

EFFECTS OF BEHAVIORAL INTERACTIONS ON THE CATCHABILITY OF AMERICAN LOBSTER, *HOMARUS AMERICANUS*, AND TWO SPECIES OF *CANCER* CRAB

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ABSTRACT

Intraspecific and interspecific behavioral interactions may affect the probability of capturing *Cancer irroratus*, *C. borealis*, and *Homarus americanus* in lobster traps. To test this hypothesis, the catch per unit of effort (CPUE) of each of these species in traps stocked with *C. irroratus*, *C. borealis*, or *H. americanus* was compared with that obtained from empty baited traps (controls).

In traps stocked with lobsters, the catch of all three species was significantly reduced. Traps stocked with 8 lobsters caught significantly fewer crabs than traps containing 3 lobsters. The only effect of stocking traps with crabs was to increase the catch of *C. borealis* in traps stocked with 3 crabs of either species. Results of laboratory experiments comparing crab CPUE in control traps with crab CPUE in traps stocked with 8 lobsters concurred with the field results.

When *H. americanus* was stocked in the holding section (parlor) of the trap, a greater proportion of the crab catch was found in the entrance section (kitchen). This behavioral response may facilitate escape of crabs from traps containing *H. americanus*. The distribution of the lobster catch was unaffected by stocking *H. americanus* or *Cancer* crabs in the parlor.

Behavioral mechanisms underlying reductions in crab CPUE were investigated by laboratory observation of an actively fishing trap. When *H. americanus* was stocked, *C. borealis* avoided entering traps. *Cancer irroratus* entered the kitchen of traps containing *H. americanus*, but the proportion entering the parlor was reduced. The escape rate of both crab species increased in traps stocked with *H. americanus*. The position underneath the entrance to the parlor was preferred by all species. When both *H. americanus* and *Cancer* crabs were present in the trap, *H. americanus* occupied that position.

A number of environmental and biological factors are known to affect the probability of capturing crustaceans in traps. Water temperature and salinity are positively correlated with capture rates of rock lobster, *Panulirus cygnus*, (Morgan 1974), and a linear relationship between temperature and the catchability of American lobster, *Homarus americanus*, was found by McLeese and Wilder (1958). Biological rhythms and physiological changes, such as those associated with the molt cycle (e.g., Chittleborough 1975), may affect feeding and other activities (e.g., Bennett 1974; Morgan 1974) and thus cause fluctuations in catchability. In addition, behavioral attributes such as avoidance of dead conspecifics (Hancock 1974; Morgan 1974; Chapman and Smith 1979), intraspecific attraction (reviewed in Hancock 1974), or competitive relations

(Bennett 1974; Ricker 1975; Caddy³) may affect catch rates. The potential importance of such interactions between animals converging on a trap has been recognized by several authors (Bennett 1974; Bennett and Brown⁴; Caddy footnote 3; Miller 1978, 1979a, b, 1980; Fogarty and Borden 1980).

The present study was designed to determine whether trap efficiency, the number of individuals captured as a fraction of those detecting the gear (Caddy footnote 3), for Jonah crab, *C. borealis*, rock crab, *C. irroratus*, and *H. americanus* is affected by the presence of others of these species in the traps. Additional null hypotheses were that 1) trap efficiency is independent of the density of other species in the trap, and 2) the

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³Caddy, J. F. 1977. Some considerations underlying definitions of catchability and fishing effort in shellfish fisheries, and their relevance for stock assessment purposes. ICES Shellfish and Benthos Committee Ref. Gear and Behavior Committee, No. 18, 22 p.

⁴Bennett, D. B., and C. G. Brown. 1976. The problems of pot immersion time in recording and analyzing catch-effort data from a trap fishery. ICES Special Meeting on Population Assessments of Shellfish Stock, No. 6, 9 p.

location of animals within the trap is unaffected by the presence of other species. Laboratory observations of the behavior of the two crab species in and around traps were made to assess processes influencing their catch rates and to investigate the allocation of space in the trap by captured animals.

METHODS

Trap Efficiency

Field studies were carried out from 27 July to 30 August 1979 to investigate the effects of intraspecific and interspecific interactions on the catch per unit of effort (CPUE) of *C. irroratus*, *C. borealis*, and *H. americanus*. The catch obtained in lobster traps stocked with these three species was compared with the catch obtained in unstocked traps. It was assumed that equal numbers of animals were attracted to all traps; thus

any differences in CPUE would be due to differences in trap efficiency caused by animals stocked in the traps.

