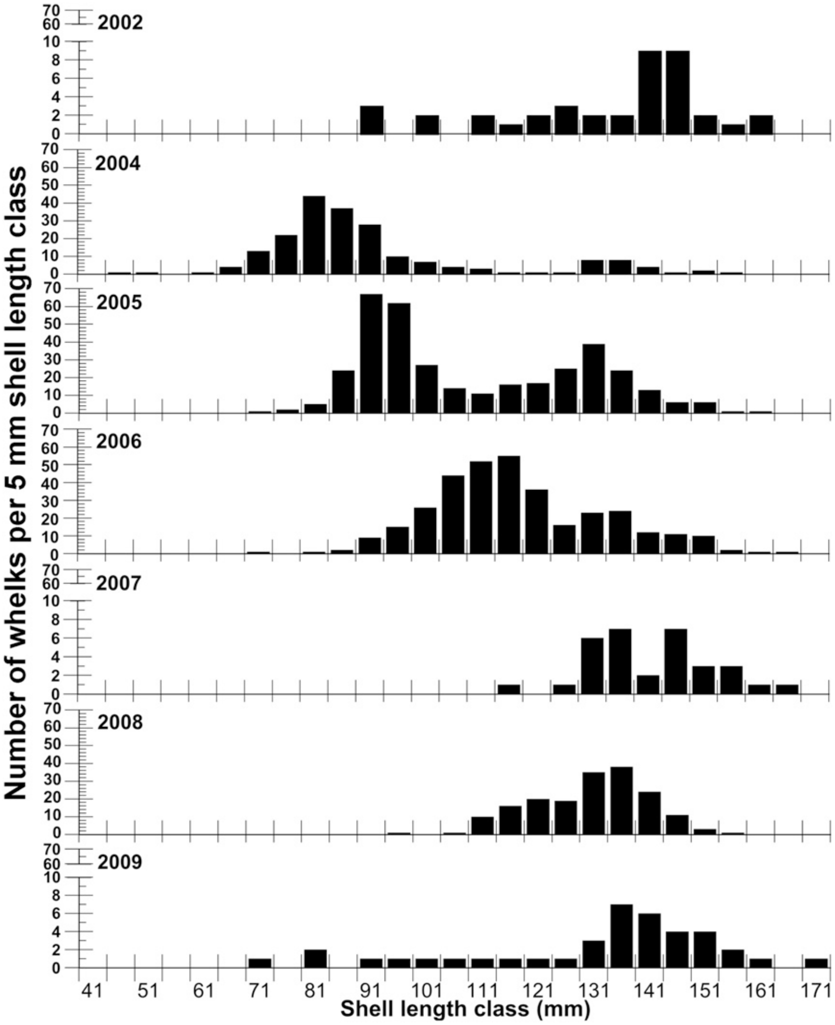

Figure 9. Rapa whelk SL (mm) frequency distribution for James River zone 1 from 2002 to 2009 by 5-mm length class. The smallest SL within a length class is used to refer to that group. No whelks were collected from January through May in 1999, 2000, 2001, or 2003 from zone 1.

