

BIASES IN CRAB TAG RECOVERY DATA

Nancy Diamond and David G. Hankin

Department of Fisheries
Humboldt State University
Arcata, California 95521

Introduction

During the years 1981-1983, we tagged and released 12,037 adult female Dungeness crabs in northern California as part of project activities designed to determine basic life history parameters and movements of female crabs. Realizing these objectives required that we place substantial reliance on tag recovery data from the northern California commercial fishery. Although these and other data allowed us to develop a remarkable description of the life history of adult female Dungeness crabs (Hankin et al., this Symposium), analyses of tag recovery data were seriously confounded by sampling biases. In particular: 1) movement analyses were biased by temporal and spatial departures of fishing effort from random or uniform distributions; and 2) estimation of annual molting probabilities was biased by a) commercial crab trap size selection, and b) loss of tags through molts.

The observation that analysis of tag recovery data for movements of crabs or other fishes is biased by the distribution of fishing effort is not new. Edwards (1979), Bennett and Brown (1983), and McKoy (1983), among others, have all presented qualitative considerations of the possible impacts of non-random fishing effort on attempted analyses of tag recovery data for movement patterns. It is obvious that animals can be recovered only at (a) locations where animals are present, and (b) locations where fishermen are present. Tag recovery data therefore give no information on movements of animals at (a) locations where animals are present, but (b) fishermen are not. Previous attempts at discerning movements of Dungeness crabs based on tag recovery data have not ignored this problem (Gotshall 1978), but analyses have been intuitive and subjective rather than quantitative and objective. That is, inferences concerning apparent movements have been drawn largely from visual inspection of tag recovery data rather than through use of statistical methods. In this paper we show that circular statistics may

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be used to test for the significance of directed movements of adult female Dungeness crabs and we briefly contrast our results with Gotshall's earlier work.

To our knowledge, there have been no previous attempts to adjust for biases that result from size selection of commercial trap gear in estimation of annual molting probabilities. Hancock and Edwards (1967), in their analysis of annual molting probabilities of *C. pagurus*, made no adjustments for size selection biases because they felt that commercial recovery gear was nonselective over the range of sizes with which they were concerned. However, they mentioned the possible importance of size selection in their paper and this problem cannot be ignored in analyses of tag recovery data for Dungeness crabs. Size selection of commercial Dungeness crab traps (in northern California) results from the large mesh size (70-100 mm on diagonal) of traps, the usual requirement for two (109 mm diameter) escape ports (to minimize capture and handling of sub-legal male and female crabs), and provision of one or two large width (about 50 mm) triggers on entrance tunnels to traps. These features of crab trap design cause retention rates for small crabs to be far less than for large crabs. In the context of estimation of annual molting probabilities, this means that tagged crabs that molt to larger sizes will have higher probabilities of being recovered in commercial gear than will crabs of the same size at tagging that fail to molt. Thus, size selection by crab traps results in a positive bias in estimates of annual molting probabilities; molted crabs are more likely to be recovered than are nonmolted crabs. In contrast, tag loss through molting results in a negative bias in molting probability estimates. Crabs that lose tags through molts cannot be recovered, and it is likely that tag loss among crabs that molt is greater than tag loss among those crabs that fail to molt. Use of crab tag recovery data for estimation of annual molting probabilities thus requires that one account for both of these kinds of biases.

The intention of this paper is to illustrate the nature and potential impacts of those biases which confounded our analyses of crab tag recovery data and, where possible, to point out some steps which could or should be taken to adjust for or minimize those biases. Because more formal peer-reviewed manuscripts are in preparation or review on both the subjects of annual molting probabilities of female Dungeness crabs and on their movements, presentation of the nature of biases and of possible responses to those biases has been limited in scope and detail. However, future publications will provide full details of presented analyses and existing and/or contemplated publications have been referenced as appropriate.

Materials and Methods

Adult female Dungeness crabs were captured, tagged, measured and released from a contracted commercial crab fishing vessel out of Trinidad Bay (41°03'N), California, during January through March of 1981, 1982 and 1983. In all years, tagging was completed prior to the start of the annual molting/mating season which takes place from early April through May in northern California. Most tagging took place between the mouth of the Mad River (40°55'N) and Freshwater Lagoon (41°51'N) at depths of 18-22 m (10-12 fathoms) in 1981 and 1982, and 22 and 44 m (12 and 24 fathoms) in 1983. Carapace widths were measured to 0.1 mm across the carapace excluding the tenth anterolateral

spines. Numbered FLOY anchor tags (Model # FD68B) were inserted at the posterior epimeral suture to ensure high retention rates through molts (see Poole 1967; Edwards 1965; and Butler 1957 for previous suture tagging studies with Cancer crabs).