The 18 lobster traps were $91 \times 25 \times 46$ cm, constructed from galvanized aluminum mesh (2.54 cm² openings) with no escape gaps (Fig. 1). Traps were set three to a string, with three strings at each of two locations in Narragansett Bay, R.I. One location was an area of coarse sand overlain with boulders, a substratum where *C. borealis* and *H. americanus* are typically found. The other location was a predominantly sand bottom where *C. irroratus* and *H. americanus* occur (Jeffries 1966; Fogarty 1976). Traps within strings were about 13 m apart, strings in each location were 15 to 60 m apart, and the locations were separated by about 1 km. Water depth varied from 8 to 14 m.

In each string of three traps, the middle trap was stocked with 8 individuals of a given species, one end trap contained 3 individuals of that species, and the other end trap was not stocked and

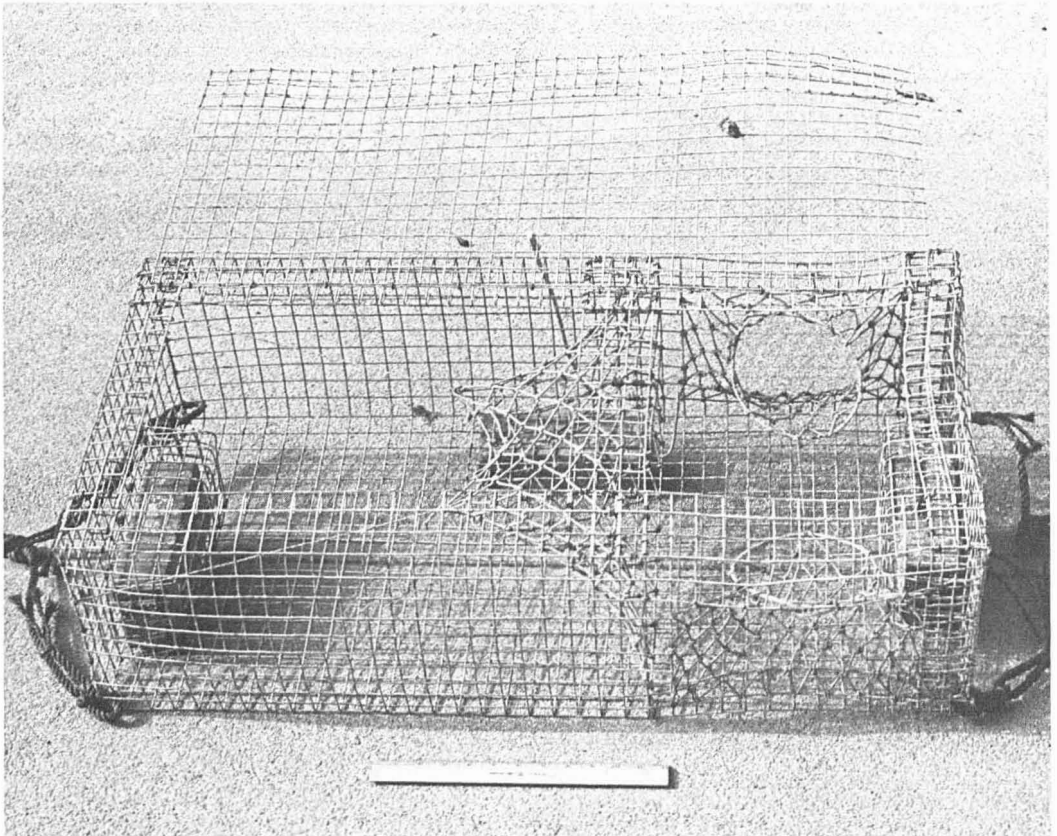


FIGURE 1.—Lobster trap used in field experiments.

served as a control. This arrangement was necessitated by poaching of the 8-lobster treatments when they were at the ends of strings. The stock rates approximated natural catch rates for lobsters, but were considerably lower than could be achieved for crabs. The use of two stocking densities allowed us to assess the effects of both the species identity and the stocking density upon catch rates.

Traps were hauled daily, weather permitting, rebaited with about 1 kg of flounder or flounder carcasses, and experimental traps were restocked if necessary. The number, size, sex, and proportion of the catch in each trap compartment were recorded for each of the three species. A total of 336 trap hauls were made.