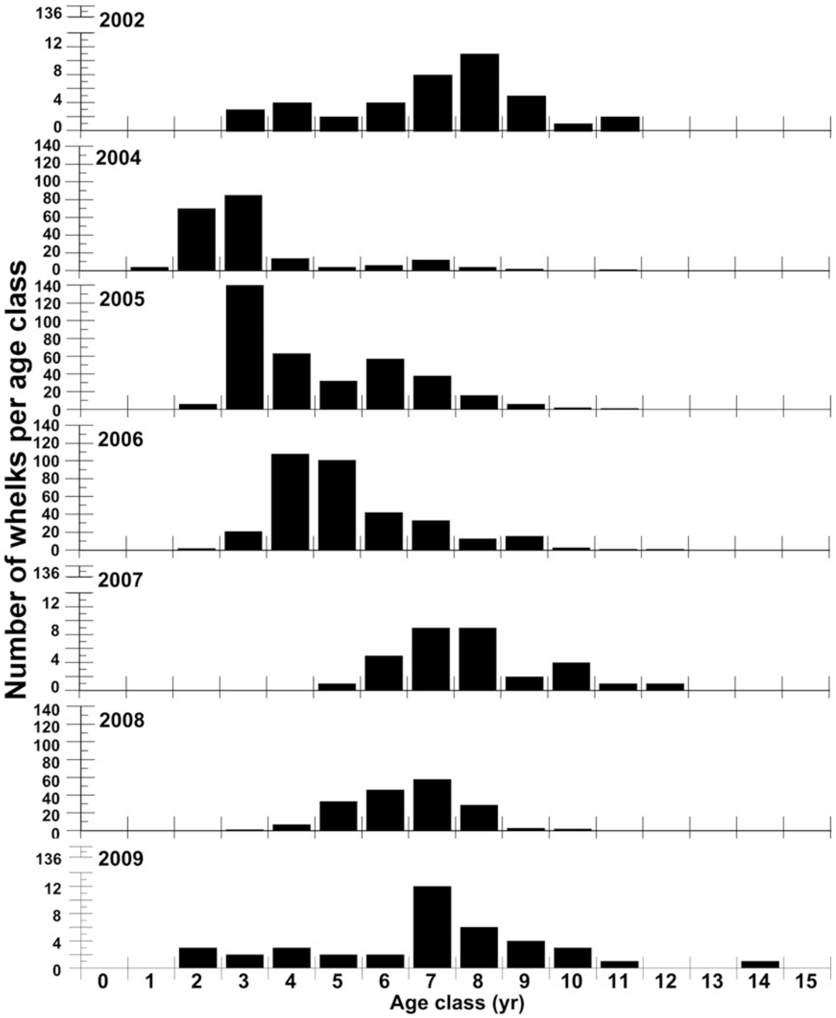

Figure 10. Age-frequency distribution for James River zone 1 rapa whelks from 2000 through 2009. No whelks were collected during 2003.

salinity in these habitats is usually between 17 and 21 as demonstrated by 2002. The tidal nature and spatial extent of these regions guarantees that the ambient environmental conditions are dynamic and likely to return to a range within physiological tolerances at tidal scales (approximately 6 h). Estuarine volume and tidal exchange modulate rapid excursions from typical environmental conditions during extreme events at basin (e.g., Tropical Storm Agnes) or smaller (e.g., local summer thunderstorms) spatial scales at time scales that typically allow rapa whelks to leave marginal habitats and enter habitats with suitable environmental conditions.

Wreck Shoal salinity ranged from 8 to 20 (Table 13, Fig. 13) during 2002 in contrast to locations below the James River SR–258 bridge and in the mainstem Bay. During years with abnormally high precipitation, such as 2003, Wreck Shoal salinity may be as low as 5–6 for spring months with fall salinity in the 8–10 range, which is as much as 5–6 salinity units below the 30 y average (Fig. 13). Low salinity events at Wreck Shoal are typical of zones 2 and 3 as well as the upper portion of zone 1, effectively forcing adult rapa whelks out of these areas during wet years when salinity is below 12–15 for most, if not all, of the year.

Wreck Shoal salinity offers insight into observed demographic trends for zone 1 whelks. No whelks were collected from zone 1 between January and May 2003 (Figs. 9 and 10). In 2003, salinity from January through May ranged from 5 to 10 with a salinity of approximately 6 observed in March, April, and May (Table 13, Fig. 13). Whelks could have taken refuge in the adjacent channel habitats and/or migrated a short distance downstream when salinity was below 12–15. Rapa whelks usually begin to actively forage and seek both mates and egg capsule deposition sites during these spring months. In contrast, Wreck Shoal salinity was greater than 10 from May 2000 through March 2001 and from May 2001 through October 2002 (Table 13, Fig. 13). Salinity during most of 2001 and all of 2002 was above the decadal averages (Table 13, Fig. 13). The elevated Wreck Shoal salinity associated with the dry years of 2001 and 2002 likely facilitated whelk range expansion into zone 1.

DISCUSSION

The Chesapeake Bay *Rapana venosa* invasion began as early as 1981. At a watershed level, the Chesapeake Bay habitats occupied by rapa whelks in 2009 remain south of Smith Point at the Potomac River mouth and essentially unchanged from 2005 through 2009. Deballasting stations in the lower Bay are almost certainly the sites of first introduction. The related rapa whelk

TABLE 12.

Summary of two sample Kolmogorov–Smirnov tests on the rapa whelk SL and age frequency distributions for whelks collected between January 1 and May 31 from James River zone 1 from 2004 to 2009.

SL		2005	2006	2007	2008	2009
	2004	*	*	ND	*	ND
	2005		*	ND	*	ND
	2006			ND	*	ND
	2007				ND	ND
	2008					ND
Age		**2005**	**2006**	**2007**	**2008**	**2009**
	2004	*	*	*	*	*
	2005		*	*	*	*
	2006			*	*	*
	2007				ND	ND
	2008					ND

No whelks were collected from January to May 1998.
* Demographics that were significantly different at alpha = 0.05; ND, demographics that were not significantly different at alpha = 0.05.

veligers probably came from the Black Sea via coal carrier ballast water (Mann & Harding 2000, Chandler et al. 2008) or they may have been produced within the Chesapeake Bay by adult broodstock that had been introduced as larvae even earlier; potentially as early as 1981. Rapa whelk life expectancy has been estimated at 15–18 y (Harding & Mann 2005, Harding et al. 2008), but the maximum longevity estimates supported by these analyses are 24–26 y.

