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Differences in Relative Predation Vulnerability Between Native and Non-native Oyster Larvae and the Influence on Restoration Planning in an Estuarine Ecosystem

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Abstract The costs and benefits of non-native introductions as a restoration tool should be estimated prior to any action to prevent both undesirable consequences and waste of restoration resources. The suggested introduction of non-native oyster species, *Crassostrea ariakensis*, into Chesapeake Bay, USA, provides a good example in which the survival of non-native oysters may differ from that of native oysters, *Crassostrea virginica*, during the larval stage. Experiments were conducted to compare the predation vulnerability of native and non-native oyster larvae to different predator types (visual vs. non-visual, benthic vs. pelagic). The results suggest that the non-native larvae are more vulnerable to visual and non-visual pelagic predators. Although vulnerability was similar for larvae exposed to benthic non-visual predators, the consumption of one non-native strain was higher than the consumption of native *C. virginica* larvae. When vulnerability data are combined with predator feeding rates, the predation mortality for non-native larvae in the wild can be much higher than for native larvae. Small changes in larval mortality rates can yield large changes in total larval delivery to the reef for settlement, so these differences among species may contribute to differences in settlement success. These results provide an example of how a comprehensive examination of the perceived benefits of non-native introductions into complex ecosystems can provide important information to inform management decisions.

Keywords Oyster · Larvae · Ecosystem management · Estuary

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Introduction

Non-native species introductions can have substantial influence on aquatic ecosystems including habitat alteration (Baker et al. 1998), displacement or replacement of native species (Dunham et al. 2004), and introduction of novel parasites and pathogens (Ruiz and Dobbs 2004). Non-native introductions can be non-intentional, such as ballast water transport (Dunstan and Bax 2008), but also include intentional introductions by management agencies (Dunham et al. 2004; Hegaret and Mazurie 2005) to achieve specific objectives. Intentional introductions for ecosystem management are unique as they represent an investment to improve ecosystem services, such as fishing or aquaculture production, but also pose a risk that the interactions of native and non-native species may have unintentional consequences. In most documented cases of intentional introductions, much uncertainty existed at the onset with regards to both the anticipated benefits and the ecosystem risks (Hegaret and Mazurie 2005; Knapp et al. 2001).

Native oyster populations (e.g., *Crassostrea* spp.) have declined in many locations due to overharvest and the prevalence of parasitic diseases, which has resulted in

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increased interest in the introduction of non-native species that are more disease resistant. For example, the introduction of the non-native Asian Suminoe oyster (*Crassostrea ariakensis*) into Chesapeake Bay, USA, was proffered as a solution to the drastic decline in the native American oyster (*Crassostrea virginica*) over the last 25 years (NRC 2004). The native stocks of *C. virginica* are estimated to be less than 0.1% of historic biomass observed during the nineteenth century (Jordan and Coakley 2004; Newell 1988). This decline has drastically reduced the commercial oyster fishery and is thought to have had broad influences on the Chesapeake Bay ecosystem, such as reductions in benthic primary productivity, decreased water clarity, and reduced resilience to eutrophication (Newell 1988; Newell et al. 2005). The most recent rapid decline is thought as largely due to the effects of the parasitic diseases MSX, carried by *Haplosporidium nelsoni*, and Dermo, carried by *Perkinsus marinus*. The resistance of *C. ariakensis* to these diseases (Calvo et al. 2001) was a central justification for a non-native rebuilding plan (NRC 2004). *C. ariakensis* is an optimal alternative choice for restoration as it is a relatively fast-growing, reef-building oyster species similar to *C. virginica* (Zhou and Allen 2003).

Two broad questions need to be addressed prior to the introduction of a non-native oyster species into a sensitive estuarine ecosystem. First, the risk of a non-native introduction both to the native oyster population as well as to other sensitive members of the ecosystem needs to be assessed. Equally important, however, is an assessment of the likely benefit of the introduction that will justify both the cost of the action and any established risk (Ruesink et al. 2005).

The desired benefit of an intentional introduction of a non-native species will vary based on the objectives of the introduction program (e.g., restore ecosystem services, fishery enhancement). Yet the establishment of a self-sustaining population as an inherent requirement of achieving the desired benefits and population sustainability of a species in a new environment is always uncertain (Landis 2004; Miller et al. 2007). In situations such as the introduction of non-native oysters into Chesapeake Bay, the non-native species partially replaces a native species, and if the population dynamics and life history of the two are sufficiently similar then data regarding the native species may be used as a guide to predict the likely sustainability of the introduced species in the same system. However, assumptions of similarities between two species, particularly oysters, which have complex life histories, should be based on careful observation and experimentation.

Both *C. virginica* and *C. ariakensis* have a motile larval stage followed by a sessile juvenile and adult stage. The larval stage is a period for population dispersal, but it is also a highly vulnerable period for both species and greater than 95% of mortality occurs at this time largely due to predation (Eckman 1996) and dispersal away from an optimal settlement habitat (North et al. 2008). The larval stage is also a period when these two oyster species appear to differ in ways that may have significant impacts on survival.

There are observed differences in the coloration, size, and swimming behavior, which are potentially important to predation vulnerability, between *C. ariakensis* and *C. virginica*. Side-by-side comparisons in the laboratory of the larvae of both species fed the same diet show that *C. ariakensis* larvae are red to pink in color in contrast to the *C. virginica* larvae, which are brown. The coloration of *C. ariakensis* differs from the color of the turbid water column typical of Chesapeake Bay, while the coloration of *C. virginica* matches that background. As a result, it is easier to visually identify individual *C. ariakensis* larvae in a turbid water column (Luckenbach, personal observation). Larval *C. ariakensis* are also larger at the eyed stage (mean shell height (SD), μm—*C. virginica* 273.3 (16.5), *C. ariakensis.* 330.4 (17.7); M. Luckenbach, unpublished data) and may reside lower in the water column than the *C. virginica* larvae of the same age (Manuel et al. 2008). Further, larval size and swimming speed (Troost et al. 2008b) increase, and the larvae become more bottom- and reef-oriented (Kennedy 1996) as they shift from the veliger to the pediveliger (i.e., foot) stage between 12 and 20 days after hatching. These differences may result in different mortality rates between the early- and late-larval stages due to the changes in encounter rates with predators residing at different depths and differences in capture probability for visual vs. non-visual predators.