The sizes of stocked animals were *C. borealis*, 95-115 mm carapace width (CW); *C. irroratus*, 90-115 mm CW; and *H. americanus*, 75-85 mm carapace length (CL). Carapace width of crabs was measured as the distance between the two most lateral notches on the carapace; carapace length of lobsters was the distance between the posterior edge of the carapace and the posterodorsal edge of the eye socket, parallel to the longitudinal axis. Stocked animals were assigned to traps unsystematically with respect to size and sex.

To further assess the effects of lobsters on catch rates of crabs, laboratory studies were undertaken from July through October of 1979. Two rectangular wooden lobster traps (69 × 34 × 51 cm) were covered with 2.5 cm mesh wire to simulate the mesh size of traps used in the field experiments. The baited traps containing either 8 or 0 (control) lobsters (70-85 mm CL) were placed in the center of two large indoor tanks (3.4 × 1.5 × 0.5 m and 3.1 × 1.5 × 0.5 m) supplied with ambient seawater running at about 2 l/min. Inflow and outflow were at opposite ends of the tanks, thus the water flowed through the traps. Each tank was provided with 10 clay pipe shelters (10.2 cm in diameter, 31 cm long, with two open ends). For each trial, 15 individuals of *C. irroratus* (80-110 mm CW) or *C. borealis* (85-115 cm CW) were placed in the tank. After about 24 h the catch was counted and removed, and the location of animals in the trap was recorded. Crabs were used only once; stocked lobsters were used twice, in different traps. Prior to experimentation, each species was held separately in large outdoor tanks supplied with running seawater and fed every third day with a variety of species of fresh fish. Individual traps were alternated as

experimental and control treatments to avoid bias due to differences between traps and tanks. Ten replicates of each experiment were performed.

Behavior

Behavioral mechanisms affecting trap efficiency were investigated by direct observation in the laboratory. A rectangular wooden lobster trap was modified to improve visibility by replacing the top with 2.5 cm mesh wire and painting the bottom white. The trap was baited with thawed whole flounder or flounder carcasses, stocked with 5 or 0 (control) lobsters (70-85 mm CL), and placed in a 3.1 × 1.2 × 0.6 m tank provided with 10 clay pipe shelters and ambient seawater running at about 2 l/min. An hour after the trap was placed in the tank, 20 *C. irroratus* or *C. borealis* (80-110 mm CW) were added. Tape-recorded observations began 15 min later and continued during alternate 15-min periods. A 25-watt incandescent red light suspended 1.2 m above the tank provided the only light. Kennedy and Bruno (1961) have shown lobsters to be relatively insensitive to these wavelengths.

Observations were carried out intermittently from July through October 1979. One sunset-to-sunrise observation for each combination of stock treatment (0 or 5 lobsters) and catch species (*C. irroratus* or *C. borealis*) revealed that activity peaked between sunset and midnight. Subsequent observations were made during these hours. Lobster-stocked and control observations for each crab species were done within 2 wk of each other to minimize seasonal effects. A total of 11.5 h of observation in three separate periods was made on each combination of stock treatment and catch species.

All animals were held in conditions similar to those described previously for tank experiments, and were in captivity from 2 d to 1 mo before use. No animal was used more than once.

Data collected included frequency and nature of inter- and intraspecific interactions and trap entry and escapement. Positions of animals in the trap were recorded every 15 min.

RESULTS

Trap Efficiency

We assumed that the relative effect of the experimental treatments would not differ between

field locations. Contingency table analyses indicated no significant differences between locations in 8 of 9 tests ($P > 0.05$, Table 1). Therefore the catches from both field locations were combined according to treatment. The number of trap hauls for each stock species was made equal by randomly deleting observations. The hypothesis that the CPUE of *C. irroratus*, *C. borealis*, and *H. americanus* is not affected by the presence of other animals inside traps was tested by comparing the total catch of each species in stocked traps with the total catch in control traps. Catches obtained after 24 h immersion time were compared using a χ^2 goodness of fit test (Zar 1974).

