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# Lobster trap video: in situ video surveillance of the behaviour of Homarus americanus in and around traps

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Abstract. A lobster-trap video (LTV) system was developed to determine how lobster traps fish for *Homarus americanus* and how behavioural interactions in and around traps influence catch. LTV consists of a low-light camera and time-lapse video cassette recorder (VCR) mounted to a standard trap with optional red LED arrays for night observations. This self-contained system is deployed like a standard lobster trap and can collect continuous video recordings for >24 h. Data are presented for 13 daytime deployments of LTV (114 h of observation) and 4 day and night deployments (89 h of observation) in a sandy habitat off the coast of New Hampshire, USA. Analyses of videotapes revealed that traps caught only 6% of the lobsters that entered while allowing 94% to escape. Of those that escaped, 72% left through the entrance and 28% through the escape vent. Lobsters entered the trap at similar rates during the day and night and in sandy and rocky habitats. Lobsters generally began to approach the trap very shortly after deployment, and many appeared to approach several times before entering. These data confirm the results of previous laboratory-based studies in demonstrating that behavioural interactions in and around traps strongly influence the ultimate catch.

Extra keywords: saturation, catch, crustacean

## Introduction

All crustacean traps, regardless of their materials and configuration, selectively sample the target population. Although some of this selectivity is intentional (e.g., escape vents minimize retention of small lobsters), much of it is not, and the factors that influence trap selectivity are not fully understood (Krouse 1989; Miller 1990; Addison and Bell 1997; Fogarty and Addison 1997; Addison and Bannister 1998). Most studies of how lobsters interact with traps have been carried out either in semi-natural settings in the laboratory (Richards et al. 1983; Karnofsky and Price 1989; Miller and Addison 1995) or by divers in the field (Auster 1985; Miller 1989, 1995). Laboratory studies are very effective because long-term observations are feasible, but the degree to which lobsters exhibit normal behaviour is uncertain. Diver observations are very enlightening, but they are expensive, bottom time is limited, and dives are generally restricted to daylight hours.

Laboratory studies of the behaviour of *Homarus* americanus around traps indicate that only a small proportion (11%) of the lobsters that encounter a trap actually enter it, and of those only 2% are subsequently

caught (Karnofsky and Price 1989). Field studies of Nephrops norvegicus (Bjordal 1986) confirm these data, and the prestocking studies of Richards et al. (1983) suggest one of the main factors limiting catch of *H. americanus* is the interaction between lobsters inside and outside the trap. As a result of these findings, and others, many recent studies of catchability have concluded that catch per unit effort is not necessarily a good indicator of the density of lobsters (Addison 1995; Addison 1997; Fogarty and Addison 1997) and that '... considerably more research is needed on behavioural and ecological factors affecting trap encounter and entry before traps can be a truly effective device for measuring lobster abundance' (Cobb 1995). To address this need, we developed an in situ video surveillance technique to observe the behaviour of lobsters in and around traps in the field.

Underwater video monitoring has been used in marine research to observe the behaviour, distribution, and abundance of fish and invertebrates since the 1950s (Barnes 1955; Myrberg 1973). Video techniques used to study lobsters in the past have included towed video sleds (Chapman 1979; Chapman 1985), hand-held video cameras (Potts *et al.* 1987; Lawton and Lavalli 1995), remotely

operated vehicles (ROVs) (Spanier et al. 1994), drop cameras (Mayfield et al. 1999), and submersibles (Anonymous 1997; Steneck pers. comm.). In situ video systems are advantageous because they (1) increase observation time (2) reduce many types of diver-related disturbances (3) obtain continuous permanent records of behaviours that can be viewed repeatedly and thus analysed more thoroughly, and (4) provide access to habitats in areas (e.g., deep ocean) or times (e.g., night) that would be difficult or impossible for divers to observe. These many advantages, along with improvements in technology, have led to an increased use of mounted video systems to study the behaviours of marine animals in situ (Witman and Sebens 1992; Burrows et al. 1994; Ramsay et al. 1997; Gibson 1998; Burrows et al. 1999; Willis and Babcock 2000). These video surveillance systems, when connected to a time-lapse recording device, allow for long-term continuous monitoring of behaviour in the natural environment while minimizing disturbance.

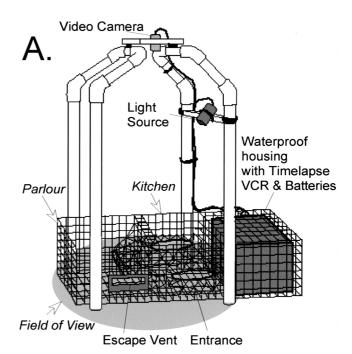
The data obtained in the present study, from an *in situ* video system used to study the behaviour of lobsters in and around traps, support previous reports that lobster traps are selective in sampling natural populations and provide additional evidence suggesting that aggressive interactions between lobsters play a key role in limiting catch.