Visual predators are likely to be important sources of oyster larval mortality both for veliger larvae throughout the water column and for pediveliger larvae near the oyster substrate. Differences in both size and body coloration among prey types have been observed to significantly affect the relative vulnerability to predation on zooplankton (Annett 1989; Bakker et al. 1997; Browman and Marcotte 1987; Curio 1976; Zaret and Kerfoot 1975). The potential visual predators of oyster larvae include larvae of demersal oyster reef resident fishes (e.g., naked goby, *Gobiosoma bosc*), which are highly abundant and spatially associated with oyster larvae. The differences between *C. ariakensis* and *C. virginica* in swimming speed and behavior may also lead to different predation rates from non-visual predators. Lobate ctenophores, *Mnemiopsis leidyi*, are important consumers of zooplankton and ichthyoplankton in the mesohaline areas of coastal estuaries such as Chesapeake Bay (e.g., Cowan and Houde 1993; Purcell et al. 1994), and their peak abundance and consumption coincide with the spawning activity of both *C. virginica* and *C. ariakensis* (Allen et al. 2005; Kennedy et al. 2005). *M. leidyi* readily

consume *C. virginica* larvae, digest nearly all veligers ingested, and are sufficiently abundant in Chesapeake Bay to consume a significant fraction of larval production (Purcell 2005; Purcell et al. 1991).

Benthic non-visual predators, including adult *C. virginica* (Tamburri and Zimmer-Faust 1996) and the barnacle, *Balanus improvises* (Steinberg and Kennedy 1979), may also be important predators of oyster larvae particularly close to settlement. *Balanus* spp. are ubiquitous members of the benthic invertebrate community and highly abundant on hard bottom such as oyster reefs (Rodney and Paynter 2006). The importance of benthic invertebrates to larval mortality has been reported to be minor for *C. virginica* (White and Wilson 1996), but it is important to test the relative contribution of benthic predators to larval mortality. In this study, we take an empirical approach to compare the vulnerability of *C. virginica* and *C. ariakensis* larvae to visual and non-visual as well as benthic and pelagic predator functional groups. The objectives of this study are to (1) compare the predation vulnerability of *C. virginica* and *C. ariakensis* during the larval stage, (2) test whether larval predation vulnerability changes among different predator functional groups, and (3) test whether larval predation vulnerability differs over the larval period.

Methods

Experimental System All experiments were conducted at the Smithsonian Environmental Research Center (SERC) in Edgewater, MD, USA. Oyster larval predation experiments were conducted under constant conditions of temperature, salinity, and light levels in a controlled experimental space. Water temperature was maintained at 20°C for all trials based on the rearing and maintenance temperature chosen for larval *G. bosc*, rotifers, and ctenophores. Salinity was set at the midpoint between the source salinities of the predator, rotifers, and oyster larvae (see below). All three groups were acclimated to this midpoint salinity by adjusting the salinity of their holding tanks over 2–3 days. Salinity ranged between 13 and 15 across all trials. Light for the experimental trials was from a low-irradiance LED light source directly above the experimental tanks and other sources of light were eliminated by isolating the experimental system behind black sheeting in a dark room.

Experimental tanks were arranged in sets of eight and were of two sizes. Large 100-l opaque plastic cylindrical containers (diameter—56 cm, water depth—41 cm) were arranged on the floor and used for trials in which *M. leidyi* was the predator. Small 10-l cylindrical glass jars (diameter—22.4 cm, water depth—25.4 cm) were arranged on a metal rack and were used for trials in which either larval *G. bosc* or adult *Balanus* spp. were used as the predator. These glass jars were wrapped in black plastic to eliminate lateral light penetration. Both the large and the small tanks were chosen to provide a reasonable amount of vertical height relative to predator and prey size to allow for changes in vertical position by both predators and prey. Experimental tanks were filled with water pumped from the adjacent Rhode River and filtered at 0.1 μm to remove any potential confounding species. Temperature and salinity were adjusted in the experimental system at least 24 h prior to the introduction of prey or predators.

Predators All predator collection and handling were conducted according to prescribed protocols known to minimize stress and maximize the number of individuals behaving normally in the experimental system. Ctenophores, *M. leidyi*, were collected from the Rhode or Patuxent rivers with a 0.5-m, 202-μm-mesh plankton net and transported to SERC 2–3 days prior to the beginning of each trial day. Ctenophores were fed both rotifers and oyster larvae prior to the trial day but were moved to prey-free water 24 h prior to any experiments. Larval naked gobies, *G. bosc*, were cultured in the laboratory from eggs collected in the Patuxent River before the beginning of an experimental period. Cultured larvae were fed rotifers ad libitum and used as predators at 5–7 days post-hatch (dph; early-stage trials) and 12–15 dph (late-stage trials) to ensure that the oyster larval size was matched to the larval goby gape width. Barnacles, *Balanus* spp., were collected from the tops of plastic trays placed in the Rhode River prior to the beginning of the experimental season. The tray tops were cut into small sections containing 15–20 barnacles and maintained in unfiltered water pumped from the Rhode River until they were moved into prey-free water 24 h prior to the onset of experiments.

Oyster Larvae All oyster larvae were obtained from a quarantined research hatchery at the Virginia Institute of Marine Science Eastern Shore Laboratory (VIMS-ESL) located in Wachapreague, VA. In both 2006 and 2007, the larvae of the three larval types, *C. virginica*, *C. ariakensis* (Oregon strain), and *C. ariakensis* (South China strain), were spawned at separate times during the experimental season (June to August) so that only one larval type was available at any one time. [The Oregon strain was derived from stocks of *C. ariakensis* imported to the US Pacific coast from Japan in the 1970s (Breese and Malouf 1977) and subsequently domesticated in hatcheries on the West Coast. The South China strain was an F3 generation stock imported to quarantine hatcheries in Virginia from South China in 2002.] When the larvae were 5–7 dph in age, a 1–2 million larvae aliquot was transported in a chilled cooler to SERC. Travel time from the VIMS-ESL to SERC is approximately 4 h.