In traps containing 8 or 3 lobsters, the total catch of *C. irroratus*, *C. borealis*, and *H. americanus* was significantly reduced ($\chi^2_{(2)} = 277.8$, 35.1, 18.2, respectively, $P < 0.001$) (Table 2). In addition, the catch of both species of crabs was significantly lower in 8-lobster treatments than in 3-lobster treatments (*C. irroratus*, $\chi^2_{(1)} = 22.9$,

$P < 0.001$; *C. borealis*, $\chi^2_{(1)} = 6.1$, $P < 0.025$). The catch of lobsters was not affected by the density of stocked lobsters ($\chi^2_{(1)} = 2.42$, $P > 0.05$). The only effect of stocking traps with crabs was to increase the catch of *C. borealis* in traps stocked with either 3 *C. borealis* or 3 *C. irroratus* (for both treatments, $\chi^2_{(1)} = 8.6$, $P < 0.005$). Stocking traps with crabs had no effect on the catch of lobsters ($P > 0.05$).

The average size of animals captured did not differ between treatments for any of the species (Student's *t* test, $P > 0.05$) (Table 3).

The results of the laboratory experiments in which lobsters were stocked concurred with those from the field. The catch of both *C. irroratus* and *C. borealis* was significantly reduced when *H. americanus* was in the parlor (Table 4).

Behavior

Location Within Trap

The spatial distribution of animals caught in a trap may be affected by behavioral interactions among the trap occupants. To test this hypothesis, the proportion of the catch found in the entry section, or "kitchen," in control traps was compared with the proportion in the kitchen in stocked traps. All comparisons of proportions were made using the normal approximation for differences between two proportions (Zar 1974). Stocked animals were placed in the parlor.

In both field and laboratory experiments, a

TABLE 1.— χ^2 values for 3×2 contingency tables comparing strings of each treatment type for *Homarus americanus* (Ha), *Cancer irroratus* (Ci), and *C. borealis* (Cb) between locations. A separate contingency table was made for each species caught. * = $P < 0.05$, @ = expected frequency of one cell was < 5 .

Species caught	Comparison of locations for		
	Ha treatments	Ci treatments	Cb treatments
<i>C. borealis</i>	0.980 @	0.920	2.675
<i>C. irroratus</i>	3.880	48.357*	2.594
<i>H. americanus</i>	0.348 @	0.146	1.816

TABLE 2.—Total numbers of *Cancer irroratus*, *C. borealis*, and *Homarus americanus* caught after 24-h immersion time in field experiments. Catch per trap haul is indicated in parentheses; control = empty baited traps; treatment refers to species stocked; *n* = no. of trap hauls for each treatment level.

Species caught	<i>H. americanus</i> -stocked			<i>C. borealis</i> -stocked			<i>C. irroratus</i> -stocked		
	Control	3	8	Control	3	8	Control	3	8
<i>C. irroratus</i>	319(7.60)	100(2.38)	42(1.00)	300(8.82)	371(10.91)	300(8.82)	342(9.50)	365(10.14)	355(9.86)
<i>C. borealis</i>	70(1.67)	36(0.86)	17(0.40)	61(1.79)	99(2.91)	78(2.29)	65(1.81)	102(2.83)	70(1.94)
<i>H. americanus</i>	54(1.29)	31(0.74)	19(0.45)	23(0.68)	21(0.62)	33(0.97)	29(0.81)	29(0.81)	29(0.81)
<i>n</i>	42	42	42	34	34	34	36	36	36 $\Sigma n = 336$

TABLE 3.—Average size (mm) and standard deviation (SD) of *Homarus americanus*, *Cancer borealis*, and *C. irroratus* caught in all traps, locations combined. Size of crabs is carapace width; size of lobsters is carapace length.

Species caught	<i>H. americanus</i> -stocked			<i>C. borealis</i> -stocked			<i>C. irroratus</i> -stocked			
	Control	3	8	Control	3	8	Control	3	8	
<i>C. irroratus</i>	\bar{X}	91.7	91.8	92.2	90.6	91.1	92.2	91.5	89.5	92.1
	SD	(10.1)	(11.5)	(13.2)	(9.9)	(11.3)	(10.4)	(10.6)	(11.8)	(8.6)
<i>C. borealis</i>	\bar{X}	92.8	94.8	94.8	93.3	94.5	92.3	94.4	94.6	92.7
	SD	(9.5)	(9.2)	(6.5)	(10.6)	(8.4)	(8.1)	(7.9)	(6.9)	(9.0)
<i>H. americanus</i>	\bar{X}	68.3	73.4	74.8	72.2	71.1	73.2	71.2	72.2	71.8
	SD	(7.9)	(6.8)	(8.1)	(6.7)	(9.1)	(9.6)	(7.6)	(7.0)	(12.5)

TABLE 4.—Total number of *Cancer irroratus* or *C. borealis* caught in 10 laboratory trials of each treatment and catch species. ** = $P < 0.001$, χ^2 goodness of fit test.