Commercial fishermen were asked to return tagged crabs with the date, depth and location (either LORAN-C readings or specific coastal landmark) of recovery. As incentive for return of tagged crabs, an annual \$500 drawing was held in which one tag was drawn from all those tags returned during a fishing season; the fisherman who had returned the winning tag received the award.

Movement vectors (straight line distances from release to recovery) were determined for crabs that were recovered at distances exceeding 2 km from the release site for two seasonal periods: a) the winter of tagging (December through February), and b) the spring following tagging (March through July). These two seasons were adopted so as to allow comparison with earlier movement analyses by Gotshall (1978), and also because they allowed separation of crab movements into those before and during the annual spring molting/mating season. Individual movement vectors within each of four designated release areas (which differed in habitat characteristics) were summed using vector algebra, and then circular statistics (Rayleigh and Moore's tests; see Batschelet 1981) were used to determine the possibility of significant directional movement (Diamond and Hankin, in review). (Movements less than 2 km were judged to be within the measurement error surrounding release and recovery locations and were assigned (0,0) rectangular coordinates with no polar equivalents). Because analysis of recovery data for movements was performed by period of recovery, and because we found no statistical dependence of distance travelled on numbers of days at large, number of days at large before recovery were not incorporated in analyses.

Size selection curves for commercial crab traps were determined by parallel fishing of nonselective experimental traps and selective commercial traps as recommended by Beverton and Holt (1957) and Pope (1975). Experimental nonselective traps were custom-built, designed on the basis of laboratory and field investigations, and had mesh size of 55 mm on diagonal, six 25 mm wide triggers per entrance tunnel, and closed escape ports. Retention in these experimental traps was 100% for crabs exceeding 85 mm carapace width. Based on the number of crabs retained at size in nonselective and selective commercial traps, parameters of a commercial gear selection curve were estimated following procedures presented in Pope (1975; see also Diamond 1983, Appendix A). Traps were usually fished for two days, but soak time ranged from two to seven days. Comparison of numbers and sizes retained in nonselective and selective traps showed that soak time did not influence size selection and retention rates when traps were fished for two days or longer before being pulled.

However, during the early part of the fishing season in northern California, fishermen frequently fish traps for periods of one day or less with the result that crabs are still actively feeding on bait and/or have not had the time or developed the "desire" to attempt escape from traps. This short soak time prevented commercial traps from exhibiting their true selective properties (which appear to require soaks of two days or longer). Actual tag recovery rates for "small"

crabs (135-145 mm) as compared to "large" crabs (≥ 155 mm) were much higher than would have been predicted on the basis of the commercial trap selection curve for soaks of two days or longer. Therefore, we developed an alternative method by which to quantify the relative recovery rates for crabs of differing sizes. For this method we used recovery data from crabs that were recovered during the early part of the season following tagging (prior to March 1). Because these crabs did not have an opportunity to molt, size at recovery was the same as size at tagging. We computed size-specific recovery rates essentially as the actual numbers recovered for a certain size interval divided by the numbers released. Relative size-specific recovery rates were then obtained by dividing the (a) (expected) recovery rate for crabs that molted to a particular (expected) size by (b) recovery rate for crabs of the same initial size that had failed to molt. The expected recovery rates for molted crabs were thus based on recovery rates for nonmolted crabs of the same size as those crabs that had molted. More satisfying descriptions of the logic behind procedures and more detailed descriptions of actual calculations are presented in Diamond (1983).

Tag loss during molting was estimated from laboratory experiments in which premating embrace females were tagged prior to molting in the laboratory. To test the possibility that tags might be lost due to the mating process itself, rather than due to molting per se, we compared tag loss between groups of females that (a) molted in the absence of males and (b) molted in the presence of males and mated at that time. Time from tagging until molting in the laboratory ranged from 1 to 37 days.

Results

Movements and migrations

The seasonal pattern of commercial fishing effort in northern California is governed by a combination of weather conditions and Dungeness crab life history. Gotshall (1978) stated that effort is distributed fairly evenly at depths of 18-75 m at the start of the season (1 December) continuing through about March. As large ocean swells and surf subside, fishing effort moves inshore during the spring months, culminating in what our local fishermen call the "beach run" (usually during April or May) when fishing effort is concentrated in shallow waters (< 18 m) along beach areas. This "beach run" coincides with the spring mating season at which time often dense aggregations of legal-sized male Dungeness crabs congregate inshore in shallow sandy areas to mate with newly molted females. Thus, the early distribution of fishing effort approximates a random distribution within the areas bounded by 18-75 m, whereas the distribution of fishing effort during the spring is highly concentrated in shallow beach areas.

