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PREDATION BY THE OYSTER TOADFISH *OPSANUS TAU* (LINNAEUS) ON BLUE CRABS AND MUD CRABS, PREDATORS OF THE HARD CLAM *MERCENARIA MERCENARIA* (LINNAEUS, 1758)¹

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ABSTRACT The oyster toadfish, *Opsanus tau* (Linne), reduces predation by xanthid and portunid crabs on juvenile hard clams, *Mercenaria mercenaria* (Linne), in field cultures. This study examined the influence of size and species on the predator-prey relationship between toadfish and crabs. The mud crabs *Eurypanopeus depressus* (Smith), *Neopanope sayi* (Smith), and *Panopeus herbstii* Milne Edwards of 5-40 mm carapace width and blue crabs *Callinectes sapidus* Rathbun of 77-105 mm carapace width were offered to toadfish of 70-322 mm total length. Toadfish predation rates on mud crabs were higher with increasing toadfish size and lower with increasing crab size. Toadfish injured or killed mud crabs that were one tenth of their total length or approximately one half of their mouth width. Predation of juvenile hard clams by blue crabs was reduced when toadfish were present.

KEY WORDS: predation, toadfish, *Opsanus*, crabs, hard clams, *Mercenaria*

INTRODUCTION

Crabs prey on juvenile hard clams in field culture systems (Eldridge et al. 1976; MacKenzie 1977, 1979; Castagna and Kraeuter 1981; Gibbons and Blogoslawski 1989). Culture techniques used to exclude predators include rafts, trays, cages, and nets (Castagna and Kraeuter 1981; Jory et al. 1984). Biological methods have been used to protect shellfish from predation with varying degrees of success. In particular, the oyster toadfish, *Opsanus tau* (Linne), has been shown to be a biological control of crab predation on juvenile hard clams, *Mercenaria mercenaria* (Linne), cultured in cages with gravel aggregate (Gibbons and Castagna 1985). This laboratory study further investigates the feeding behavior and predation rates by oyster toadfish on four species of crabs that prey on juvenile hard clams.

Opsanus tau is a benthic, non-migratory fish found along the Atlantic coast of the United States (Gudger 1910; Schwartz and Dutcher 1963). It preys mainly on crustaceans, with mud crabs (Decapoda: Xanthidae) and blue crabs (Decapoda: Portunidae) forming the bulk of stomach contents (McDermott 1964; Wilson et al. 1982; Gibbons and Castagna 1985). During the day toadfish ambush prey from their burrows, while at night they stalk prey (Phillips and Swears 1979). The sympatric mud crabs *Eurypanopeus depressus* (Smith), *Neopanope sayi* (Smith), and *Panopeus herbstii* Milne Edwards, and the blue crab, *Callinectes sapidus* Rathbun, are predators of the hard clam, *M. merce-*

naria, (Gibbons and Blogoslawski 1989) and live in similar habitats as the oyster toadfish, *O. tau* (Williams 1984). The oyster toadfish preys upon these crabs but not hard clams (Gibbons and Castagna 1985).

The oyster toadfish normally ranges from 180-300 mm total length (TL) with a maximum reported size of 368 mm (TL), (Gudger 1910; Schwartz and Dutcher 1963). Of the three mud crab species examined, the carapace widths (CW) of adult *E. depressus* and *N. sayi* overlap in size and reach 22 mm, while adult *P. herbstii* are larger reaching 62 mm CW (Williams 1984). The larger *C. sapidus* may attain 227 mm CW (Williams 1984). *Callinectes sapidus*, *E. depressus*, and *N. sayi* prey on hard clams up to 33% of the crabs' CW (Carriker 1961; Castagna and Kraeuter 1981; Gibbons 1984). *Panopeus herbstii* is capable of opening significantly larger hard clams, up to 65% of CW (Whetstone and Eversole 1981), because of a large molariform tooth on the dactyl of the master claw. This study examined the influence of toadfish size on predation of mud crabs of various size classes. The effect of toadfish on blue crab predation upon juvenile hard clams was examined in the presence and absence of substrate.