Once the aliquot arrived at SERC, it was immediately placed in a glass beaker of water, slowly acclimated to ambient temperature, and observed for larval swimming activity. Once significant larval swimming activity was observed, the aliquot was poured into a 64-μm sieve and transferred to a 100-l holding tank that was matched in salinity and temperature to the source system at VIMS. The larvae were fed cultured microalgae (*Isochrysis galbana* and *Tetraselmis striata*) as supplied by the VIMS hatchery once per day until the beginning of experiments. Larval transport and acclimation always occurred at least 36 h prior to any trial day. This entire process was repeated when the larvae were 12–15 dph, providing for an early-larval stage (5–7 dph; 108–145 μm) and a late-larval stage (12–15 dph, 160–282 μm) trial set for each larval type. On each experimental day, the density of actively swimming oyster larvae in the holding tank was estimated based on triplicate 50-ml counts examined in a Ward clear acrylic counting wheel (www.wildco.com).

Alternative Prey Marine rotifers, *Branchionus* spp., were obtained from the University of Maryland Center of Marine Biotechnology (COMB) and maintained in a small-scale system at SERC. Rotifers were fed live or frozen algae (Instant Algae, Reed mariculture, Campbell, CA) and rotifer densities were checked daily. In addition to experiments, cultured rotifers were also used to feed *G. bosc* larvae. Twenty-four hours prior to each experimental day, a sub-sample of the rotifer culture, poured into a 64-μm sieve, was removed by siphon for use in experiments. The density of this sub-sample was estimated on the morning of the experimental day from triplicate 1-ml counts of actively swimming rotifers examined at ×100 magnification in a Sedgwick-rafter cell.

Experimental Trials Experiments were conducted with each oyster larval type separately in 2- or 3-day blocks with a single predator type used on each day. The predator order was haphazard but not rigorously randomized. On each trial day, each of the eight trial tanks was randomly assigned to a target prey density. Target prey densities differed by predator type and year (Table 1). In particular, the three lowest densities used in year 1 for ctenophores were increased in year 2 because minimal feeding was observed at these densities. Rotifers and oyster larvae were added to each trial tank at the appropriate density to achieve a 50/50 mix at the target prey density based on volume and allowed to move freely in experimental chambers for 15 min prior to the start of the trial period. Only actively swimming prey were selected for experiments by gently removing larvae or rotifers from the top two thirds of the water column with a beaker. The trial period began with the collection of replicate water samples to estimate actual prey density. These samples were collected with a vertical tube sampler lowered onto a rubber stopper placed on the bottom of the tank, which sampled the entire tank water column but not the tank bottom. Prey samples were sieved onto 64-μm mesh and preserved in 10% buffered formalin for analysis. Immediately after prey sampling, ten predator individuals were introduced into the tank at mid-water column (ctenophores, fish larvae) or bottom (barnacles). Once the predators were in the tank, they were allowed to forage for either 30 (*M. leidyi*) or 45 min (*G. bosc* and *Balanus* spp.). At the end of this foraging period, the experiment was stopped by removing the predators from the system into a dish containing food-free water. In the case of *G. bosc*, 10 mg of MS-222 was added to the trial tank just prior to predator removal to anesthetize the larvae and minimize regurgitation during handling. A second triplicate set of post-experiment prey samples was collected as described to estimate prey depletion/mortality. Once removed, the predators were preserved individually in 10% buffered formalin for gut content analysis. Ctenophores dissolve in formalin, so no further processing was required. The digestive track of both *G. bosc* and *Balanus* spp. was removed by dissection and the contents of the foregut were examined and counted by prey type. Individual lengths were recorded for *M. leidyi* prior to preservation. The

Table 1 Target prey densities (ml^{-1}) for each year and predator type. The target densities in 2007 were adjusted based on the observed total feeding rates in 2006. The three lowest densities for the ctenophore trials were changed by an order of magnitude and are italicized in the table

2006		2007		
Ctenophores	Larval gobies	Ctenophores	Larval gobies	Barnacles
0.01	0.1	0.1	0.1	0.1
0.02	0.25	0.25	0.25	0.25
0.05	0.5	0.50	0.50	0.50
0.1	0.75	0.75	0.75	0.75
0.2	1.0	1.0	1.0	1.0
0.5	1.5	1.5	1.5	1.5
1.0	2.0	2.0	2.0	2.0
3.0	4.0	3.0	3.0	3.0

lengths of *G. bosc* were estimated based on a sub-sample of 25 larvae taken from the source cohort on each trial day. Shell heights of *Balanus* spp. were measured at the time of sample processing (see below). Tanks were arbitrarily numbered one to eight and the trials in individual tanks were completed in an ascending, overlapping series. After the trials had been completed in all eight replicate tanks, all remaining water was siphoned into a holding tank and treated according to an approved biosecurity protocol. The contents of both prey density and predator gut samples were counted at ×1–8 magnification.

Data Analysis Chesson's electivity index was calculated for each individual predator based on gut and prey density samples.

$$\alpha_i = \frac{\frac{p_i}{q_i}}{\sum_k \frac{p_k}{q_k}}$$

where p_i is the proportion of prey type *i* in the predator gut and q_i is the proportion of prey type *i* in the trial tank. The neutral selection for prey type *i* is indicated by a Chesson's α value equal to 1/*n* where *n* is the number of prey types present (i.e., 0.5). In our experiments, positive selection is indicated by values above 0.5 and the negative selection by values below 0.5. The mean selectivity value for each of the trial tanks was used for analysis. The selectivity data for oyster larvae were compared with a two-way ANOVA for each predator type with prey type (n=3) and stage (n=2) as independent variables. Replicates (i.e., tanks) were excluded from these calculations if fewer than 50% of the individuals in the replicate had at least ten prey items in the gut sample. Each observation (i.e., tank mean) was also weighted by the deviation of q_i from 0.5 to account for changes in behavior of Chesson's α when the relative proportion of prey items differ by more than 5–10% in a two-prey model (Confer and Moore 1987).