Figure 1 shows the four release areas which were considered in movement analyses: Area I - an exposed sandy beach; Area II - a protected rocky coast; Area III - an exposed rocky coast; and Area IV - an exposed sandy beach. Visual examination of winter movement vectors for one of these areas (Area I) suggested a possible northward movement during the winter period (Figure 2). However, statistical tests of the summed resultant vectors within this and other areas, as well as for all areas combined, failed to support an hypothesis of significant

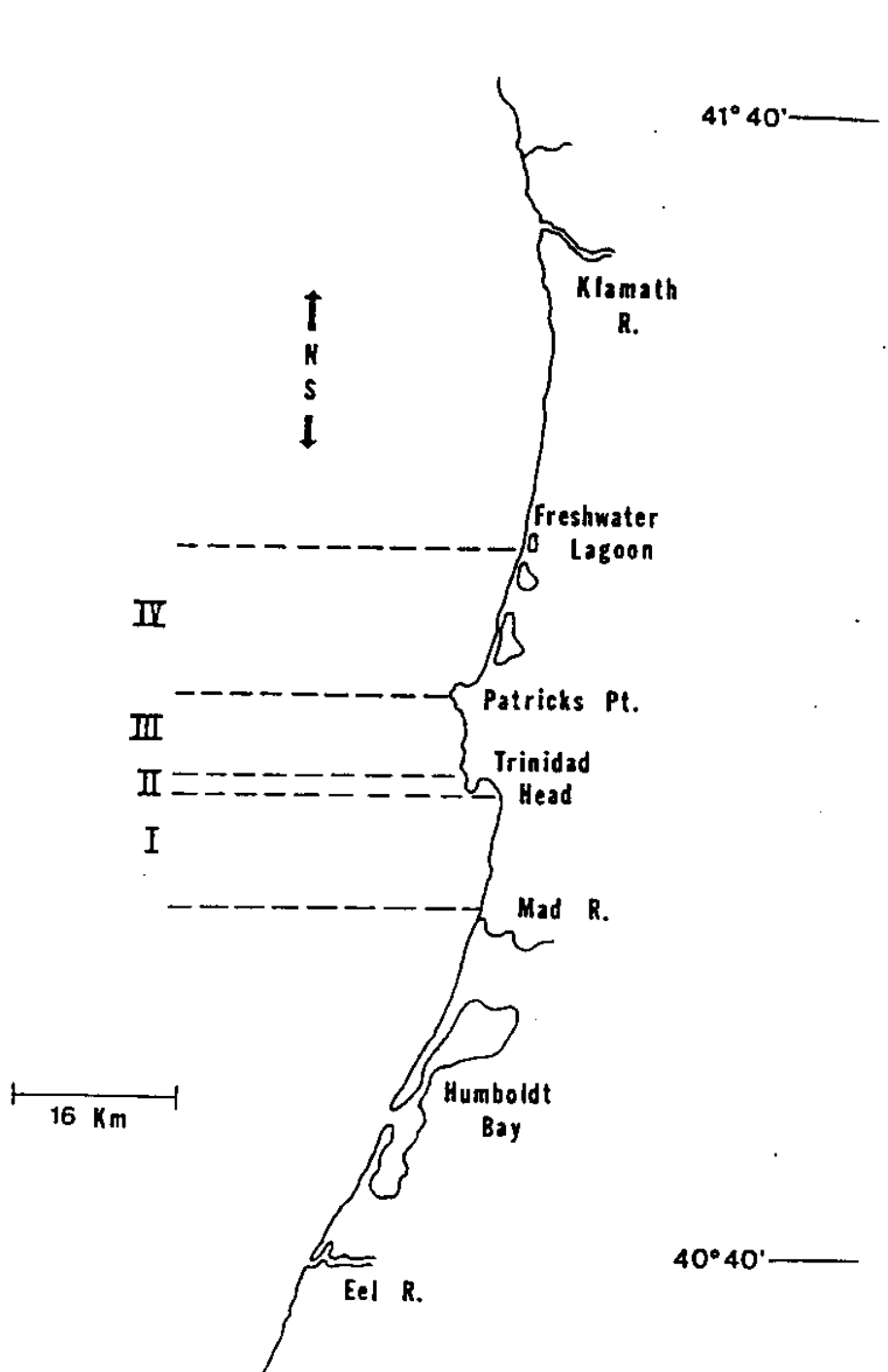


Figure 1. Map of release locations in northern California. Physical characteristics of the four distinct release locations (I-IV) are briefly described in text.