MATERIALS AND METHODS

Nine laboratory experiments were conducted from July to September 1986. Temperature and salinity of ambient seawater were monitored during all experiments. Crabs and toadfish were collected locally and held in flowing seawater. Juvenile hard clams were cultured at the Virginia Institute of Marine Science Wachapreague Laboratory. Toadfish were used only once and were starved for 48 hr

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prior to each experiment. Experimental chambers (49 × 40 × 26 cm) received ambient seawater at the rate of 2 L/min. Within each chamber a 15 cm high standpipe covered with fiberglass insect screening prevented crab escape. Except where specified, neither structures nor substrate were present in the chambers. Toadfish and crabs from specific size classes were selected randomly for each trial. Experimental treatments and controls were replicated three times. Predation rates of toadfish were recorded as the number of crabs killed/toadfish/24 hr.

Predation by toadfish on mud crabs

Five experiments (I–V) were performed to examine the influence of size on the predator-prey relationship between toadfish and mud crabs. Due to the logistics of obtaining sufficient toadfish and mud crabs, a full factorial design was not carried out. Sizes of toadfish and mud crabs used are shown in Table 1. Toadfish were divided into five size classes based on total length. In addition, mouth width (MW) of each toadfish was measured as the medial distance between the articulation of the articular and quadrate bones on each side of the mouth. Owing to their similar appearance and their sympatric relationship, mud crabs *E. depressus*, *N. sayi*, and *P. herbstii* were divided into four size classes based on carapace width without consideration of species. Therefore, implications were drawn for mud crabs as a group not single species. A random sample from each size class was selected for estimation of species-size distribution; this distribution was similar to those in other studies (Ryan 1956, McDonald 1982, Williams 1984) (Table 2).

For each experiment treatment chambers held one toadfish and one size class of mud crabs. Control chambers held

crabs without toadfish. After 24 hr, predation rates by toadfish and mortality of crabs from confamilial interference were determined. Dead and injured crabs were replaced with live crabs of the same size class and the experiment continued for an additional 24 hr to see if predation may be reduced by satiation. Temperature and salinity ranged from 24–31°C and 30–34 ppt, respectively, during Experiments I–V.

In Experiment I, three toadfish of the smallest size class (70–90 mm TL) were offered the smallest size class of mud crabs (5–10 mm CW). Each toadfish was placed in a treatment chamber with ten crabs. In Experiment II, twelve toadfish of the next larger class (120–140 mm TL) were each offered only one of the four size classes of mud crabs. Ten crabs were used for each size class except the largest class (35–40 mm CW) which was represented by three crabs per replicate. For Experiments III–V, each of the four size classes of mud crabs were offered to twelve oyster toadfish of 170–190, 220–240, and 270–290 mm TL. The largest size class of mud crab was represented by only five crabs per replicate.

Interactions between toadfish, blue crabs, and hard clams

Experiments VI–IX examined the effects of toadfish on predation by blue crabs upon juvenile hard clams with various substrates. Sizes of animals are given in Table 3. Temperature and salinity ranged from 19–26°C and 29–32 ppt, respectively, during the experimental period.

Experiment VI tested the interaction of toadfish with blue crabs in the absence of any substrate. Individual toadfish of 196–320 mm TL were placed in a chamber with one blue crab of 77–96 mm CW. Toadfish and crabs were examined daily for injury or mortality. Blue crabs were exam-

TABLE 1.
Sizes of toadfish and mud crabs used in Experiments I–V.

Experiment	Total Length (mm) of Toadfish			Corresponding Mouth Width (mm) of Toadfish
	Size class	Mean ± SD	N	Mean ± SD
I	70–90	84.3 ± 3.1	3	14.9 ± 0.2
II	120–140	128.4 ± 6.1	12	23.3 ± 1.7
III	170–190	178.0 ± 5.0	12	37.1 ± 2.1
IV	220–240	225.6 ± 5.4	12	47.0 ± 2.3
V	270–290	283.0 ± 6.3	12	65.6 ± 2.9
Carapace Width (mm) of Mud Crabs				
	Size class	Mean ± SD	N	
	5–10	8.0 ± 1.4	50	
	15–20	18.9 ± 1.4	40	
	25–30	28.0 ± 1.6	40	
	35–40	37.5 ± 1.5	18	

TABLE 2.
Percent size distribution of three species of mud crabs in each size class offered toadfish (N = 10 per class).

Species	Size Class (mm Carapace Width)			
	5-10	15-20	25-30	35-40
<i>Eurypanopeus depressus</i>	20	10	20	
<i>Neopanope sayi</i>	80	50		
<i>Panopeus herbstii</i>		40	80	100

ined for missing appendages and punctures of the carapace. There were nine replicates. The experiment was terminated after 96 h as more than half of the crabs were preyed upon.