Within the OV–HB–JRship regions, the site of introduction, establishment and source region for lower Bay, the whelk SL and age-frequency distributions from 1999 to 2009 describe a broad demographic with ongoing recruitment confirming establishment and sufficient propagule pressure to maintain and then "fill in" the existing demographic. Although seasonal range extension into the Elizabeth and Lafayette Rivers was consistently observed beginning in 2000 with increasing intensity (indicated by numbers of whelks collected) throughout the time series, both of these tributaries are relatively shallow and it is likely that colder winter temperatures dictate seasonal evacuation of these areas with reinvasion each spring. The annual ambient water temperature and salinity conditions within the OV, HB, and mesohaline (10–23) James River habitats appear to be within the range of the physiological tolerances for benthic rapa whelks (juvenile and adult). Whelk occupancy of OV, HB, and lower James River habitats will not be restricted solely on the basis of either water temperature or salinity.

TABLE 13.

Decadal average WT and S values with standard error (SE).

	1979–2009 average		1989–2009 average
Month	**VIMS WT (SE)**	**WS S (SE)**	**VIMS/MG S (SE)**
January	5.32 (0.08)	9.70 (0.10)	19.94 (0.09)
February	5.29 (0.07)	9.12 (0.10)	18.89 (0.10)
March	8.39 (0.07)	8.16 (0.09)	17.72 (0.11)
April	13.65 (0.08)	8.40 (0.08)	16.59 (0.10)
May	19.11 (0.07)	9.32 (0.08)	17.06 (0.09)
June	24.08 (0.06)	11.60 (0.11)	17.86 (0.09)
July	26.87 (0.04)	13.81 (0.10)	19.25 (0.07)
August	27.26 (0.04)	14.95 (0.11)	19.70 (0.10)
September	24.61 (0.06)	14.63 (0.13)	19.41 (0.16)
October	19.41 (0.09)	14.21 (0.13)	20.46 (0.10)
November	13.58 (0.08)	12.11 (0.13)	21.04 (0.08)
December	8.41 (0.09)	10.37 (0.11)	20.49 (0.08)

WT, water temperature; S, salinity; MG, Middle Ground; WS, Wreck Shoal. Water temperatures at VIMS, Gloucester Point, York River are equivalent to water temperatures at WS (James River zone 1) and the lower James River (JRship, Elizabeth, Lafayette). Salinity at Gloucester Point is similar to salinity at MG in the lower James River as discussed in text. Wreck Shoal salinity was estimated from discharge data as discussed in text.

Local circulation patterns carry planktonic larval whelks and set the initial footprint of "inoculation" in combination with propagule pressure (larval supply) but the observed spatial distribution of recruits and older whelks results from postsettlement processes including whelk behavior. Rapa whelks require hard substrate for successful metamorphosis (Harding 2006) and live epifaunally for at least several months postsettlement (Harding, unpublished data). At SL less than approximately 25 mm, rapa whelks are still capable of dispersal via water currents to new hard substrate habitats because they can inflate their feet and float (Harding 2011). During this epifaunal period, juvenile whelks co-occur with a broad suite of native predators associated with Chesapeake Bay mesohaline hard substrates that are likely capable of eating recently settled rapa whelks including errant polychaetes [e.g., *Neanthes* (=*Nereis*) *succinea* (Frey & Leuckart, 1847)]; mud crabs [e.g., *Panopeus herbstii* (H. Milne Edwards, 1834), *Eurypanopeus depressus* (Smith, 1869)]; blue crabs, and demersal fishes [e.g., *Opsanus tau* (Linnaeus, 1766)]. Whelks are still vulnerable to predation at least by small blue crabs until they attain SL of approximately 30–40 mm (Harding 2003).

Within the mesohaline James River estuary, rapa whelk range expansions observed between 2004 and 2009 likely reflect year-round occupancy promoted by bathymetry, physical oceanography, and the availability of food resources. The JRship region marks a transition zone for ecology as well as habitat parameters. The deep (6–10 m) depositional channel that promotes tidal incursion of marine water likely acts as a salinity and temperature refuge as well as a conduit for whelks to up-estuary locations (Wood & Hargis 1971, Ruzecki & Hargis 1989). Infaunal benthic channel habitats remain relatively cool and salty year-round as the water column stratifies seasonally (Pritchard 1952, Ruzecki & Hargis 1989) unlike the shallow (typically 1–3 m) well-mixed habitats that extend to the banks on either side of the dredged channel. Thus, the James River shipping channel is an important geomorphological feature that facilitates range expansion upriver because it is a reservoir of relatively salty water. Rapa whelk use of shallow habitats from Wreck Shoal upriver through Deep Water Shoal appears to be dictated by seasonal freshwater discharge patterns and the resulting salinity. Adult whelks likely follow the isohalines and avoid salinity less than 10–12 much like the native muricid oyster drills (Zachary & Haven 1973).