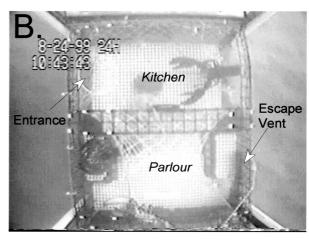
#### Methods

The lobster-trap video (LTV) system is a modular, low-cost, underwater video system designed to be easily used by lobster biologists and fishery managers. The approach we have taken, and advocate, for underwater video surveillance is to use the most economical solution that will address the hypotheses at hand, but to keep the system modular so that it can be upgraded if the hypotheses change or new ones are explored.

# LTV System

LTV consists of a traditional double-parlour wire-mesh lobster trap  $(122 \times 61 \times 34 \text{ cm})$  with equipment in a waterproof housing in one parlour so that the trap essentially fishes like a single parlour trap (Fig. 1). The wire-mesh top has been replaced with Plexiglas, which facilitates observation of the interior of the trap. Lobsters enter the kitchen of the trap, which contains a bait bag filled with approximately 1-2 kg of frozen herring, through two standard circular heads 6 inches (15.3 cm) in diameter (Fig. 1). The parlour has one standard escape vent (15.9 × 4.5 cm). A low-light, black-and-white, CCD video camera (0.05 lux, 3.6-mm lens, Model RHP-320WP, Rock House Products, Middletown, New York) mounted 100 cm above the trap allows for observation of the interior of the trap, as well as a field of view of an area 0.5 m larger than the perimeter of the trap (Fig. 1). A custommade PVC underwater housing holds a 12-VDC time-lapse VCR (Panasonic AG-1070DC), six 12-VDC sealed rechargeable gel cell batteries, and a timer that switches the electronics on and off to conserve power. The system is capable of collecting data for at least 24 h, so it can continuously record all lobster approaches within the field of view, as well as entries, exits, and intra- and interspecific behavioural interactions. When collecting data at night we used an array of 36 near-red LED lights (650 nm) because lobsters seem to have limited light detection capability at wavelengths >600 nm (Wald and Hubbard 1957). Using this lighting, we were able to observe





**Fig. 1.** Lobster trap video (LTV) system. A. LTV is an *in situ* time-lapse video-recording system attached to a standard lobster trap. Optional lights and recording equipment can be turned on and off by a timer in the waterproof case that contains all electronics. Movement of lobsters around the trap (within the field of view) and inside the trap can be continuously recorded. B. A single frame from an LTV time-lapse video with the time and date in the upper left of the image. Three lobsters are in the trap, one clearly visible entering the kitchen section of the trap and two retained in the parlour (for video, see Watson 2001).

entries, exits, and behavioural interactions inside the trap at night, but not approaches. Because LTV is self-contained, it can be deployed by two people in a small boat in remote locations, interspersed with traditional traps. Although the modifications necessary to fit the trap with electronics may have altered the way it fishes, control traps fished with LTV showed similar catch rates (see results).

A single frame from a section of video obtained during the summer of 1999 is shown in Fig. 1, and short sections of actual video are

available at our web site (Watson 2001) or as an Accessory Publication to the present paper at (http://www.publish.csiro.au/journals/mfr).

#### Field Experiments

Most deployments of LTV (n = 13) were conducted in a 10 000-m<sup>2</sup> study area marked with buoys off Wallis Sands Beach, New Hampshire (43°01'15" N, 70°43'40" W). This site is 4-6 m in depth and dominated by a sandy substrate that facilitates visualizing lobsters around LTV and obtaining accurate estimates of lobster abundance by means of SCUBA surveys. Densities of lobsters in the area determined by transects conducted by SCUBA divers generally ranged from 0.001 to 0.06 lobsters/m<sup>2</sup> (unpublished data). No other fisherman used this site, presumably because catch of lobsters is assumed to be generally low in sand habitats. This type of habitat is not typical lobster habitat, so comparative LTV deployments were made on five occasions in a rocky habitat approximately 0.5 km south of the sandy habitat. Each deployment in the rocky habitat was made within 1 week of a paired sandy-habitat deployment. Densities determined by SCUBA surveys at the rocky-habitat site (0.01–0.06 lobsters/m<sup>2</sup>) were similar to those obtained at the sandy-habitat site (unpublished data).

LTV (n = 13), and 3–5 single parlour (control) traps (n = 56), were deployed between 0900 hours and 1400 hours, June–October in 1997–2000. During each deployment, time-lapse video was obtained for an average of 19 h (range 10–25 h). A timer was used to turn off the electronics at night to save batteries except for the four deployments when lights were used to observe night-time entries. Thus, depending upon ambient visibility, observable video was obtained from deployment to dusk and then from dawn to retrieval on the following day. Typically, all traps were hauled on the day after deployment, and all lobsters caught in the LTV trap and the control traps were measured and released back at the study site.