Experiment VII tested the effect of toadfish upon predation by blue crabs on juvenile hard clams in the absence of any substrate. Treatments included the presence of single toadfish of 297-318 mm TL, effluent water from toadfish, and the absence of toadfish (control). One blue crab of 67-94 mm CW was placed into each chamber with 30 hard clams of 5.4 mm mean (4.8-6.3 mm) shell height (SH). Mortalities of clams and blue crabs were determined after 24 h and the experiment was terminated because of the high mortality of clams in the control replicate treatments.

The influence of a sand substrate on the toadfish-blue crab-hard clam interactions was examined in Experiment VIII. Treatments included the presence of one toadfish and sand, presence of one toadfish without sand, no toadfish but sand present, and absence of both toadfish and sand (control). Sand was placed in chambers at a depth of 50 mm and hard clams were allowed to burrow into the substrate. Each chamber received one blue crab of 80-96 mm CW and 30 hard clams of 5.8 mm mean (4.7-6.5 mm) SH. After 48 h the mortalities of hard clams and blue crabs were determined.

The addition of a crushed gravel aggregate to sand substrate was tested for influence on the interactions between hard clams, blue crabs, and toadfish in Experiment IX. Treatments included the presence of gravel and toadfish, toadfish without gravel, gravel without toadfish, and absence of both toadfish and gravel (control). All chambers received sand at a depth of 50 mm, 30 hard clams of 5.2

mm mean (4.3-6.3 mm) SH, and one blue crab of 72-105 mm CW. Gravel of 5-15 mm diameter was added at a depth of 25 mm on top of the sand substrate in the chambers. Mortalities of hard clams and blue crabs were determined after 48 hr.

Statistical analyses

Predator-prey size ratios were determined for toadfish by comparing the carapace width of the mud crabs preyed on to the total length of toadfish. Although no predator-prey size relationship was studied in the toadfish-blue crab Experiments (VI-IX), the sizes of those blue crabs preyed upon (injured or killed) by the toadfish were noted and a size comparison was made. Mud crab mortalities between the test and control replicates for Experiments I-V were compared using two-way analysis of variance (ANOVA) after log (x + 1) transformation with toadfish presence and exposure time as variables. Hard clam mortalities for Experiments VII-IX were analysed using one-way ANOVA after log (x + 1) transformation. Differences between numbers of blue crabs preyed on (injured and dead) versus numbers of uninjured blue crabs for Experiments VII-IX were tested with one-way ANOVA after log (x + 1) transformation. Significant differences in treatment means of hard clam mortalities and number of blue crabs preyed on were further analysed using Duncan's new multiple-range test (Steel and Torrie 1960).

RESULTS

Predation rates by oyster toadfish generally increased with decreasing mud crab size and increased with increasing toadfish size (Fig. 1). Mortality of the smallest size class of mud crabs (5-10 mm CW) was significantly higher (d.f. = 1, $p < 0.001$) in the presence of toadfish for toadfish size classes of 70-90 mm TL ($F = 114.6$), 120-140 mm TL ($F = 154.8$), 170-190 mm TL ($F = 162.9$), 220-240 mm TL ($F = 84.0$), and 270-290 mm TL ($F = 43.9$). Mud crabs of 15-20 mm CW had significantly higher mortality in the presence of toadfish size classes of 170-190 mm TL ($F = 227.0$, d.f. = 1, $p < 0.001$), 220-240 mm TL ($F = 169.9$, d.f. = 1, $p < 0.001$), and 270-290 mm TL ($F = 11.9$, d.f. = 1, $p =$

TABLE 3.
Sizes of toadfish, blue crabs, and hard clams used in Experiments VI-IX.