directed movement during winter (Figure 3); all tests were non-significant ($p > .05$). In contrast, individual movement vectors during the spring suggested highly directed inshore movements, particularly in Area II (Figure 4); summed resultant vectors for Areas II and III, and for all areas combined (Figure 5), were indeed significantly directed inshore ($p < .05$). However, because tag recovery data were clearly biased toward recovery of crabs that had moved inshore during the

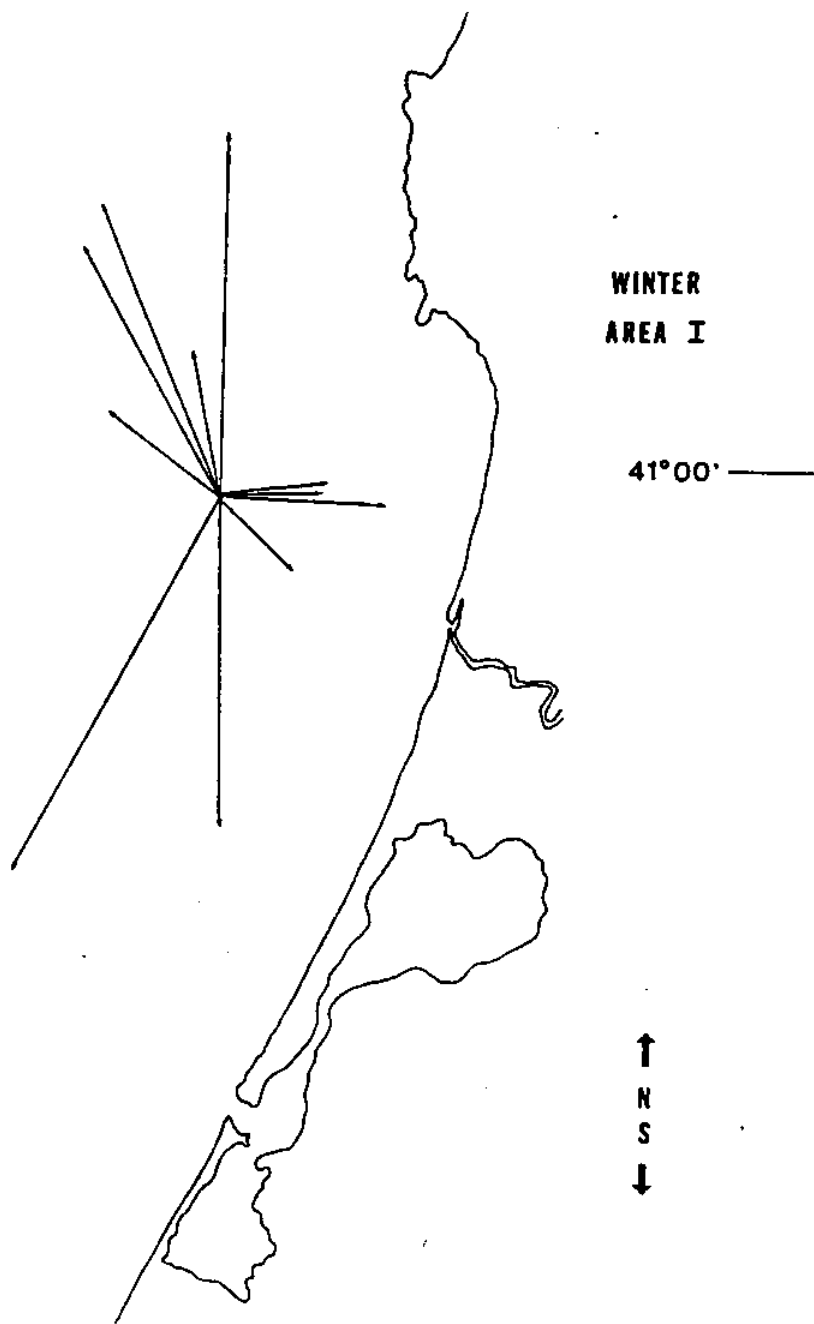


Figure 2. Winter movement vectors for female Dungeness crab tagged and released from Area-I (see Figure 1). Note that, although the majority of movement vectors appear to suggest a general northward trend, circular statistics used to test for such a trend failed to support an hypothesis of directed winter movement. Vectors are drawn to scale of coastline.