### Video Analysis

Videotapes were viewed at the University of New Hampshire Image Analysis Laboratory, and counts were made of all the lobsters viewed in the following behavioural categories: (1) approach, any individual entering the field of view of the camera (because most lobsters were not individually identifiable, we assume that many lobsters were counted multiple times as they left the field of view and then returned); (2) entry, lobsters fully entering a trap; (3) half-entry, lobsters entering more than half a body-length into a trap (this category included individuals that entered just enough to feed but never left the entrance; see Karnofsky and Price 1989 or Auster 1985 for a detailed description of this behaviour); (4) exit, lobsters leaving the trap through either an entrance (kitchen) or the escape vent (parlour) and; (5) catch, the number of lobsters in the trap at the end of each hour (see Fig. 2 for a sample of the relationship of these behaviours over time). We determined sizes of lobsters that entered the trap by digitizing individual frames and then measuring lobsters with NIH Image software calibrated to a ruler on the bottom of the trap (Fig. 1). Lobsters ≥80 mm carapace length (CL) were considered 'large' lobsters, whereas those <80 mm CL were categorized as 'small'. Size data are presented for the deployment on 6 August 1997. Finally, times spent in the kitchen and in the parlour were recorded for all individuals that entered the trap.

# Results

LTV has provided a unique method for collecting information about the behavioural factors that influence catch in lobster traps (Fig. 1, see Watson 2001). LTV appears to fish in the same way as standard traps because catch per unit effort in control traps  $(2.66 \pm 0.29, n = 56)$  was similar to that in LTV  $(2.38 \pm 0.50, n = 13; p > 0.10,$ 

Mann Whitney U-test). The average size of lobsters caught by LTV (76.3  $\pm$  1.2 mm CL) was also similar to that of lobsters caught in control traps (75.2  $\pm$  0.7 mm CL). (All variation is reported as standard error (SE) throughout the results.)

Although the behaviour and ecology of lobsters may be different in rocky and sandy habitats, we found that between June and September they differed little in catch per unit effort  $(2.5 \pm 0.65 \text{ on sand}; 2.2 \pm 0.82 \text{ on rock})$  or entries per hour  $(2.0 \pm 0.86 \text{ on sand}; 2.4 \pm 0.67 \text{ on rock})$ . The data used for comparison were obtained from five deployments of LTV at the rocky site paired with five deployments of LTV at the sandy site (a subset of the 13 deployments presented below) made within the same one-week period. Although these data are not definitive because of low sample sizes, they do suggest that traps in the sandy habitat at Wallis Sands fished similarly to those in more typical rocky habitats. All data presented below are from LTV deployments at the Wallis Sands location because the analyses of approaches and behavioural interactions were more reliable at the sandy site, where the visual contrast between lobsters and the substrate was much greater.

# Trap dynamics

Approaches, entries, exits, and catch per hour from deployment to dusk on the first day were determined (n =13) (Table 1, Figs 2 and 3). Analyses of these videotapes showed that a large number of lobsters approached the trap, but of these only 4% entered (n = 331). Of those entering the trap, only 6% were captured, whereas 94% escaped. Of those escaping (n = 310), 72% escaped from the kitchen, and 28% escaped from the parlour. Lobsters can escape from the parlour back into the kitchen and then out of the trap, but they did so infrequently. Although most of the lobsters observed were estimated to be of sublegal size (<83 mm CL) and could readily escape from the parlour through the entrances and escape vents, even larger, legal-sized lobsters often escaped from the traps through the entrances. For example on 6 August 1997, 5 of the 7 large lobsters observed entering the trap (mean size  $86.9 \pm 3.9$  mm CL, range 80-93) escaped. Of the small lobsters observed entering the trap (mean size 62.8 ± 1.6 mm CL, range 34-79, n = 38) all but three escaped before the end of the observation period (12 h). (See also Watson 2001).

Immediately after entering the trap, most lobsters began feeding and spent an average of 9 min 50 s ( $\pm$  4 min 8 s) in the kitchen (Fig. 3). Lobsters that did not escape through the entrances but entered the parlour section of the trap spent an average of 18 min 8 s ( $\pm$  13 min 11 s) in the parlour (this group does not include large lobsters that were ultimately captured when the trap was hauled because these individuals were in the trap for several hours) (Fig. 3*B*).