Experiment	Total Length (mm) of Toadfish		Carapace Width (mm) of Blue Crabs		Shell Height (mm) of Hard Clams	
	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N
VI	252.9 \pm 48.1	9	87.2 \pm 6.3	9	0	
VII	308.0 \pm 12.2	6	80.2 \pm 7.7	9	5.4 \pm 0.5	30
VIII	310.5 \pm 10.9	6	88.8 \pm 5.1	12	5.8 \pm 0.5	30
IX	308.5 \pm 6.0	6	84.5 \pm 9.3	12	5.2 \pm 0.5	30

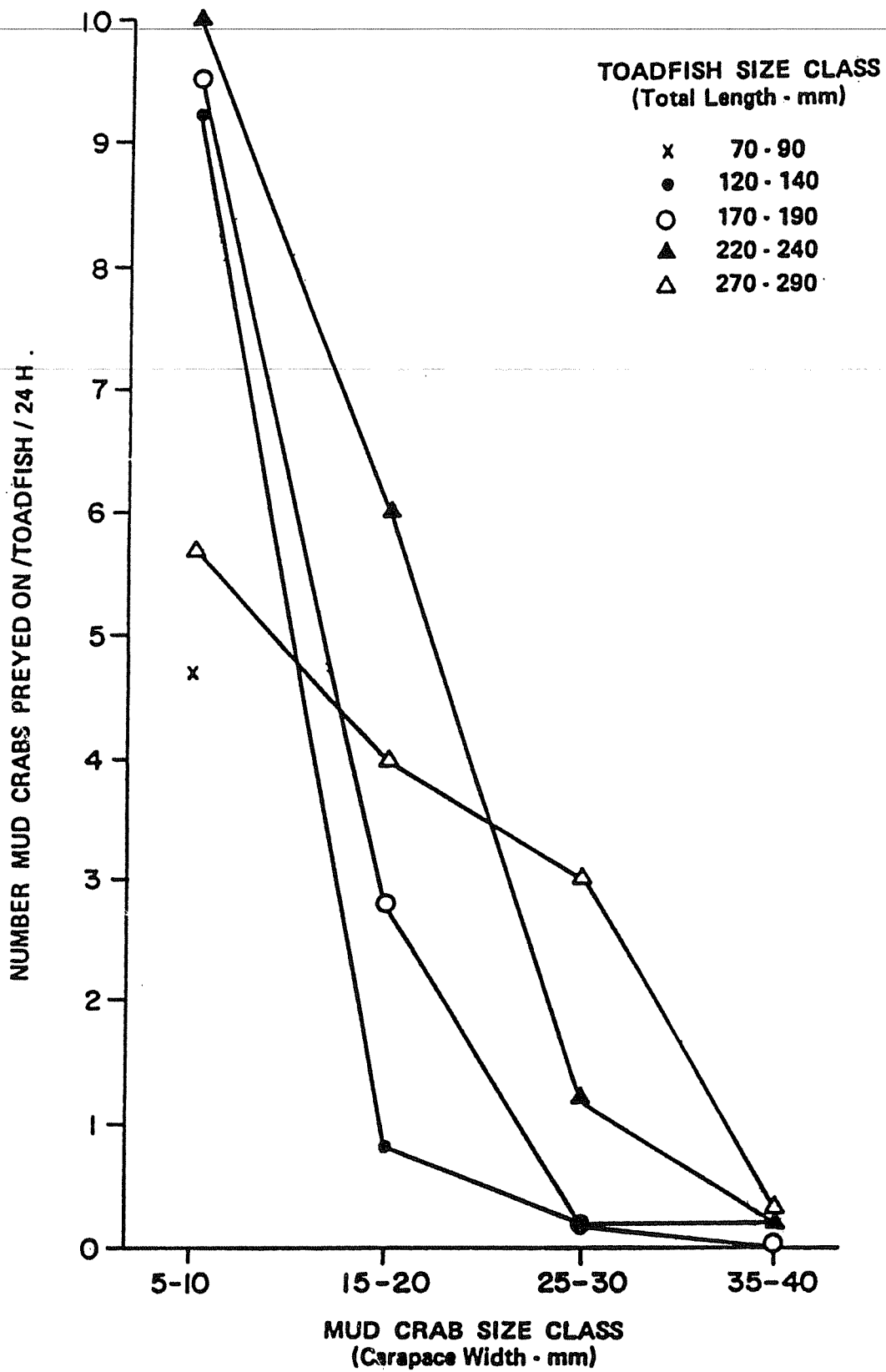


Figure 1. Predation rates by toadfish on mud crabs from Experiments I-V.

0.008). Significant mortalities of mud crabs of 25–30 mm CW occurred in the presence of toadfish of 220–240 mm TL ($F = 11.4$, d.f. = 1, $p = 0.009$) and 270–290 mm TL ($F = 268.6$, d.f. = 1, $p < 0.001$). No significant differences ($p = 0.05$) in predation rates occurred between 24 hr and 48 hr. Toadfish could prey on up to 10 mud crabs/toadfish/24 hr. Although there was no significant predation by toadfish on mud crabs of the largest size class (35–40 mm CW) which was composed of only *P. herbstii*, one crab was eaten by a toadfish of the largest size class (270–290 mm TL).