The shallow shoulders on either side of the James River shipping channel include habitats with living oysters and associated oyster shell substrate (Haven et al. 1978, Mann

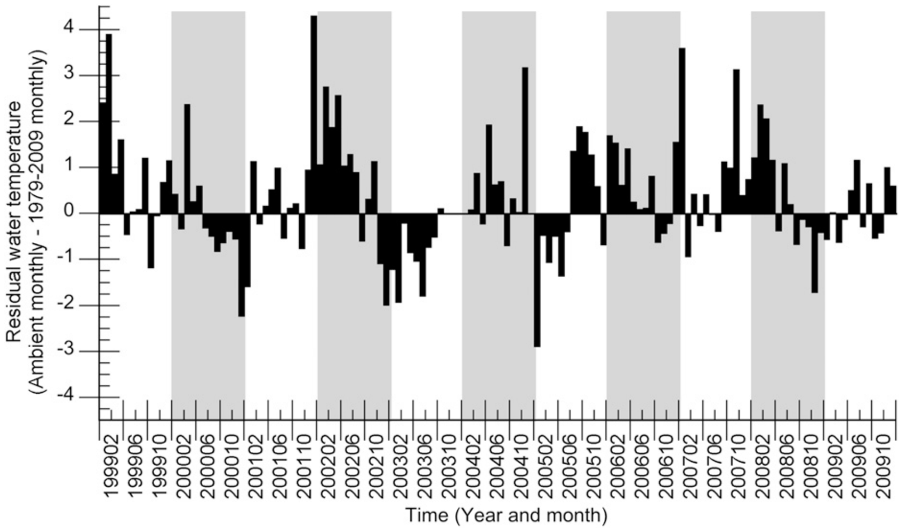

Figure 11. Monthly water temperatures from 1999 to 2009 presented as residuals relative to the 1979 to 2009 decadal average monthly water temperatures. Grey boxes distinguish even from odd years. Data from October 2003 through February 2004 are not available.

et al. 2009a, 2009b; Fig. 1) that are the remnants of the massive oyster reef system that developed during the Holocene epoch as the modern Chesapeake Bay formed (Hargis 1999). Although the spatial distribution of modern oyster populations is reduced compared with their historic footprint (Winslow 1882), mesohaline James River oyster habitats remain from Newport News Point to Mulberry Point (Haven et al. 1978, Mann et al. 2009b; Fig. 1). By 2009, the observed rapa whelk spatial distribution in this area seasonally overlapped with the distribution of extant commercially fished oyster populations. Salinity less than 10–15 during seasonal (late winter-spring) wet periods will force whelk egress from the shallow areas to the channel, potentially even forcing whelks downstream in the channel (depending on the volume of freshwater discharge relative to tidal influx) and release oysters from whelk predation pressure. Oysters survive exposure to salinities as low as 5–7 (Shumway 1996). Salinity ranging from approximately 7 to 12 would promote oyster survival but potentially exclude rapa whelks from the same area.

Miller et al. (2007) describe salinity tolerance as one of the primary factors in the success or failure of molluscan invasion success in estuaries. The distribution of the isohalines and faunal salinity tolerances dictate the occupied range, that is, the fundamental niche. Selection over geological time in geographically isolated locations creates species with unique fundamental and realized niche boundaries. When anthropogenic actions transport species to novel locations with differing or even absent biological and/or physical boundaries of these evolved niche specifications, then the invader will, over time, stabilize in an occupied or underused niche. Successful invaders are able to occupy the edges or boundaries between niches occupied by natives and thus establish a foothold in the receptor habitat.

Ecosystem disruptions that alter historic patterns of resource use provide niche opportunities and potential advantages to invaders, particularly if the invaders use resources differently than natives (Sherr & Hyatt 1999, Davis et al. 2000, Shea & Chesson 2002). Prior to 1972, modern Chesapeake predatory gastropods occupied two distinct salinity zones. Native oyster drills (*Urosalpinx cinerea* and *Eupleura caudata*), potential competitors with recently settled rapa whelks, occurred at a minimum salinity of 9–12 (Federighi 1931, Carriker 1955, Manzi 1970, Zachary & Haven 1973) with preferred salinity greater than 15 (Federighi 1931, Stauber 1943, Menzel & Nichey

TABLE 14.

Summary of Pearson correlations between monthly WT or S and the total number of whelks collected from January to May within a year from OV-HB-JRship, the Elizabeth and Lafayette Rivers, and James River zone 1.