Consumption rate was measured as the mean total prey consumed by predators within a single tank (n=10) during each experimental trial. The consumption rate of oyster larvae was examined as a function of total prey density, larval stage, and larval type with an ANCOVA to identify a functional response for each predator. The consumption rate data were ln (X+1) transformed to correct for heteroscedasticity. All statistical tests were conducted with a type 1 error rate of 5% (i.e., α=0.05).

Differences in relative mortality due to predation (*d*) among larval types were calculated based on observed feeding rates for each predator type adjusted for observed differences in predator preference for each larval type relative to alternative prey by multiplying the mean feeding rate by the appropriate mean Chesson's α. The adjusted feeding rate was converted to a relative estimate of instantaneous mortality rate based on a 12-h feeding period per day and a 24-day larval period.

$$N_1 = N_0 \times C_i \times \alpha_i \times 60 \times 12$$

$$M_x = \ln\left(\frac{N_1}{N_0}\right) \times 24$$

$$d_{\mathrm{Ca}} = \frac{M_{\mathrm{Ca}}}{M_{\mathrm{Cv}}}$$

where N_0 is the cohort size at hatch, N_1 is the cohort size 1 day after hatch, C_i is the observed consumption rate (min^{-1}) of predator *i* from our experiment, and α_{i} is the observed preference value in our experiments. The parameter M_x is the instantaneous mortality rate for cohort *x* between hatch and settlement. The parameter *d* is the ratio of *M* for a non-native species and *M* for *C. virginica.* This value does not estimate the total predator impact in the natural world but rather the relative change in the instantaneous mortality rate due to predation (*M*) over the entire larval period assuming a complete replacement of native oyster larvae with one of the non-native larval types.

Results

Prey Preferences The patterns of preference for oyster larvae differed as a function of predator type, oyster larval type, and oyster larval stage. Ctenophores were the only predator type that had consistently positive feeding rates on early-stage oyster larvae. Larval *G. bosc.* fed very inconsistently on early-stage oyster larvae and *Balanus* spp. fed only on later-stage oyster larvae. The mean sizes of predators are given in Table 2 and did not differ significantly across oyster larval strains within predator type or larval stage (ANOVA, all $F_{0.05,2,802}$<3.75, all p>0.06).

Ctenophore preference for oyster larvae was significantly different across oyster larval type and stage ($F_{0.05,\ 2,58}$= 12.593, p<0.0001) with the preference for *C. virginica* significantly lower than the preference for either *C. ariakensis* strain for both early-stage ($q_{3,58}$=5.2; p<0.0001) and late-stage oyster larvae ($q_{3,58}$=6.7; p<0.0001) based on a Dunnett's test (Fig. 1). The mean preference values for early-stage oyster larvae in the 2006 trials were consistently less than 0.5, indicating that all three oyster larval types were less preferred than rotifers by ctenophores (Fig. 1a). However, while the mean preference was negative for early-stage *C. virginica* larvae (mean Chesson's α was below 0.5) in 2007, it was strongly positive (mean Chesson's α=0.74 and 0.89) for the *C. ariakensis* South China and Oregon strain,

Table 2 Mean size and SD of the predators and oyster larvae (shell height, μm) used in the feeding experiments as well as the mean (SD) total feeding rate (FR; individual per minute) of predators across all treatments within the larval stage. The size data are presented separately for early (E)- and late (L)-stage trials. The size data for oyster larvae are separated by year

	Year	Stage	Mean	SD	FR
Predator					
Ctenophores (length, cm)		E	5.2	1.3	7.6 (9.0)
		L	5.7	1.5	15.6 (24.2)
Larval naked goby (total length, mm)		E	4.1	0.62	0.0014 (0.003)
		L	5.2	0.88	0.014 (0.004)
Barnacles (shell height, cm)		E	0.94	0.19	0
		L	0.94	0.19	2.35 (0.50)
Oyster larvae					
C. virginica	2006	E	136	24.59	
		L	248	22.51	
	2007	E	145	18.41	
		L	276	49.7	
C. ariakensis OS	2006	E	154	11.4	
		L	282	49.7	
	2007	E	134	23.02	
		L	188	31.96	
C. *ariakensis* SC	2006	E	108	8.37	
		L	248	13.04	
	2007	E	118	19.24	
		L	160	29.15	

respectively (Fig. 1b). Despite the observed difference between years, the preference for both strains of *C. ariakensis* larvae was significantly higher than the preference for *C. virginica* larvae overall. The ctenophore preference for late-stage oyster larvae was consistently positive across all oyster larval types in both years (Fig. 1c, d).

Larval naked gobies had low predation rates relative to other predators and fed consistently only on the late-stage