One of the most striking and consistent observations was that the number of approaches by lobsters to a trap greatly

#### Table 1. Lobster trap dynamics summary.

Numbers of approaches, entries, escapes, and catches were determined for the duration of a given deployment of the LTV. Only data taken between deployment and dusk of the first day are included (n = 13). # caught: refers to the number of lobsters present in the trap at the end of the last hour of the observation time, not necessarily when the traps were hauled. These data provide the basis for the trap dynamics diagram shown in Fig. 3

Date	Observation time (h)	# approaches	# entries	# escapes, kitchen	# escapes, parlour	# caught
6 Aug 97	12	3058	45	23	17	5
3 July 98	11	45	2	1	1	0
25 Sept 98	9	1603	43	37	5	1
21 June 99	10	11	7	6	1	0
7 July 99	10	122	10	7	2	1
15 July 99	5	253	4	2	2	0
9 Aug 99	8	503	38	25	10	3
12 Aug 99	10	256	34	21	11	2
17 Aug 99	7	246	28	21	5	2
24 Aug 99	10	705	47	32	11	4
13 Sept 99	7	237	18	8	9	1
10 July 00	8	284	3	3	0	0
25 July 00	7	699	52	35	15	2
Totals	114	8023	331	221	89	21

exceeded the number of lobsters entering it (Table 1, Figs 2 and 3). This approach behaviour began very shortly after the trap was deployed. Because of the difficulties in accurately quantifying the number of individual lobsters that approach a trap, the relationship between approach to the trap and catch remains unclear.

# Temporal variability in catch

Red lights were used on four LTV deployments to illuminate the inside of the trap, making it possible to compare rate of entry during the night (56 h of videotape) and the day (33 h of video tape). Although lobsters are generally considered nocturnal (Cobb 1971; Stewart 1972; Reynolds and Casterlin 1979; Cooper and Uzman 1980; Lawton 1987; Karnofsky *et al.* 1989; Lawton and Lavalli 1995; Jury 1999), we observed no significant difference between the rate of entries during the day and that during the night (p > 0.05, Mann Whitney U-test). An average of  $3.3 \pm 1.3$  entries/h occurred in the daytime and  $2.5 \pm 1.1$  entries/h at night (Fig. 4). These data suggest that, although lobsters may be more active at night and may even approach the trap more frequently, they do not enter the trap at a higher rate at night.

Comparison of entries per hour between deployment and dusk (n = 13) with entries per hour between dawn and recovery (n = 13) revealed no statistically significant difference in rate of entry (p > 0.5, paired t-test) between successive periods. On average  $1.8 \pm 0.5$  lobsters entered the trap each hour during Day 1 and  $1.7 \pm 0.5$  lobsters/h entered

during Day 2. Entry rate during both periods closely matched exit rate in any given hour, and any small difference in rates resulted in changes in ultimate catch (Fig. 2).

#### Behavioural interactions

Entries into, and exits out of, the trap appeared to be strongly influenced by the length of time that lobsters fed on the bait as well as antagonistic interactions between lobsters in the kitchen and lobsters attempting to enter the trap. When the lobster entering was larger, it usually chased the smaller lobster out of the kitchen. If the lobster attempting to enter the trap was smaller, the lobster in the kitchen defended the bait and prevented it from entering. Lobsters in the kitchen eventually stopped feeding spontaneously when there were no lobsters in the trap. To quantify this observation, we determined from one videotape the numbers of half-entries and full entries into the kitchen when another lobster was already in the kitchen and when the kitchen was not occupied (see Watson 2001). The results show that, when the kitchen was occupied (n = 222)observations), 89% of lobsters displayed half-entries (i.e., began to enter and then retreated); while only 11% fully entered. When the kitchen was not occupied (n = 39)observations), 64% fully entered without hesitation, and only 36% displayed half-entries. The difference was statistically significant (Fisher's Exact Test, p < 0.001) and demonstrates the strong influence of conspecifics on entry rate.

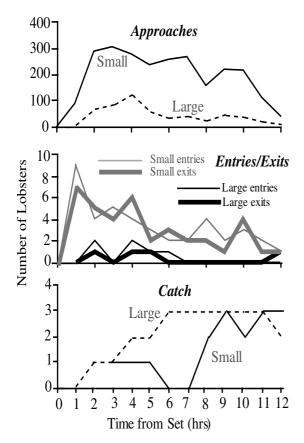
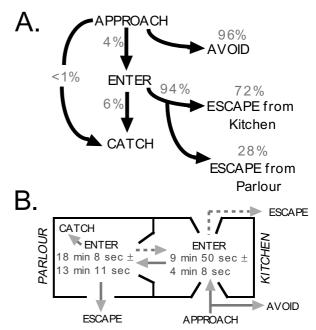


Fig. 2. Comparison of approaches, entries, exits, and total catch of large and small lobsters vs. time from one 12-h deployment of LTV on 6 August 1997. For this analysis large lobsters (≥80 mm carapace length) were considered to be 'catchable'. Small animals appeared to enter and exit the trap at approximately the same rate every hour, whereas large animals entered the trap and were usually retained. The retention of large lobsters and the differential between entries and exits each hour leads to the catch per hour seen in the bottom panel.