	OV-HB-JRship				Elizabeth/Lafayette Rivers				Zone 1			
	VIMS WT		VIMS S		VIMS WT		VIMS S		VIMS WT		WS S	
Month	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*
December*	–0.28	0.60	0.20	0.64	–0.22	0.78	0.12	0.88	–0.04	0.39	–0.54	0.14
January	–0.33	0.42	0.24	0.50	–0.43	0.33	0.43	0.33	–0.14	0.73	–0.53	0.12
February	–0.01	0.97	0.23	0.51	–0.55	0.16	0.24	0.57	0.20	0.59	–0.44	0.20
March	–0.29	0.38	0.31	0.35	–0.67	0.07	–0.09	0.84	–0.20	0.59	0.09	0.81
April	–0.05	0.88	0.44	0.18	–0.53	0.18	–0.08	0.85	0.09	0.80	0.11	0.76
May	0.22	0.52	0.12	0.73	–0.22	0.59	–0.02	0.96	–0.24	0.50	0.19	0.61

WT, water temperature; S, salinity; WS, Wreck Shoal; *R*, Pearson correlation test statistic; *P*, significance value.
* Previous calendar year.

TABLE 15.

Summary of Pearson correlations between quarterly WT or S and the number of whelks collected from January to May within a year from OV–HB–JRship, the Elizabeth and Lafayette Rivers, and James River zone 1.

	OV–HB–JRship				Elizabeth/Lafayette Rivers				Zone 1			
	VIMS WT		VIMS S		VIMS WT		VIMS S		VIMS WT		WS S	
Quarter	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*
October–December†	0.09	0.80	0.46	0.25	–0.48	0.28	0.03	0.96	0.62	0.07	–0.42	0.26
January–March	–0.14	0.68	0.27	0.42	–0.77	0.03*	0.04	0.92	0.23	0.52	–0.36	0.31
April–June	0.07	0.83	0.23	0.49	–0.67	0.07	–0.18	0.67	–0.18	0.61	0.21	0.56

WT, water temperature; S, salinity; WS, Wreck Shoal in the James River; *R*, Pearson correlation test statistic; *P*, significance value.
* Statistical significance at alpha = 0.05.
† Previous calendar year.

1958). Channel and knobbed whelks, native predatory gastropods that are potential competitors with adult rapa whelks, were (and are) restricted by their salinity tolerances to down-estuary habitats with salinity greater than 18–20 (Castagna & Kraeuter 1994), and typically are found at salinity greater than 25–28 (Maghales 1948, Castagna & Kraeuter 1994, Power et al. 2002, Walker et al. 2008).

Tropical Storm Agnes (June 1972) reset the distribution and abundance of native oyster drills in the lower Chesapeake Bay (Andrews 1973, Mann & Harding 2003, Harding & Harasewych 2007), creating a niche opportunity. Excessive freshwater inflow depressed salinity, whereas the accompanying sediment killed epifaunal bivalve prey (particularly oysters) for several weeks after the storm (Andrews 1973). In the wake of Tropical Storm Agnes, viable oyster drill populations were restricted to main-stem Chesapeake Bay locations near the Bay mouth (Andrews 1973). Surviving native drill populations have been reinvading their original range, but the pace and success of this process are

TABLE 16.

Chesapeake Bay rapa whelk spawning season duration (wk) in relation to water temperatures for 1981 to 2009.

Year	Date WT >18°C	Date WT >28°C	WOY WT >18°C	WOY WT >28°C	Estimated spawning season duration (wk)
1981	May 14, 1981	August 10, 1981	20	33	13
1982	May 7, 1982	July 28, 1982	19	31	12
1983	May 6, 1983	August 11, 1983	19	33	14
1984	May 6, 1984	August 14, 1984	19	33	14
1985	April 23, 1985	August 10, 1985	17	32	15
1986	May 9, 1986	July 16, 1986	19	29	10
1987	May 17, 1987	July 22, 1987	21	30	9
1988	May 16, 1988	August 2, 1988	21	32	11
1989	May 14, 1989	August 10, 1989	20	32	12
1990	April 28, 1990	July 22, 1990	17	30	13
1991	May 4, 1991	July 8, 1991	18	28	10
1992	May 15, 1992	August 10, 1992	20	33	13
1993	May 7, 1993	July 6, 1993	19	28	9
1994	April 29, 1994	July 5, 1994	18	28	10
1995	May 12, 1995	July 16, 1995	19	29	10
1996	May 5, 1996	August 10, 1996	19	32	13
1997	May 20, 1997	August 15, 1997	21	33	12
1998	May 5, 1998	July 21, 1998	19	30	11
1999	May 9, 1999	July 22, 1999	20	30	10
2000	May 7, 2000	August 9, 2000	20	33	13
2001	May 2, 2001	August 9, 2001	19	32	13
2002	April 18, 2002	July 17, 2002	18	29	11
2003	May 2, 2003	August 22, 2003	20	34	14
2004	April 25, 2004	July 20, 2004	20	30	10
2005	May 12, 2005	July 13, 2005	21	29	8
2006	April 25, 2006	July 18, 2006	19	29	10
2007	May 1, 2007	August 1, 2007	20	31	11
2008	April 28, 2008	July 19, 2008	19	29	10
2009	April 29, 2009	August 4, 2009	19	32	13
				Average	11.5

WOY, week of the year; WT, average daily water temperature (°C).