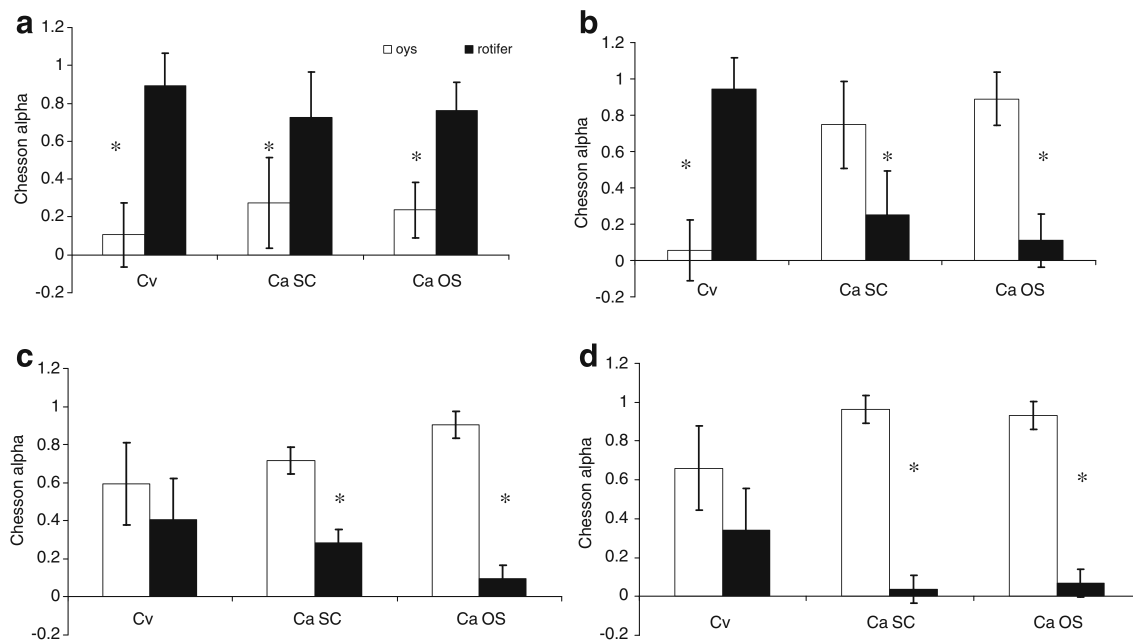

Fig. 1 Mean relative preference (±SD) of lobate ctenophores, *M. leidyi*, for early-stage (**a**, **b**) and late-stage (**c**, **d**) oyster larvae (*Crassostrea* spp.) mixed with rotifers (*Branchionus* spp). Data are given separately for trials conducted in 2006 (**a**, **c**) and 2007 (**b**, **d**). Data are given separately in each panel for *C. virginica* (*Cv*), *C. ariakensis* Oregon strain (*Ca OS*), and *C. ariakensis* South China strain (*Ca SC*). *Asterisks* indicate a significant difference at α=0.05

oyster larvae, yet they also displayed a stronger preference for *C. ariakensis* larvae than *C. virginica* larvae in comparison to alternative prey. Larval goby preference for oyster larvae in comparison to alternative prey was consistently above 0.6 for all oyster larval types, indicating a positive preference for late-stage oyster larvae relative to the alternate prey. The preference for oyster larvae differed significantly among oyster larval types ($F_{0.05,\ 2,19}$=5.14, p= 0.016). The preference for *C. virginica* was significantly lower than the preference for both strains of *C. ariakensis* larvae based on a Dunnett's test ($q_{3,19}$=6.9, p<0.0001; Fig. 2a).

Barnacles consumed oyster larvae and rotifers but displayed neither positive nor negative preference for any individual prey type. Barnacles fed only on late-stage oyster larvae most likely because of their inability to access a prey distant from the substrate to which they are attached. The mean preference for oyster larvae did not differ from 0.5 across all larval types ($\overline{X}$ = 0.55, SE=0.04; Fig. 3a) and did not differ significantly among oyster larval types ($F_{0.05,\ 2,11}$= 2.582, p=0.12).

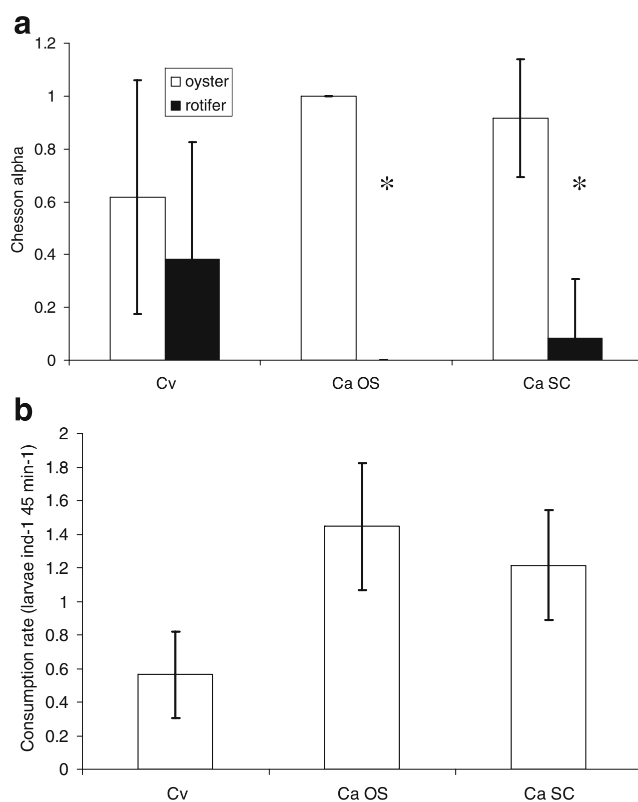

Fig. 2 Mean relative preference (±SD) of larval gobies, *G. bosc*, for late-stage oyster larvae (**a**) and mean foraging rate (±SD) of *G. bosc* on late-stage oyster larvae (**b**). Data are given separately for *Crassostrea virginica* (*Cv*), *C. ariakensis* Oregon strain (*Ca OS*), and *C. ariakensis* South China strain (*Ca SC*). *Asterisks* indicate a significant difference at α=0.05