Species caught	Treatment		χ^2
	Control	8 <i>Homarus americanus</i>	
<i>C. irroratus</i>	49	15	23.8**
<i>C. borealis</i>	66	20	14.9**

greater proportion of the crab catch was found in the kitchen of 8-lobster treatments than of controls (Tables 5, 6). Stocking traps with 3 lobsters had no effect on the distribution of crabs, and lobsters were unaffected by either stock density of lobsters ($P > 0.05$).

Interspecific interactions between *C. irroratus* and *C. borealis* apparently influenced the distribution of these species inside traps. In traps stocked with either 3 or 8 *C. irroratus*, the proportion of the *C. borealis* catch found in the kitchen was significantly greater than in controls ($Z = 2.50, P < 0.01$). In traps containing 3 *C. borealis*, the proportion of the *C. irroratus* catch found in the kitchen was significantly greater than in controls ($Z = 2.50, P < 0.01$), but no effect was seen in traps stocked with 8 *C. borealis* ($P > 0.05$) (Fig. 2).

TABLE 5.—In field experiments, spatial distribution of *Cancer irroratus*, *C. borealis*, and *Homarus americanus* catch in traps stocked with *H. americanus* (Ha). All data obtained after one setover day are included. Proportion of catch found in the kitchen of stocked traps was compared with controls using normal approximation for differences between two proportions (Z) (Zar 1974). n = number of trap hauls; * = $P < 0.05$, ** = $P < 0.001$.

Species caught	Treatment	n	Proportion in kitchen	Z
<i>C. irroratus</i>	8 Ha	42	0.29	8.67**
	3 Ha	54	0.06	0.91 ns
	Control	51	0.03	
<i>C. borealis</i>	8 Ha	42	0.35	2.00*
	3 Ha	54	0.09	0.67 ns
	Control	51	0.13	
<i>H. americanus</i>	8 Ha	42	0.00	0.94 ns
	3 Ha	54	0.00	1.25 ns
	Control	51	0.03	

TABLE 6.—In laboratory experiments, spatial distribution of the *Cancer* crab catch in traps stocked with *Homarus americanus* (Ha). Proportion of catch found in the kitchen of stocked traps was compared with controls using normal approximation for differences between two proportions (Z) (Zar 1974). n = no. of trap hauls, * = $P < 0.0001$.

Species caught	Treatment	n	Proportion in kitchen	Z
<i>C. irroratus</i>	8 Ha	10	0.27	5.19*
	Control	10	0.08	
<i>C. borealis</i>	8 Ha	10	0.70	5.27*
	Control	10	0.09	

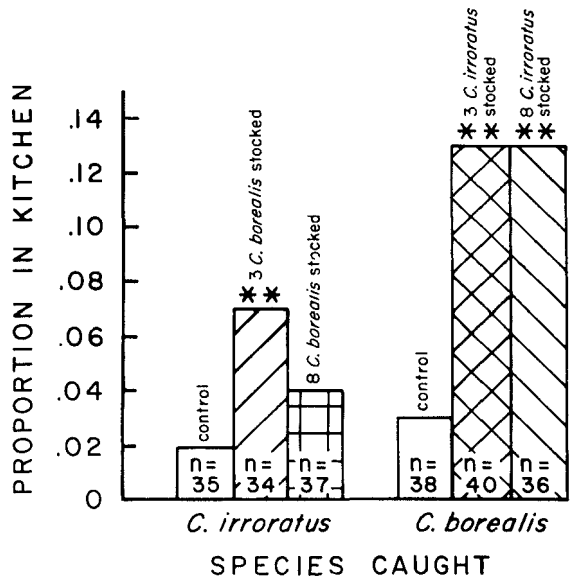


FIGURE 2.—Proportion of *Cancer irroratus* and *C. borealis* found in the kitchen of traps stocked with congeners in field experiments. All data obtained after one setover day are included. n = number of trap hauls, ** = significant difference ($P < 0.01$) between treatment and control, using normal approximation for differences between two proportions (Zar 1974).