# Discussion

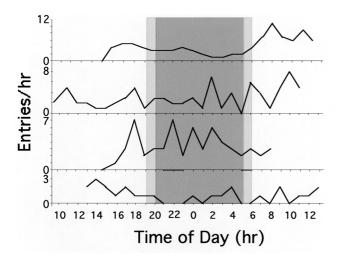
We were surprised to discover that traps catch such a small percentage of the lobsters that approach and enter and how closely these data matched laboratory studies of trap dynamics (Karnofsky and Price 1989). In addition, our observations of the behavioural interactions between lobsters makes it clear that they play an extremely important role in determining the flow of lobsters through a trap and ultimately the catch. Although the present paper does not address questions of how lobster density influences these interactions and subsequent catch, it does provide the framework for further analyses (Watson and Jury in prep.).

Diver-held underwater video cameras, time-lapse video, and tethered ROVs have been used previously to observe lobster behaviour in the field (Auster 1985; Wahle and Steneck 1992; Barshaw and Spanier 1994; Burrows *et al.* 1994; Spanier *et al.* 1994), but few have systematically examined how lobsters interact with traps. In one study of



**Fig. 3.** Overview of LTV trap dynamics. A. Approaches, entries, escapes, and catch were determined for daytime observations with the LTV system (n=13) (see Table 1). Many approaches were observed but were probably not unique individuals. B. Schematic of trap showing the time course of entry and escape. Lobsters generally enter the kitchen through one of two entrances, feed for a set amount of time (minutes and seconds  $\pm$  SE) and then either escape or enter the parlour. They then remain in the parlour for some time (minutes and seconds  $\pm$  SE) and then either escape or remain to be ultimately caught.

H. americanus, a time-lapse camera and strobe system was used to study the effect of changing current velocities on foraging behaviour in a 0.5-m<sup>2</sup> area around bait staked to the bottom (Auster 1985). Frames were taken every minute for one 50-h deployment, but no lobsters or crabs were observed, and the bait was gone when the system was recovered. ROVs have been used to observe lobster behaviour in the field but the noise and possibly lights appeared to alter some lobster behaviours significantly (Spanier et al. 1994). Finally, a system similar to LTV was used to demonstrate that only 6% of Norway lobsters (N. norvegicus) observed near traps were actually caught (Bjordal 1986). The explanations put forth to explain this low catch rate included (1) temporal changes in feeding motivation (2) difficulty in locating trap entrances (3) frequent aggressive behaviours (small individuals were chased away by larger ones), and (4) failure by one third of the observed individuals to contact the trap at all. The data presented here are consistent with Bjordal's findings and provide additional insight into some of the mechanisms that may lead to low catch efficiency. In particular, aggressive interactions between lobsters appear to be one of the dominant factors limiting both rate of entry into traps and rate of exit from traps.



**Fig. 4.** Changes in the rate of entry of lobsters into a lobster trap during four deployments in August–September 1999. Entry data are presented from both daytime and night-time recordings from each deployment. The shaded area represents night-time observations. These data demonstrate that there is little diel change in entry rate.

One of the most striking and consistent observations was that the number of lobster approaches to a trap greatly exceeded the number of lobster entries into the trap (Table 1, Figs 2 and 3).). The disparity resulted, in part, because many individual lobsters appeared to stay in the vicinity of the trap and approached it many different times before entering, if they entered at all. SCUBA observations of LTV, as well as time-lapse observations of LTV by a separate camera mounted 2-3 m away, have confirmed these observations (unpublished data). Karnofsky and Price (1989), in their laboratory study, found similar results showing that individual lobsters that ultimately entered a trap approached their traps an average of 27 times (range = 0-54), whereas individuals that never entered a trap approached an average of 15 times (range = 1-50). Despite the large individual variability, Karnofsky and Price (1989) did find that 'large individuals which approached more tended to be caught more... although there were numerous exceptions'. If these numbers are also typical of field behaviours, then we can roughly estimate the number of individual lobsters approaching a trap in the present study by dividing observed approaches by a factor of 15-25. If this 'correction' factor is accurate, then the number of approaches by individual lobsters is fairly close to the number of entries (see Table 1) suggesting that a large proportion of the lobsters that are attracted to a trap will eventually enter.

Several studies have shown that lobsters are nocturnally active (Cobb 1971; Stewart 1972; Reynolds and Casterlin 1979; Cooper and Uzman 1980; Lawton 1987; Karnofsky *et al.* 1989; Lawton and Lavalli 1995; Jury 1999), and it is often suggested that they are therefore more likely to be

captured at night. However, recent recordings from the feeding muscles of blue crabs (Callinectes sapidus), also generally considered a nocturnal forager, indicate that they feed throughout the day (Wolcott and Hines 1989). A study on the crab Scylla serrata also showed no evidence to support the long-standing belief that night catches are higher than day catches (Robertson 1989). The results of the present study suggest that entry rate of H. americanus into traps does not significantly increase at night. In a separate set of trap studies, we also found very little difference in catch per unit effort between traps deployed for 12 h during daytime and traps deployed for 12 h at night (Watson, unpublished data). Therefore, even though laboratory studies and field observations indicate that the American lobster is generally nocturnal, the relationship of catch to diurnal and nocturnal activity is unclear (Karnofsky and Price 1989). We suggest that, even though lobsters may be more active and approach traps more often at night, entry rate and subsequent catch are limited by competitive interactions. Thus differences between daytime and nighttime activity are not generally reflected in catch data.