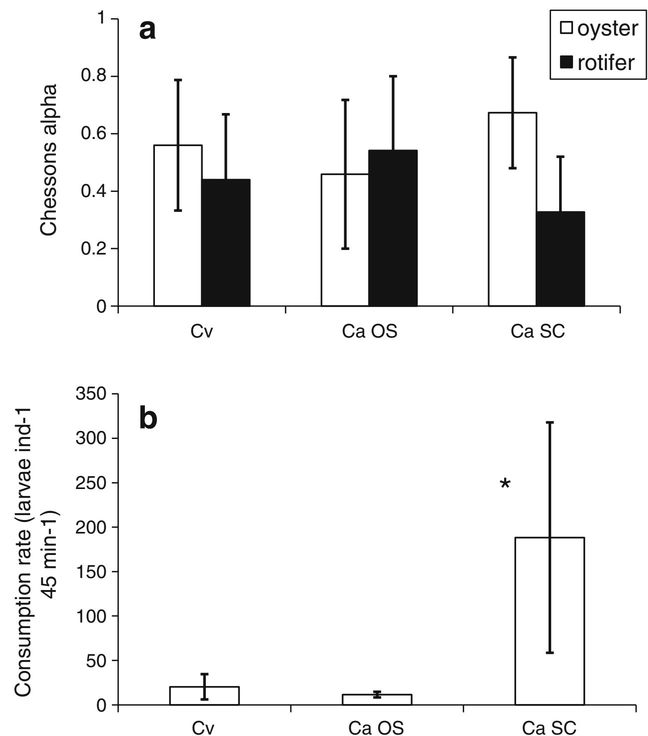

Fig. 3 Mean relative preference (±SD) of barnacles, *Balanus* spp., for late-stage oyster larvae (**a**) and mean foraging rate (±SD) of *Balanus* spp. on late-stage oyster larvae (**b**). Data are given separately for *C. virginica* (*Cv*), *C. ariakensis* Oregon strain (*Ca OS*), and *C. ariakensis* South China strain (Ca SC). *Asterisk* indicates a significant difference at α=0.05

Predator Foraging Rate Ctenophore foraging rate (min^{-1}) on oyster larvae in the presence of alternative prey differed as a function of oyster species, oyster larval stage, and total prey density. For early-stage larvae, foraging rate was highest when feeding on *C. ariakensis* larvae. Ctenophores did not display a significant functional response ($F_{0.05,\ 1,22}$=0.189, p=0.67) when feeding on early-stage oyster larvae but the mean foraging rate did differ among oyster larval types ($F_{0.05,\ 2,22}$=9.1, p<0.001; Fig. 4a). The ctenophore foraging rate was significantly higher for the two *C. ariakensis* strains in comparison to *C. virginica* based on a linear contrast (Scheffe's test; p<0.0001). No significant functional response was observed for ctenophores feeding on rotifers in early-stage trials ($F_{0.05,\ 1,22}$=0.46, p=0.504; Fig. 4b), but the mean foraging rate on rotifers was significantly lower when paired with *C. ariakensis* South China strain than with either *C. virginica* or *C. ariakensis* Oregon strain based on a linear contrast (Scheffe's test; p=0.009).

The ctenophore foraging rate for late-stage oyster larvae increased with prey density but did not change between *C. virginica* and *C. ariakensis*. Ctenophores displayed a significant positive functional response for late-stage oyster larvae ($F_{0.05,\ 1,35}$=80.5, p<0.0001; Fig. 4c), and foraging rate did not differ among oyster

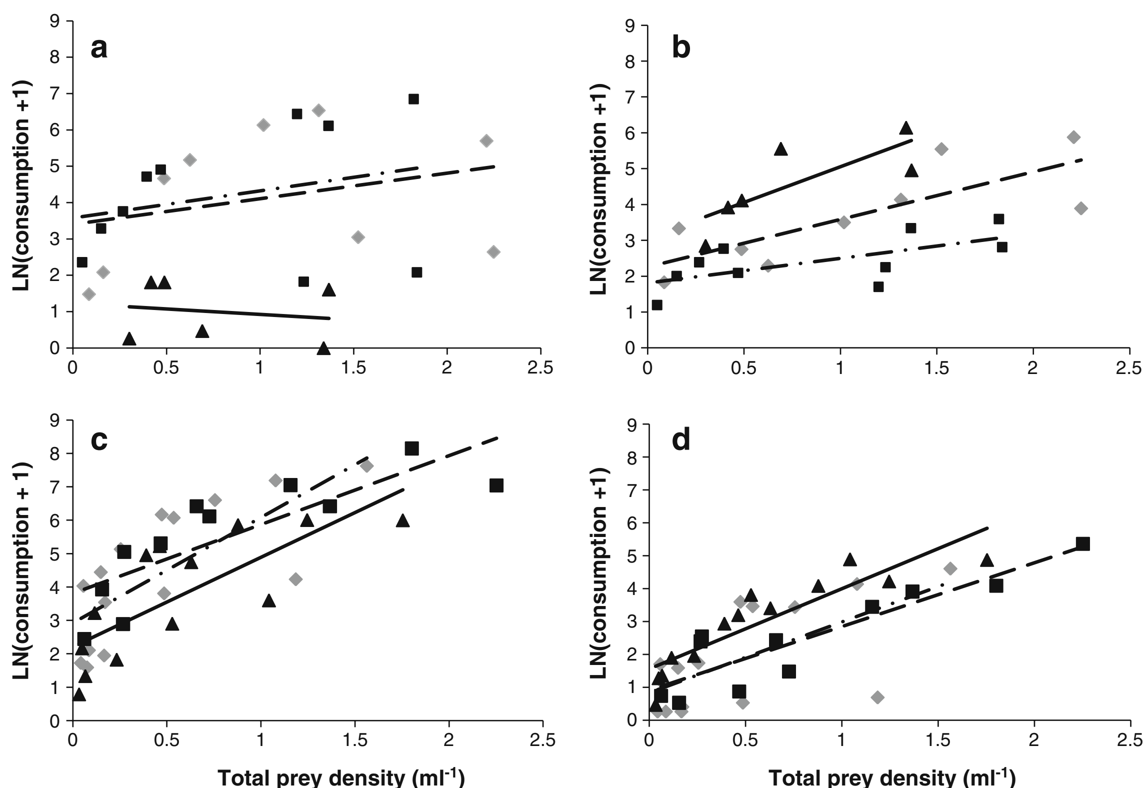

Fig. 4 Foraging rate as a function of total prey density for *M. leidyi* feeding on oyster larvae (**a**, **c**) and rotifers (**b**, **d**). Data are given separately for trials involving the mixtures of rotifers with early-stage larvae (**a**, **b**) or rotifers and late-stage larvae (**c**, **d**). *Symbols* indicate data for the three strains of oyster larvae: *C. virginica* (*filled triangles*), *C. ariakensis* Oregon strain (*filled squares*), and *C. ariakensis* South China strain (*filled diamonds*). *Lines* indicate best fit linear regressions for *C. virginica* (*solid line*), *C. ariakensis* Oregon strain (*mixed hash line*), and *C. ariakensis* South China strain (*single hash line*)

larval types ($F_{0.05,\ 2,35}$=5.1, p=0.07). Ctenophores also had a significant positive functional response to rotifers in the late stage trials ($F_{0.05,\ 1,35}$=15.3, p=0.019; Fig. 4d) and mean foraging rate differed for rotifers paired with different oyster larval types ($F_{0.05,\ 2,35}$=23.1, p=0.001). The foraging rate of ctenophores on rotifers was highest when mixed with *C. virginica* than either *C. ariakensis* Oregon strain or *C. ariakensis* South China strain (Scheffe's test; p=0.038).