Competition Inside Traps

To further investigate how the location of animals in a trap is affected by behavioral interactions, competition for preferred areas in the trap was studied in the laboratory. Frequency of occupation was used as an index of preference and was measured as the number of times a given position was occupied when censused every 15 min. The observed distribution of animals was compared with an expected uniform distribution using a χ^2 goodness of fit test. For lobsters and for each crab species in the absence of lobsters, the preferred position in the parlor was underneath the entry head (*C. irroratus*, $\chi^2_{(4)} = 202.0, P < 0.001$; *C. borealis*, $\chi^2_{(4)} = 51.8, P < 0.001$; *H. americanus*, $\chi^2_{(4)} = 744.2, P < 0.001$). When lobsters were present, the number of crabs in the parlor decreased sharply, so comparisons between lobster-stocked and control traps were made using proportions. In the presence of lobsters, the preference of both crab species changed (*C. irroratus*, $Z = 2.26, P < 0.01$; *C. borealis*, $Z = 5.97, P < 0.001$). *Cancer irroratus* occupied the middle of the parlor, and *C. borealis* occupied the corners most frequently when *H. americanus* was

present (*C. irroratus*, $\chi^2_{(4)} = 82.3$, $P < 0.001$; *C. borealis*, $\chi^2_{(4)} = 52.5$, $P < 0.001$) (Table 7).

Space inside the trap was partitioned into vertical strata. Both crab species showed a significant increase in occupation of the top part of the trap when lobsters were present (*C. irroratus*, 0.47 vs. 0.79, $Z = 4.87$, $P < 0.001$; *C. borealis*, 0.21 vs. 0.38, $Z = 1.76$, $P < 0.05$). This contrasts with 99% occurrence of lobsters in the bottom portion of the trap.

from the parlor did not increase in lobster-stocked traps for either species (*C. irroratus*, $Z = 1.37$, $P > 0.05$; *C. borealis*, $Z = 0.37$, $P > 0.05$).

DISCUSSION

Trap Efficiency

The results of the field and laboratory experiments demonstrate that the presence of lobsters

TABLE 7.—Laboratory-observed frequency and relative frequency of occupation of positions in the parlor by *Cancer irroratus*, *C. borealis*, and *Homarus americanus*. Counts were weighted to compensate for unequal availability of positions due to trap design. * = significant ($P < 0.01$) χ^2 values for frequency of occupation and preferred positions; + = significant ($P < 0.01$) differences in occupation of a particular position in lobster-stocked traps and controls; ctl = control; lob = 5 lobsters stocked.

Species caught	Position occupied									
	Under head		Corner		Corner by head		Side		Middle	
	ctl	lob	ctl	lob	ctl	lob	ctl	lob	ctl	lob
<i>C. irroratus</i>										
Frequency	129*	27	12	9.3	32	8	9	8	60	57*
Relative frequency	0.53	0.25+	0.05	0.09	0.13	0.07	0.04	0.07	0.25	0.52+
<i>C. borealis</i>										
Frequency	93*	3	32	42.5*	42.5	17.3	23	9	42	15
Relative frequency	0.40	0.04+	0.14	0.49+	0.18	0.20	0.10	0.10	0.18	0.17
<i>H. americanus</i>										
Frequency	—	555*	—	204.8	—	38.6	—	109	—	471
Relative frequency	—	0.40	—	0.15	—	0.03	—	0.08	—	0.34

Trap Entry and Escapement

Laboratory observations revealed that *C. irroratus* and *C. borealis* respond differently to traps stocked with *H. americanus*. The presence of *H. americanus* did not affect the number of *C. irroratus* entering the kitchen (39 vs. 33, $\chi^2_{(1)} = 0.35$, $P > 0.05$); however, significantly fewer *C. borealis* entered when *H. americanus* were stocked (35 vs. 8, $\chi^2_{(1)} = 18.2$, $P < 0.001$).

The proportion of *C. irroratus* which moved from the kitchen to the parlor was significantly reduced in lobster-stocked traps (0.81 vs. 0.23, $Z = 2.73$, $P < 0.0001$). The proportion of *C. borealis* entering the parlor did not decrease significantly when *H. americanus* was present (0.53 vs. 0.31, $Z = 0.58$, $P > 0.05$); however, the number of *C. borealis* that had entered the kitchen was relatively low.

The proportion of both *C. irroratus* and *C. borealis* which escaped the kitchen increased significantly in the presence of *H. americanus* (*C. irroratus*, 0.23 vs. 0.55, $Z = 2.86$, $P < 0.005$; *C. borealis*, 0.26 vs. 0.63, $Z = 1.97$, $P < 0.025$). Escape

reduces the CPUE of crabs, and provide a possible explanation for the inverse relationship between lobster and crab catches seen in other studies (e.g., Stasko 1975; Krouse 1978; Fogarty and Borden 1980). This effect appears to be density-dependent since fewer crabs were captured when a large number of lobsters were present.