A predator-prey size ratio of 0.10 (CW/TL) was determined for toadfish preying on mud crabs. When mouth width was considered, toadfish could prey on mud crabs that were almost one half of the mouth width (CW/MW). Mud crabs killed by toadfish were either partially or entirely consumed, or had a punctured carapace. Shell parts from partially digested crabs appeared after 48 hr via regurgitation by toadfish. Mortality of mud crabs in the controls averaged 2.7% per 24 hr for all experiments. Some of this mortality was due to predation and interference behavior by other crabs.

A predator-prey size ratio of 0.32 (CW/TL) was determined for toadfish preying on blue crabs in Experiments VI–IX. Oyster toadfish attacked blue crabs by removing their legs and chelae and puncturing the carapace. Blue crabs were either partially or entirely consumed. Injuries and deaths of blue crabs did not occur until 72 hr after exposure to toadfish in Experiment VI (Table 4), but occurred within 24–48 hr in Experiments VII–IX (Table 5). Toadfish were not injured by blue crabs.

Blue crabs reacted to the presence of toadfish by remaining distant, and some crabs escaped from the experimental chambers (Experiment VI) (Table 4). Blue crabs were returned to the chambers from which they escaped. When sand substrate was available, blue crabs hid by burrowing. Blue crabs did not burrow into the gravel substrate.

No significant differences in blue crab mortalities were found in Experiment VII (Table 5). Blue crab injuries and death in Experiment VIII were significantly higher ($p = 0.05$) in the presence of toadfish with no differences detected between substrate type (Table 5). Experiment IX had significantly higher ($p = 0.05$) blue crab injuries and death in treatments with toadfish and gravel substrate combined than with toadfish present with sand only or treatments without toadfish. Blue crabs did not show any behavioral reaction to toadfish effluent. More injuries and deaths of blue crabs occurred in the presence of toadfish when exposed for 48 hr (Experiments VIII and IX) than 24 hr (Experiment VII). There was no mortality of blue crabs in controls.

In the presence of toadfish, blue crab predation on hard clams was reduced without regard to blue crab condition (i.e. uninjured, injured, or killed). Mortality of hard clams

TABLE 4.

The daily condition of blue crabs held with toadfish for 96 hours in Experiment VI.

Elapsed time in hours	Condition of Crab			
	Uninjured	Injured	Dead	Escaped
24	8	0	0	1
48	6	0	0	3
72	6	2	0	1
96	3	1	4	1

from blue crab predation was significantly lower ($p = 0.05$) in the presence of toadfish than in the presence of toadfish effluent or the absence of toadfish in Experiment VII (Table 5). Experiment VIII tests had significantly lower ($p = 0.05$) clam mortality in the presence of toadfish (Table 5). Toadfish did not consume hard clams.

When considering the gravel on sand substrate in the presence of toadfish in Experiment IX (Table 5), only slightly lower clam mortality occurred than without toadfish. Significantly lower ($p = 0.05$) clam mortality occurred in Experiment IX from treatments having toadfish and gravel on sand, or treatments without toadfish and having gravel on sand, or from treatments having toadfish and without gravel than from treatments without either toadfish or gravel. The sand substrate alone provided no protection for hard clams against blue crabs.

DISCUSSION

The oyster toadfish, *O. tau*, preys on mud crabs, *E. depressus*, *N. sayi*, and *P. herbstii*, and the blue crab, *C. sapidus*. In general, toadfish preyed on mud crabs that were no more than one tenth their size (CW/TL). Toadfish had predation rates as high as 10 mud crabs/toadfish/24 hr. Higher predation rates are possible as the toadfish were not fed mud crabs *ad libitum*. Toadfish consumed higher numbers of mud crabs as mud crab size decreased or toadfish size increased (Fig. 1).

The species distribution in mud crab size classes may influence the size effects on predation rates. There was some mortality of mud crabs in chambers without toadfish, probably from interspecific and intraspecific aggression. Mud crabs such as *N. sayi* have ritualized behavioral patterns that reduce aggressive encounters (Swartz 1976).