The foraging rate of larval naked goby or barnacles feeding on oyster larvae did not change among oyster larval types or as a function of prey density. Goby larvae did not display a significant functional response ($F_{0.05,\ 1,16}$=0.137, p=0.716) for oyster larvae and the mean feeding rate on late-stage oyster larvae did not differ significantly among oyster larval types ($F_{0.05,\ 2,16}$=1.306, p=0.295) although the feeding rate on both *C. ariakensis* larval types were consistently higher than for *C. virginica* larvae (Fig. 2b). The barnacles did not display a significant functional response for late-stage oyster larvae ($F_{0.05,\ 1,10}$=0.136, p= 0.172). The mean barnacle feeding rate did, however, differ significantly among oyster larval types ($F_{0.05,\ 2,10}$=22.8, p< 0.001) with the feeding rate for *C. ariakensis* South China strain significantly higher than both *C. ariakensis* Oregon strain and *C. virginica* based on a linear contrast (Scheffe's test; p<0.001; Fig. 3b).

Oyster Larvae Mortality Rate The differences in both the preference and the feeding rate among predators translated into differences in relative mortality rate (d). Ctenophores appear to be the more important predator of the three in terms of total estimated consumption as they displayed both significant differences in preference among larval types in comparison to alternative prey and a higher feeding rate. The larval naked gobies showed a significantly higher preference for *C. ariakensis* larvae but had a low feeding rate (Table 2). The barnacles displayed no preference but increased their feeding rate for *C. ariakensis* larvae. The relative mortality rate of early-stage larvae due to ctenophores shifted from essentially no mortality for *C. virginica* to a relative M of 0.01 for *C. ariakensis* South China strain and 0.05 for *C. ariakensis* Oregon strain, which translated to a d-value of 21 over a 24-day larval period. The predation mortality by *M. leidyi* on late-stage larvae had a relative mortality difference of 9 and 17.7 for *C. ariakensis* Oregon strain and South China strain, respectively. The

differences in relative predation mortality for *G. bosc* were 20 and 35 for *C. ariakensis* South China strain and Oregon strains respectively. Only the feeding rates differed significantly among the larval types for barnacles, and this translated to a difference in relative mortality of 9.3 and 0.56 for *C. ariakensis* South China and Oregon strains, respectively.

Discussion

The introduction of a non-native species into any ecosystem has a high potential to alter that ecosystem and the costs and benefits of such actions should be closely scrutinized. In this study, we were concerned with whether differences in relative predation vulnerability exist between the native and non-native oyster species in Chesapeake Bay that may affect the success of non-native oysters supplementing the native population. It is important to make a meaningful prediction regarding success prior to making the irreversible decision to introduce a non-native species. Such predictions will be greatly enhanced if we understand and account for differences in survival rate between native and non-native species over their entire life histories. Our examination of relative predation rates suggests that differences do exist in the relative vulnerability to predation between *C. virginica* and two strains of *C. ariakensis* during the larval stage. For all three predators tested, one or both strains of *C. ariakensis* experienced higher predation rates or was a more highly preferred prey than *C. virginica.*

The differences in relative predation vulnerability of larvae can be separated into factors likely to affect either the probability of encounter with a predator, probability of attack given an encounter, or probability of escape once encountered and attacked. Those considered indirectly here via our choice of predators are differences most likely to affect encounter rate, including visual differences such as differences in individual larval size or coloration and distributional differences such as predator vertical position. The differences in oyster larval size may also result in differences in escape potential as swimming speed has been found to be positively related to size (Troost et al. 2008b). In our experiments, the size differences between species were small particularly for the early-stage larvae, so the observed differences in vulnerability are most likely due to other factors. Many species of bivalve larvae, particularly oysters, are known to become negatively phototactic as they develop (Bayne 1964; Carriker 1951); the resulting increase in mean depth should decrease the encounter rates with pelagic predators and increase the encounter rates with benthic predators. Vertical distributions of larvae were possible in this study but were not observable. We therefore cannot directly assess the importance of variation in vertical distributions among larval types and ages to vulnerability in our experiments.

Prior to this study, the observed differences in visibility and distribution between *C. virginica* and *C. ariakensis* larvae suggested that the *C. ariakensis* larvae may be more vulnerable than *C. virginica* to visual and demersal predators. In contrast, *C. virginica* was thought to be more vulnerable to pelagic predators based on an assumption of a higher vertical distribution, but this would also be a function of predator distribution and water column stratification (Manuel et al. 2008). The results of this study only partially support these predictions. The vulnerability of *C. ariakensis* to a benthic visual predator (*G. bosc*) was higher than that of *C. virginica*, but not to a benthic non-visual predator (*Balanus* spp.), lending support to the hypothesis that the differences in visibility are important in defining the predation vulnerability of oyster larvae, particularly during the later stages close to settlement. The vulnerability to a pelagic non-visual predator (*M. leidyi*) was also higher for *C. ariakensis* than for *C. virginica*, although the results were less consistent for the early stages. Since this difference is not due to visual cues, it may be the result of either differences in predator encounter rates or differences in escape potential. Our data do not allow for any conclusions as to the ultimate cause, but this would be a fruitful area for continued study.