Factors other than behavioral interactions could cause negative correlations between lobster and crab catch rates. *Cancer irroratus* is often spatially separated from *C. borealis* and *H. americanus* in Narragansett Bay (Jeffries 1966; Fogarty 1976). Such discontinuous distributions could result in inverse catches of *C. irroratus* and *H. americanus*, or of *C. irroratus* and *C. borealis*, but do not explain the differences seen in the catch of adjacent traps in this study. Other factors known to affect catchability (e.g., size, sex, reproductive condition, molt stage) were held constant among stocked animals used in the different treatments. Temperature changed little over the course of the study (average surface temperature, $21.9 \pm 2.15^\circ\text{C}$). This and other environmental variables would have affected all treat-

ments equally. The nonrandom arrangement of treatment levels within strings could have biased catch rates through gear competition. However, we feel the assumption that equal numbers of animals were attracted to all traps is valid for the following reason. If gear competition caused the reduced crab catches in lobster-stocked strings, a similar pattern of catch rates would have been seen in crab-stocked strings. This was not the case.

Cancer irroratus is a prey item for lobsters (Squires 1970; Weiss 1970; Scarratt and Lowe 1972; Ennis 1973), suggesting that the decreased catch of this species in traps containing lobsters may be the result of predator-avoidance behavior. *Cancer borealis* and *H. americanus* are thought to compete for shelter space in rocky subtidal habitats (Stewart 1972; Fogarty 1976; Cooper and Uzmann 1977; Wang 1982). In laboratory studies (Fogarty 1976), *H. americanus* dominated *C. borealis* for possession of shelter. This dominance appeared to be the result of avoidance by *C. borealis* rather than overt aggressive interactions. Such behavior may cause reduced catches of *C. borealis* in traps containing lobsters.

The reduction in lobster CPUE when lobsters were stocked is not surprising since lobsters are known to be highly aggressive and generally inhabit shelter alone under natural conditions (Cobb 1971; Cooper and Uzmann 1980). Trap saturation apparently becomes important for lobsters at relatively low catch levels since traps stocked with 8 and 3 lobsters were equally effective in reducing the lobster catch. In a laboratory experiment reported by Smolowitz (1978), a reduction in trap entry was seen with only 1 or 2 lobsters in the trap. Reduced entry was probably important in the present study since escapement of stocked lobsters was low (10.1%).

Stock rates used for crabs were low compared with crab catches in control traps. At higher densities, crabs might have had a more significant effect on the catch of lobsters. An increased lobster catch might be expected in traps containing *C. irroratus*, a lobster prey item (Squires 1970; Weiss 1970; Ennis 1973; McLeese 1974). However, the presence of live prey may not significantly increase the attractiveness of an already baited trap. No evidence was seen of lobster predation on crabs in traps. Similarly a decrease in lobster catch might be expected in traps containing a competitor (*C. borealis*). However, *C. borealis* is less aggressive than *H. americanus*

(Fogarty 1976; Wang 1982) and occupies mutually desirable shelters through passive means rather than active displacement, as shown in Stewart's (1972) study.

Trap saturation apparently was not an important factor for crabs at the stock levels used, since crab catches in crab-stocked traps were not reduced below the level of control traps. In laboratory observations, Miller (1978, 1979a, 1980) noted that intraspecific agonistic interactions among *C. irroratus*, *Hyas araneus*, and *C. productus* aggregating downstream from baited traps often resulted in departure from the trap area. He suggested that trap saturation in these three species was due in part to "intimidation" of crabs outside the trap by those inside. However, at relatively low catch densities, the effects of aggression may be minimal.

The increased *C. borealis* catch in traps stocked with 3 crabs of either species is difficult to explain. Release of attractants from the bait by feeding activity could enhance trap entry. As crab density inside the trap increases, such enhancement may be countered by increased aggression, reducing trap entry rates and increasing escapement. These speculations do not explain why the *C. irroratus* catch was not similarly increased by a low stock density of either crab species.