The likelihood that a lobster will enter a trap and be captured appears to depend on several factors, including the number of individuals already in the trap (saturation effect), moult stage, reproductive condition, size, sex, satiation, predator density, habitat type, water temperature, season, and time of day (Ennis 1973; McCleese 1974; Miller 1978, 1979a, 1979b, 1980, 1983, 1989, 1990, 1995; Richards et al. 1983; Smith and Jameison 1985; Krouse 1989; Robertson 1989; Miller and Addison 1995; Tremblay 2000). Many of these factors may influence the tendency of lobsters to approach a trap, but the likelihood that a lobster will find a given trap may also depend on the density of lobsters in the area, the area fished by the trap, the density of traps being fished, or the foraging area of individuals (Jernakoff and Phillips 1988; Skajaa et al. 1998; Watson and Jury in prep.). Our data suggest that, once lobsters have approached a trap, the likelihood that they will enter and be captured is strikingly low. Karnofsky and Price's (1989) laboratory study of H. americanus supports this finding. They found that only 2% of approaches led to capture, and of those that entered the trap only 11% were captured. In addition only 37% of the population tested (n = 30) in their study were ever captured in any trial (103 h total observation time), and 43% of the lobsters that approached never even entered a trap. These results suggest a high degree of individual variability in the behavioural response to traps.

On the basis of our behavioural observations we hypothesize that the agonistic interactions between conspecifics are the single most important factor influencing rate of entry and catch (see Watson 2001). In particular, interactions between lobsters in the kitchen and those attempting to enter strongly limit the rate of entry. Additional competition outside the trap may also play an

important role because lobsters, and sometimes crabs, appear to compete aggressively for the opportunity to be the next individual to enter the trap. Lobsters in the parlour may influence the entry of additional individuals into the trap, but we have yet to address this question quantitatively. Richards et al. (1983) reached that conclusion after prestocking the parlours of single-parlour traps without escape vents with 3 to 8 large lobsters and examining subsequent catch. They found that the presence of lobsters in a trap reduced the catch of other lobsters, probably because of some type of interaction between the lobsters in the trap and those outside. The present study, taken together with the aforementioned laboratory and field data, suggests that lobster behaviour in and around traps leads to the phenomenon of trap saturation. As a result, traps are not very efficient, and the probability that catch directly reflects the true population density on the bottom is low.

Several recent papers have described models designed to predict the dynamics of how traps function to catch lobsters (Addison and Bell 1997; Fogarty and Addison 1997; Addison and Bannister 1998). These models incorporate behavioural parameters to allow prediction of catch over various deployment times and simulated densities of lobsters, but the dearth of in situ empirical data on these behaviours has necessitated numerous assumptions to make the models work. One goal of the LTV studies is to provide some of the necessary empirical data for models such as these and to develop a revised model to describe the various processes that dictate the dynamics of lobster movements into and out of traps. Finally we are working toward moving from the individual-trap level to the fishery level in order to determine how the density of lobsters is related to entry and escape processes and to determine how these processes are related to catch per unit effort in the field (Watson and Jury, in prep.).