We are not aware of any other published study that has compared the predation vulnerability of larval *C. virginica* to the larvae of other congenerics across a suite of potential predators; however, the vulnerability of introduced oyster larvae has been compared to the larvae of native bivalves in other systems. *Crassostrea gigas* has become well established in the Oosterschelde estuary (SW Netherlands) and this is thought to be partially due to the increased escape potential of *C. gigas* larvae compared to the native *Mytilus edulis* when exposed to filtration by adult bivalves (Troost et al. 2008a). In the Oosterschelde estuary, swimming speed, which is a function of larval size, was thought to be the primary determinant of differences in larval predation vulnerability. This finding supports the hypothesis that differences in larval size may be important, particularly when larviphagy is a significant source of mortality.

Larviphagy has been observed in many species of bivalves including *C. virginica* (Tamburri and Zimmer-Faust 1996) and may be an important source of larval mortality in estuaries with an abundance of adult bivalves. The importance of larviphagy in Chesapeake Bay is likely to be low due to the present low oyster biomass. The relative vulnerability of *C. ariakensis* and *C. virginica* larvae to predation by benthic filter-feeders, such as adult oysters and *Balanus* spp., should be governed by similar

dynamics, which suggests that differences in vulnerability will be small. Yet, predation vulnerability to adult oysters may still differ due to differences in feeding behavior and size selectivity (Barnes and Barnes 1982; Newell and Langdon 1996) and this will be a fruitful area for future study.

The real-world impact of any difference in vulnerability among native and non-native larvae will be a function of total larval consumption of a particular predator type relative to the total number of bivalve larvae in the system. The rates of oyster larval predation by invertebrate predators at natural densities have been observed to be low in marine systems (Johnson and Shanks 2003). Yet, studies of oyster larval predation in estuaries such as Chesapeake Bay have found the predation rates to be significant on oyster larvae under natural conditions (Harding 1999; Purcell et al. 1991), suggesting that the predation rate on bivalve larvae may be dependent on local prey density and the predator types present. In our experiments, the feeding rates of all predators were negligible below a prey density of 0.1 ml^{-1}, but oyster larvae are commonly found at densities as high as 200 ml^{-1} in Chesapeake Bay, particularly around oyster reefs (Chesapeake Bay monitoring program; http://www.chesapeakebay.net/data_plankton.aspx). The critical factors determining the influence of a particular predator on total larval survival are likely to be foraging rate, predator functional response, and differences in predator selectivity among larval types.

The larvae of the reef-associated benthic predator, *G. bosc*, displayed the largest selectivity difference between native and non-native oyster larvae. However, the per capita consumption rate of *G. bosc* larvae, at 0.014 prey per individual per minute, was the lowest among the predator types examined. Harding (1999) reported a peak consumption rate of 0.03 prey per individual per minute in experimental trials and stated that, at a density of ten gobies per square meter, *G. bosc* could consume 74% of the natural larval production for oysters on a reef. A conversion of our observed feeding rates to an estimate of difference in instantaneous mortality (*d*) suggests that predation mortality could be much higher for *C. ariakensis* larvae than for *C. virginica* larvae assuming that the preferences and feeding rates we observed persist through demersal larval stages of *G. bosc*. We did not observe a functional response for *G. bosc*, so the feeding rate may not change above our threshold prey density (0.1 ml^{-1}). Further, oyster larvae in later stages move in close to the reef in preparation for settlement and larval densities at this time are high (Harding and Mann 2000). So, despite their low consumption rate, *G. bosc* may be capable of having a substantial impact on the number of oyster larvae surviving to settlement.

Oyster larvae are vulnerable to pelagic predators such as *M. leidyi* earlier in the larval stage (Purcell et al. 1991) and there appear to be important differences in predation vulnerability to *M. leidyi* between native and non-native oyster larvae greater than the observed vulnerability to early-stage *G. bosc* larvae. *M. leidyi* is a voracious zooplanktivore that has the ability to clear the water of mesozooplankton during periods of high abundance in the summer (Purcell et al. 2001). Diet analysis (Purcell et al. 1994; Sullivan and Gifford 2004) and laboratory experiments (Grove and Breitburg 2005) suggest that mesozooplankton (e.g., *Acartia tonsa*) are the dominant prey item for *M. leidyi*; however, *M. leidyi* also feed on microzooplankton and show a strong preference for native oyster larvae in experiments (Purcell et al. 1991). The period of peak abundance of ctenophores also occurs during the summer months and overlaps with the peak spawning period of both *C. virginica* and *C. ariakensis* (Allen et al. 2005; Kennedy 1996). Our results suggest that the oyster larvae are positively selected relative to comparably sized zooplankton prey. Therefore, even if oyster larvae are a relatively minor component of ctenophore diets in Chesapeake Bay, the high consumption rate of ctenophores generates potential for impact on total predation mortality during the larvae period, particularly in the years of above-average ctenophore density (Purcell 1992).

Overall, our results suggest that the relative differences in the mortality rates of *C. ariakensis* and *C. virginica* larvae may be important and should be considered in an examination of the population viability of non-native oysters in Chesapeake Bay. Several studies have indicated that the variability in larval survival is less important in determining annual recruitment due to the impact of post-settlement mortality (Newell et al. 2000). Yet, with total larval survival frequently less than 1% (Rumrill 1990), even small differences in predation vulnerability during the larval stage can translate to large differences in larval delivery to the substrate (Thorson 1950) that must be accounted for in making predictions regarding population viability. Our results provide an important example of the need to incorporate all life stages into a benefits analysis of non-native introductions into complex estuarine ecosystems. More work is needed to fully understand the causative factors for these observed differences in larval vulnerability to predation. Nonetheless, the results of this study demonstrate a potentially important difference between species that should be incorporated into simulation models used to predict oyster larval distribution in order to achieve a more realistic picture of how recruitment may differ between native and non-native oysters. The outcome will be a better assessment of whether the projected benefits of a non-native introduction outweigh the projected costs, which can

provide guidance for the better use of management resources.

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