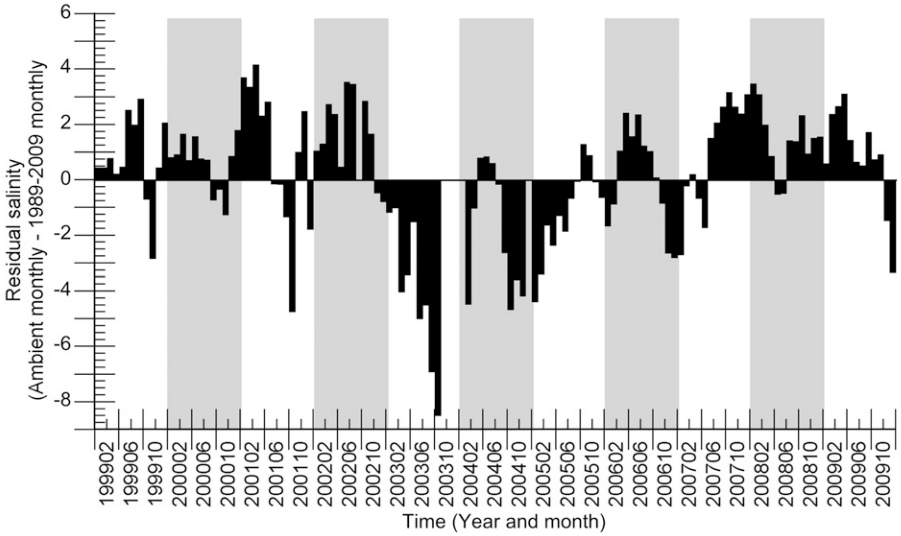

Figure 12. Middle Ground (HB, James River) monthly salinities from 1999 to 2009 presented as residuals relative to the 1989 to 2009 decadal averages. Salinity data were not available for 1979 to 1988 or October 2003 through mid-February 2004. Grey boxes distinguish even years from odd years.

limited by the absence of a planktonic larval dispersal stage and the increased patchiness and habitat fragmentation associated with declines in the coverage of oysters and oyster shell related both to disturbance from Agnes, increased sedimentation (dredging, shoreline development), and changes in oyster populations since 1972 related to disease (Andrews 1996, Burreson & Ragone Calvo 1996, Carnegie & Burreson 2011), recruitment (Southworth & Mann 2004, Mann et al. 2009a, Harding et al. 2010), and shell dynamics (Haven et al. 1978, Mann & Powell 2007, Harding et al. 2010).

Adult and juvenile rapa whelks have salinity tolerances similar to those of *Urosalpinx cinerea* and *Eupleura caudata* and have occupied the former drill habitats delineated by a lower ambient salinity threshold of 10–12 extending to fully marine waters (Golikov 1967, Tsi et al. 1983, Rubinshtein & Hiznjak 1988, Mann & Harding 2000). Adult rapa whelk use of infaunal habitats with salinity approximately 15–25 allows them to avoid direct competition with native channel and knobbed whelks for food. The rapa whelk's ability to thrive in mesohaline conditions has also facilitated its establishment in the Rio de la Plata where it also occupies a unique set of depth, temperature, and salinity conditions in nearshore coastal habitats relative to the suite of native macrobenthic gastropods (Carranza et al. 2008).

Rapa whelk life history includes traits that enhance establishment and range expansion within receptor habitats. Mixed development (egg capsules and pelagic larvae) allows tidal transport of planktonic larval forms into up-estuary habitats and across gaps in fragmented benthic habitats within a single generation versus the multiple generations required by native gastropods to crawl up-estuary. Predation by crabs and other benthic predators may select for fast-growing whelks that attain