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#### References

- Addison, J. T. (1995). Influence of behavioral interactions on lobster distribution and abundance as inferred from pot-caught samples. *ICES Marine Science Symposium* 199, 294–300.
- Addison, J. T. (1997). Lobster stock assessment: report from a workshop. *Marine and Freshwater Research* **48**, 941–44.
- Addison, J. T., and R.,C. Bannister (1998). Quantifying potential impacts of behavioral factors on crustacean stock monitoring and assessment: modeling and experimental approaches. In 'Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management'. Canadian Special Publications in Fishery and Aquatic Science 125. (Eds G. S. Jameison and A. Campbell.) pp. 167–177.
- Addison, J. T., and M. C. Bell. 1997. Simulation modelling of capture processes in trap fisheries for clawed lobsters. *Marine and Freshwater Research* 48, 1035–44.
- Anonymous (1997). Scientists use submarine to find lobster broodstock. *Lobster Bulletin*, October, Vol. 10, No. 2.
- Auster, P. (1985). Factors affecting catch of American lobster, Homarus americanus in baited traps. University of Connecticut Sea Grant Program Technical Bulletin Series CT-SG-85-1. 46 p.
- Barnes, H. (1963). Underwater television. *Oceanography and Marine Biology Annual Review* 1, 115–28.
- Barshaw, D. E., and Spanier, E. (1994). Anti-predator behaviors of the Mediterranean slipper lobster, Scyllarides latus. Bulletin of Marine Science 55, 375–82.
- Bjordal, A. (1986). The behaviour of Norway lobster towards baited creel and size selection of creels and trawls. *Fiskeridirektoratets Skrifter Serie Havundersokelser* **18**, 131–37.
- Burrows, M. T., R. N Gibson, L. Robb, and C. A Comely. (1994). Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *Journal of Experimental Marine Biology and Ecology* 177, 251-68.
- Burrows, M. T., K. Kawai, and R. N. Hughes. (1999). Foraging by mobile predators on a rocky shore: underwater TV observations of movements of blennies *Lipophrys pholis* and crabs *Carcinus maenas*. *Marine Ecology Progress Series* 187, 237–50.
- Chapman, C. J. (1979). Some observations on populations of Norway lobster, Nephrops norvegicus (L.) using diving, television and photography. Journal du Conseil, Conseil International pour l'Exploration de la Mer 175, 127–33.
- Chapman, C. J. (1985). Observing Norway lobster, *Nephrops norvegicus* (L.) by towed sledge fitted with photographic and television cameras. In 'Underwater Photography and Television for Scientists'. (Eds J. D. George, G. J. Lythgoe, and J.,W. Lythgoe.) pp. 100–108. (Clarendon Press, Oxford.)
- Cobb, J. S. (1971). The shelter-related behavior of the American lobster, *Homarus americanus*. *Ecology* **52**, 108–15.
- Cobb, J. S. (1995). Interface of ecology, behavior and fisheries. In 'Biology of the Lobster *Homarus americanus*'. (Ed. J. R. Factor.) pp. 139–152. (Academic Press. San Diego, California.)
- Cooper, R. A., and Uzmann, J. R. (1980). Ecology of juvenile and adult *Homarus americanus*. In 'The Biology and Management of Lobsters, Vol. II.' (Eds J. S. Cobb and B. F. Phillips.) pp. 97–142. (Academic Press, New York.)
- Ennis, G. P. (1973). Food, feeding, and condition of lobsters, Homarus americanus, throughout the seasonal cycle in Bonavista Bay, Newfoundland. Journal of the Fisheries Research Board of Canada 30, 1905–9.
- Fogarty, M. J., and Addison, J. T. (1997). Modelling capture processes in individual traps: entry, escapement and soak time. *ICES Journal of Marine Science* **54**, 193–205.
- Gibson, R. N., Pihl, L., Burrows, M. T., Modin, J., Wennhage, H., and Nickell, L. A. (1998). Diel movements of juvenile plaice

- Pleuronectes platessa in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. Marine Ecology Progress Series 165, 145–59.
- Jernakoff, P., and Phillips, B. F. (1988). Effect of a baited trap on the foraging movements of juvenile western rock lobsters, *Panulirus* cygnus George. Australian Journal of Marine and Freshwater Research 39, 185–92.
- Jury, S. (1999). Behavioral and physiological responses of the lobster, Homarus americanus, to temperature: a new synthesis. Ph.D. dissertation, University of New Hampshire, Durham, New Hampshire.
- Karnofsky, E. B., and Price, H. J. (1989). Behavioral response of the lobster Homarus americanus to traps. Canadian Journal of Fisheries and Aquatic Sciences 46, 1625–32.
- Karnofsky, E. B., Atema, J., and Elgin, R. H. (1989). Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. *Biological Bulletin* (Woods Hole) 176, 239–46.
- Krouse, J. S. (1989). Performance and selectivity of trap fisheries for crustaceans. In 'Marine Invertebrate Fisheries: Their Assessment and Management'. (Ed. J.F. Caddy.) pp. 307–25. (Wiley, New York.)
- Lawton, P. (1987). Diel activity and foraging behaviour of juvenile American lobsters, Homarus americanus. Canadian Journal of Fisheries and Aquatic Sciences 44, 1195–1205.
- Lawton, P., and Lavalli, K. L. (1995). Postlarval, juvenile adolescent, and adult ecology. In 'Biology of the Lobster *Homarus* americanus'. (Ed. J. R. Factor.) pp. 47–81. (Academic Press, New York.)
- Mayfield, S., Branch, G. M., and Cockcroft, A. C. (1999). Determining prey availability for rock lobsters, *Jasus lalandii*: diver-sampling versus monochrome video photography. *Marine Biology* 135, 347– 52.
- McCleese, D. W. (1974). Olfactory responses of lobsters (*Homarus americanus*) to solutions from prey species and to seawater extracts and chemical fractions of fish muscle and effects of antennule ablation. *Marine Behavior and Physiology* **2**, 237–49.
- Miller, R. J. (1978). 'Crab (*Cancer irroratus* and *Hyas araneus*) Ease of Entry to Baited Traps'. Canadian Fisheries Marine Service Technical Report 771.
- Miller, R. J. (1979a). Entry of Cancer productus to baited traps. Journal du Conseil, Conseil International pour l'Exploration de la Mer 38, 220–25.
- Miller, R. J. (1979b). Saturation of crab traps: reduced entry and escapement. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **38**, 338–45.
- Miller, R. J. (1980). Design criteria for crab traps.. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **39**, 140–47.
- Miller, R.J. (1983). Considerations for conducting field experiments with baited traps. *Fisheries (Bethesda)* **8**(5):14–17.
- Miller, R. J. (1989). Catchability of American lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) by traps. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 1652–57.
- Miller, R. J. (1990). Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences* 47, 1228–50.
- Miller, R. J. (1995). Catchability coefficients for American lobsters (*Homarus americanus*). *ICES Marine Science Symposium* **199**, 349–56.
- Miller, R. J., and Addison, J. T. (1995). Trapping interactions of crabs and American lobster in laboratory tanks. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 315–24.