Behavior

Location Within Trap

Behavioral interactions apparently affected the spatial distribution of animals in traps. A greater proportion of the crab catch was found in the kitchen when 8 lobsters were stocked in the parlor. This may have been the result of the avoidance responses discussed above and may enhance escapement of crabs from traps containing lobsters. *Cancer borealis* shifted to the kitchen in both density levels of *C. irroratus*-stocked traps, but the distribution of *C. irroratus* changed significantly only in traps stocked with 3 *C. borealis*. Perhaps the generally greater activity of *C. irroratus* (Jeffries 1966; pers. obs.) serves as a deterrent to parlor entry by *C. borealis*. Both species may be influenced by prior residence effects in which an advantage is conferred upon the individual(s) initially utilizing a resource (e.g., Sinclair 1977; Davies 1978; O'Neill and Cobb 1979). Such an effect may have been caused by the stocking procedure.

Competition Inside Traps

During scuba diving observations of lobster traps, Pecci et al. (1978) noted an apparent dominance of crabs over lobsters in occupation of mutually desirable "niches" in traps. They reported that when both crabs and lobsters were present in traps, crabs always occupied positions that were evidently preferred by both species. The observations of this study contradict those of Pecci et al. Both crab species were displaced by lobsters. It is possible that our results reflect a prior residence advantage conferred on lobsters by the stocking procedure. However, our findings agree with what is known of the relative aggressiveness of *H. americanus*, *C. borealis*, and *C. irroratus* (Fogarty 1976; Wang 1982).

Trap Entry and Escapement

In the laboratory, the presence of *H. americanus* in a trap did not affect the number of *C. irroratus* entering the kitchen, but did decrease the number of *C. borealis* entering. Just the opposite might have been expected in light of the predator-prey relationship between *C. irroratus* and *H. americanus*. We observed no interactions between animals inside the trap and those outside; thus the sensory basis for avoidance by *C. borealis* of traps containing lobsters is unknown.

The proportion of *C. irroratus* moving from the kitchen to the parlor was reduced in lobster-stocked traps. The decrease in parlor entry rate for *C. borealis* was not statistically significant; however, the number of *C. borealis* that had entered the kitchen was relatively low. Reduced parlor entry appeared to be the direct result of interactions between animals in the two trap compartments. These typically consisted of a lobster displaying (meral spread) or lunging at a crab climbing up the parlor head, resulting in retreat to the kitchen by the crab. In several instances, crabs hanging from the parlor head contacted a lobster, which responded by displaying or attacking the crab. The crab then pulled back up into the parlor head and returned to the kitchen. General lobster activity (fighting, exploring, etc.) had a similar effect on crabs in the parlor head. Only 24% of *C. irroratus* and 10% of *C. borealis* entering the parlor head actually entered the parlor when lobsters were stocked. Parlor entrants increased to 60% and 67%, respectively, in control traps.

Escapement could be a significant factor in reducing the efficiency of traps. Skud⁵ considered this the most likely explanation for declining catch rates for lobster over time. High escape rates for two species of *Cancer* have been observed by Miller (1979b) and High (1976). In this study, escape of both crab species from the kitchen increased when lobsters were present in the parlor, probably due to the behavioral interactions described above. Escape of crabs from the parlor did not increase when lobsters were stocked. This may reflect both the design of the parlor head, which makes escape more difficult, and the small sample size resulting from a low rate of entry to the parlor.

In summary, the behavioral mechanisms involved in reducing crab catches in traps containing lobsters were

- 1) For *C. borealis*, entry to the trap is reduced, and escapement of those that enter the kitchen is increased.
- 2) For *C. irroratus*, trap entry is not reduced, but entry to the parlor decreases and rate of escape from the kitchen increases.

SUMMARY

This study demonstrated that behavioral interactions between animals attracted to traps can have significant effects on the probability of their capture. The CPUE of American lobsters and of two species of commercially harvested *Cancer* crabs was significantly reduced in traps containing lobsters. Such effects may be density-dependent, since significantly fewer crabs were caught in traps containing 8 lobsters than in traps containing 3 lobsters. The proportion of captured crabs occupying each trap section changed significantly when lobsters were stocked, and behavioral observations indicated that lobsters occupy the mutually preferred positions in traps. The behavioral mechanisms responsible for decreased crab catches included both reduced entry (*C. borealis*) and increased escapement (*C. irroratus* and *C. borealis*). These results reflect the behavioral and ecological relations of the three species.

⁵Skud, B. E. 1976. Soak-time and the catch per pot in an offshore fishery for lobsters (*Homarus americanus*). ICES Special Meeting on Population Assessments of Shellfish Stocks, No. 8, 25 p.

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