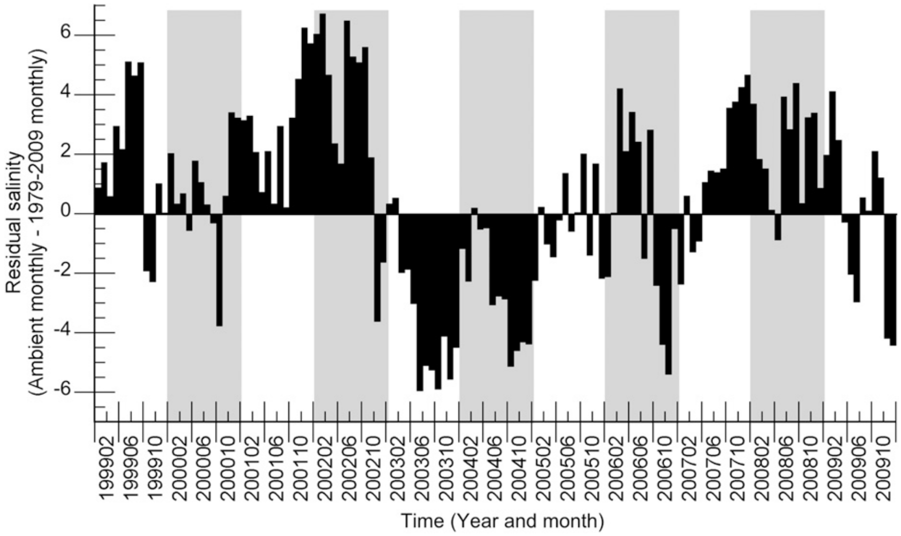

Figure 13. Monthly Wreck Shoal (zone 1, James River) salinities from 1999 to 2009 presented as residuals relative to the 1979 to 2009 decadal averages. Salinities were estimated using USGS discharge data as described in text.

a size that refuge from predation faster than native gastropods. From an invasion perspective, selection for fast growth in an invasive whelk with generation times of 10–11 mo after hatching (Harding et al. 2007a, 2008), life expectancies of more than 25 y (these data), and fecundity that scales nonlinearly with age (Harding et al. 2007b, 2008) potentially has the effect of selecting for extremely high propagule pressure.

Food limitation is probably the only factor that is likely to hinder the maintenance of rapa whelk populations within the lower Bay. Rapa whelks transition from epifaunal to infaunal habitats with ontogeny. Shifts in habitat use with age correspond to changes in prey type and attack methods. The transition from eipfaunal to infaunal habitats and concurrent changes in diet could set up a bottleneck for feeding and growth if whelks were not mobile. Whelk mobility combined with the proximity of deep channel habitat in the James River allows larger whelks access to extant oyster grounds for foraging even if (or when) suitably sized infaunal bivalve prey, notably northern quahogs, become limiting in zone 1 or areas downstream. A noteworthy tipping point in food availability will potentially be realized if submarket and market oysters (<76 mm shell height and >76 mm shell height, respectively) on oyster grounds in the lower James River become scarce due to a combination of predation [e.g., rapa whelk, blue crab, cownose ray *Rhinoptera bonasus* (Mitchill, 1815)], oyster disease, freshets, and/or fishing activity. This did not appear to be happening as of 2009 and 2010 (Southworth et al. 2010, 2011) based on modest increases in small and market oysters observed in the lower James River, a trend that continues as of this writing (2016).

Observed whelk demographics support the absence of food limitation for whelk populations in the occupied range. Black Sea rapa whelk populations have been food limited because rapa whelk predation on top of original ecological and commercial pressures drastically reduced the density and availability of native bivalves including oysters, scallops, and mussels in the 1960s (Drapkin 1963, Chukhchin 1984, Zolotarev 1996). Recent Black Sea rapa whelk SL demographics rarely extend to 100 mm (Saglam et al. 2009, Kosyan & Antipushina 2011). These truncated demographics indicate that Black Sea rapa whelks are reproducing but that growth rates are slow and whelks die as they reach sizes that require larger prey items for positive scope for growth.

The James River mesohaline dynamics offer a template for the occupancy of the Chesapeake Bay system as a whole. The initial projections of Bay-wide distribution have not yet been realized and probably will not be due to a combination of oceanography (Pritchard 1952, Mann 1988), patchy distribution of food resources (Baker & Mann 1991, Roegner & Mann 1991, Mann et al. 2005, 2009a), and ontogenetic changes in whelk prey and habitat requirements combined with the seasonal distribution of predators and salinity.

Rapa whelk establishment in the Chesapeake Bay resulted from a combination of natural and anthropogenic factors. The system-wide disturbance caused by Tropical Storm Agnes during summer 1972 disrupted trophic dynamics and created a niche opportunity (Shea & Chesson 2002) across annual and decadal time scales and basin spatial scales. The normal succession and recolonization process post-Agnes was interrupted by the colonization success of rapa whelk veligers arriving via ballast water and successfully occupying habitats that had been formerly occupied by oyster drills in evolutionary time. It is worthy of mention that these minor natural disturbances, decades rather than centuries in length and driven by atypical meteorological events, are of minor consequence in the absence of anthropogenic facilitation of invasions. Whelk veligers had probably been arriving in ballast water from the Black Sea and Mediterranean regions since at least the late 1940s given the presence of Norfolk Naval Base as well as numerous commercial shipping terminals in the Hampton Roads region. Environmental and ecological conditions during the late 1970s and early 1980s facilitated successful introduction, invasion, and ultimately establishment in the temporarily vacant niche. Ironically, implementation of the Federal Water Pollution Control Act amendments in 1972 (i.e., the Clean Water Act; 33 U.S.C. 1251 et seq) since the early 1970s has improved water quality, potentially facilitating invasion success. Continued propagule pressure from external European sources during the 1980s and 1990s is likely given geopolitical events and related shipping trends, whereby commercial coal ships move from Newport News Point to the Black Sea and ballasted bulk carriers return to the lower Chesapeake Bay 11 days later (Mann & Harding 2000).