Myrberg, A. A., Jr. (1973). Underwater television—a tool for the marine biologist. *Bulletin of Marine Science* **23**, 824–36.

- Potts, G. W., Wood, J. W., and Edwards, J. M. (1987). Scuba diver operated low-light level video system for use in underwater research and survey. *Journal of the Marine Biological Association of the United Kingdom* **67**, 299–306.
- Ramsay, K., Kaiser, M. J., and Hughes, R. N. (1997). A field study of intraspecific competition for food in hermit crabs (*Pagurus bernhardus*). Estuarine, Coastal and Shelf Science 44, 213–20.
- Reynolds, W. W., and Casterlin, M. E. (1979). Behavioral thermoregulation and activity in *Homarus americanus*. Comparative Biochemistry and Physiology **64A**, 25–28.
- Richards, R. A., Cobb, J. S., and Fogarty, M. J. (1983). Effects of behavioral interactions on the catchability of American lobster, *Homarus americanus*, and two species of *Cancer* crab. *Fishery Bulletin*, U.S. 81, 51–60.
- Robertson, W. D. (1989). Factors affecting catches of the crab *Scylla serrata* (Forskal) (Decapoda: Portunidae) in baited traps: soak time, time of day and accessibility of the bait. *Estuarine*, *Coastal and Shelf Science* **29**, 161–70.
- Skajaa, K., Ferno, A., Lokkeborg, S., and Haugland, E. K. (1998). Basic movement pattern and chemo-oriented search towards baited pots in edible crab (*Cancer pagurus L.*). *Hydrobiologia* 371/372, 143–53.
- Smith, B. D., and Jamieson, G. S. (1985). A model for standardizing Dungeness crab (*Cancer magister*) catch rates among traps which experienced different soak times. *Canadian Journal of Fisheries* and Aquatic Sciences 46, 1600–8.
- Spanier, E., Cobb, J. S., and Clancy, M. (1994). Impacts of remotely operated vehicles (ROVs) on the behavior of marine animals: an example using American lobsters. *Marine Ecology Progress Series* 104, 257–66.
- Stewart, L. L. (1972). 'The Seasonal Movements, Population Dynamics, and Ecology of the Lobster, *Homarus americanus*, off Ram Island Connecticut'. Ph.D. Dissertation, University of Connecticut, Storrs.
- Tremblay, M. J. (2000). Catchability of the lobster (*Homarus americanus*): late spring versus autumn. In 'The Biodiversity Crisis and Crustacea: Proceedings of the Fourth International Crustacean Congress, Vol. 2'. Crustacean Issues 12. (Eds J. C. von Vaupel Klein and F. R. Schram.) pp. 701–13. (Balkema: Rotterdam.)
- Wahle, R. A., and Steneck, R. S. (1992). Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology* 157, 91–114.
- Wald, G., and Hubbard, R. (1957). Visual pigment of a decapod crustacean: the lobster. *Nature (London)* **180**, 278–80.
- Watson, W. H., III (2001). 'Video and photo gallery'. Web site providing video segments of behaviors described in the text. http:// zoology.unh.edu/faculty/win/winvideos.htm. 17 May 2001.
- Willis, T. J., and Babcock, R. C. (2000). A baited underwater video system for the determination of relative density of carnivorous reef fish. *Marine and Freshwater Research* **51**, 755–63.
- Witman, J. D., and Sebens, K. P. (1992). Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia* **90**, 305–15.
- Wolcott, T. G., and Hines, A. H. (1989). Ultrasonic biotelemetry of muscle activity from free-ranging marine animals: a new method for studying foraging by blue crabs (*Callinectes sapidus*). *Biological Bulletin (Woods Hole)* **176**, 50–56.