Under certain conditions, the presence of oyster toadfish reduced predation by blue crabs on juvenile hard clams, owing to the aggressive and predatory behavior of toadfish towards blue crabs. The ability of a blue crab to escape, defend itself, or prey on hard clams was reduced by each encounter with a toadfish. Toadfish pull appendages from the blue crab's body and then kill the crab. Similar be-

TABLE 5.
The influence of toadfish on the predation by blue crabs on hard clams in Experiments VII-IX.

Experiment	Presence of Toadfish	Type of Substrate	Condition of Blue Crab			Number of Clams Eaten (Mean and Range)
			Uninj.	Inj.	Dead	
VII 24 h	present	none	1	1	1	0.7 (0-2)
	effluent	none	3	0	0	30.0 (30)
	absent	none	3	0	0	25.0 (15-30)
VIII 48 h	present	sand	1	2	0	0.3 (0-1)
	present	none	0	2	1	0.0 (0)
	absent	sand	3	0	0	19.7 (0-30)
	absent	none	3	0	0	30.0 (30)
IX 48 h	present	gravel	0	2	1	0.6 (0-1)
	present	sand only	2	0	1	10.0 (0-30)
	absent	gravel	3	0	0	2.3 (1-5)
	absent	sand only	3	0	0	30.0 (30)

havior has been observed in field experiments (Bisker, unpublished data).

Crushed gravel aggregate may act not only to reduce the effectiveness of hard clam predators, but also to enhance the effectiveness of higher-level predators upon hard clam predators. In this study, gravel added to a sand substrate reduced predation by blue crabs on juvenile hard clams, by providing a refuge for hard clams and decreasing the burrowing ability of the blue crab. The inability to burrow reduced the feeding efficiency of the blue crab and increased its risk of exposure to toadfish which resulted in increasing predation on the blue crabs by the toadfish. Predation pressure on juvenile hard clams has been reduced by the addition of crushed gravel aggregate in laboratory studies with mud crabs, *N. sayi*, calico crabs, *Ovalipes ocellatus* (Herbst), and hermit crabs, *Pagurus longicarpus* Say (Gibbons 1984), and field cultures with blue crabs, *C. sapidus*, and other crabs (Castagna and Kraeuter 1981; Arnold 1984).

Field grow-out systems for juvenile hard clams of 6-12 mm SH generally use mesh nettings or cages to exclude predators (Eldridge et al. 1976; Manzi et al. 1980; Castagna and Kraeuter 1981; Walker 1984; Kraeuter and Castagna 1985). Nets with square mesh openings of 11.1 mm or 12.0 mm will not exclude blue crabs, *C. sapidus*, of less than 39.2 mm CW or mud crabs, *P. herbstii*, of 25.2 mm CW, respectively (Bisker and Castagna 1986). Blue crabs of this size may prey on hard clams of 8 mm SH or less while *P. herbstii* can open those clams of 16 mm SH or less. Juvenile crabs are often attracted to grow-out systems for food or refuge, pass through the netted enclosures, and grow to sizes large enough to cause significant mortality on clams (Walker 1984).

The mud crabs *E. depressus* and *P. herbstii* have average densities of 40-50 crabs/m² (Dame 1979) but may

have mean densities as high as 1000 and 100/m², respectively (Bahr 1974). *Neopanope sayi* may reach densities of 54 crabs/m² (MacKenzie 1977), while the blue crab, *C. sapidus*, may reach a density of 13 crabs/m² (Larson 1974). The abundance, mobility, and high predation rates of these crabs make them serious predators of juvenile hard clams (Eldridge et al. 1976; MacKenzie 1977, 1979).

This study shows that toadfish larger than 220 mm TL can prey on mud crabs less than 30 mm CW and on blue crabs less than 70 mm CW. Hence, toadfish may be used to control crab populations within netted enclosures. In the field, toadfish of 231 mm mean TL reduced crab predation on juvenile hard clams 3 mm in shell length when cultured in cages of 25 mm square mesh with crushed gravel aggregate (Gibbons and Castagna 1985). Toadfish, larger than 170-220 mm TL, may be placed within cages, trays, or beds with crushed gravel aggregate and a mesh of 6-12 mm to control crab predation effectively and reduce manual labor for crab removal. Enclosed grow-out systems that are established in the field prior to planting of hard clams should receive toadfish several days before the addition of clams. The addition of toadfish to field grow-out systems will enable the use of smaller (<8 mm SH) hard clams, and thereby reduce expenses and efforts required to raise clams in these systems.

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