The Chesapeake Bay rapa whelk invasion chronology is more nuanced than a simple invasion story of expanding fronts, because the potential for expansion and infill behind the front resets every season based on a combination of changing ecological (predators, prey) and environmental or oceanographic conditions (salinity, temperature), where the resulting interactions vary on an interannual as well as intra-annual basis (Yackulic et al. 2015). The connectivity between the Chesapeake Bay and coastal as well as offshore waters combined with the seasonal migrations of whelk predators (e.g., blue crabs, sea turtles, cownose rays) with life histories that operate on a range of time scales and whose dynamics are individually and independently set by anthropogenic forces to a varying extent within any year makes the invasion progression even more challenging to predict. As long as a reservoir of large rapa whelks resides near the Bay mouth, there is the potential for these whelks to supply continued generations of propagules. Ballast water transport of veligers as well as hull or sea chest transport of recently settled epifaunal juveniles remain as viable vectors for continued inoculation. Modern shipping traffic to and from regions with established populations (native range, Black Sea, Mediterranean, North Sea, Rio de la Plata) continues. Whelk veliger success in the recipient Chesapeake habitat depends on the habitat, the ambient environmental conditions, and the surrounding ecology at micro (mm) and macro (basin wide) scales.

The Chesapeake Bay rapa whelk invasion provides an example of how life history and ecological traits facilitated establishment at decadal time scales. Rapa whelks have yet to be discovered in other U.S. Western Atlantic estuaries as of this writing. While recently settled whelks have been found on loggerhead turtles in Georgia (Harding et al. 2011), these whelks were almost certainly too young/small to have come from the Chesapeake Bay. Chesapeake Bay rapa whelk population dynamics offer a cautionary tale based on fundamental ecological principles. The time lag from the window of first introduction to the first discovery of adults may be on the order of decades depending on the size and complexity of the system involved and the presence or absence of regular monitoring efforts (or fisheries that would include rapa whelks as bycatch) in the context of native species inventories. Although very few estuaries remain undisturbed by anthropogenic activities, the relative temporal and spatial scales of anthropogenic and natural disturbances are relevant to invasion success (Jackson et al. 2009). Natural ecological resistance may remain sufficient to keep invaders from successful establishment until unusually large natural disturbances compound the existing anthropogenic perturbations with the end result of cumulative catastrophic disturbance that resets the system ecologically at broad spatial scales. Afterward, the natural successional sequence will be disrupted as natives and invaders alike scramble to take advantage of new niche opportunities created by changes in resource supply and distribution.

ACKNOWLEDGMENTS

Special thanks are extended to the lower Chesapeake Bay commercial fishermen and seafood processors who cheerfully and dependably collaborated with us for more than a decade. Donations by other Commonwealth of Virginia citizens as well as tourists are also gratefully acknowledged. The bounty program functioned because of the dedicated effort from Virginia Institute of Marine Science personnel including Melissa J. Southworth, Catherine Ware, Adriana Picareillo, Erica Westcott, Stephanie Gera, Meghan Harris, E. Alexander Jestel, David Kerstetter, Peter Kingsley-Smith, Meredith Fagan, Rhonda Howlett, Stephanie Haywood, Rebecca Green, Amy Bohannon, Tim Drummond, Erin Reilly, Matthew Robinson, Courtney Harris Burge, Karen Capposela, Emily Chandler, Christina Conrath, Elizabeth Darrow Condon, Mike Seebo, Pat Crewe, R. V. Carmean, Dennis Bunting, Buddy Matthews, Mike Oesterling, Paulette Topping, Carol Tomlinson, Cindy Forrester, Anita G. Reardon, Jane Lopez, and Vicki Clark. This is Contribution number 3574 from the Virginia Institute of Marine Science, College of William & Mary. Bounty funds were provided by the Virginia Marine Resources Commission Virginia Saltwater Commercial Fishing Development Fund (CF-98-19), The Aquatic Nuisance Species Research and Outreach program through National Sea Grant College Program/NOAA/Dept. of Commerce (NA96RG0025/5-29456 and VA-ANS-01-01), the National Fish and Wildlife Foundation, and the Commonwealth of Virginia. Additional support for this project was provided by Virginia Sea Grant (R/MG-98-3), and partial support to RM by the National Science Foundation (OCE-9810624).

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