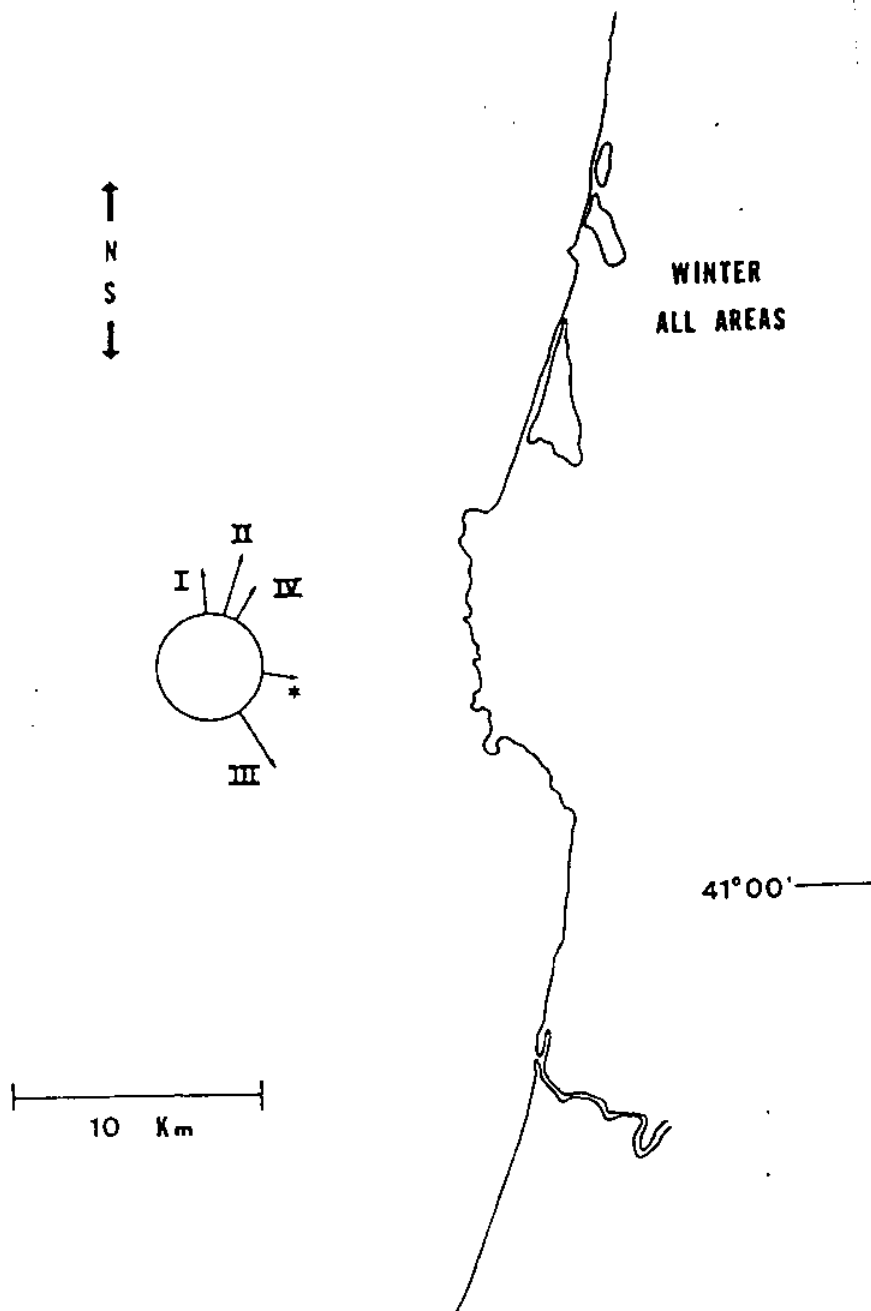


Figure 3. Summed resultant vectors for female Dungeness crabs tagged and released in Areas I-IV, and for all Areas combined, that were recovered during winter months. Note that, although three of the summed resultant vectors are in a northern direction, there were no statistically significant directional movements in any of the four areas or for all areas combined. Movement vectors are on same scale as coastline and asterisk denotes combined data.

spring, these statistical tests were of dubious validity; the test assumptions of randomly distributed fishing effort were clearly violated by the concentration of fishing effort in shallow sandy areas during this season.

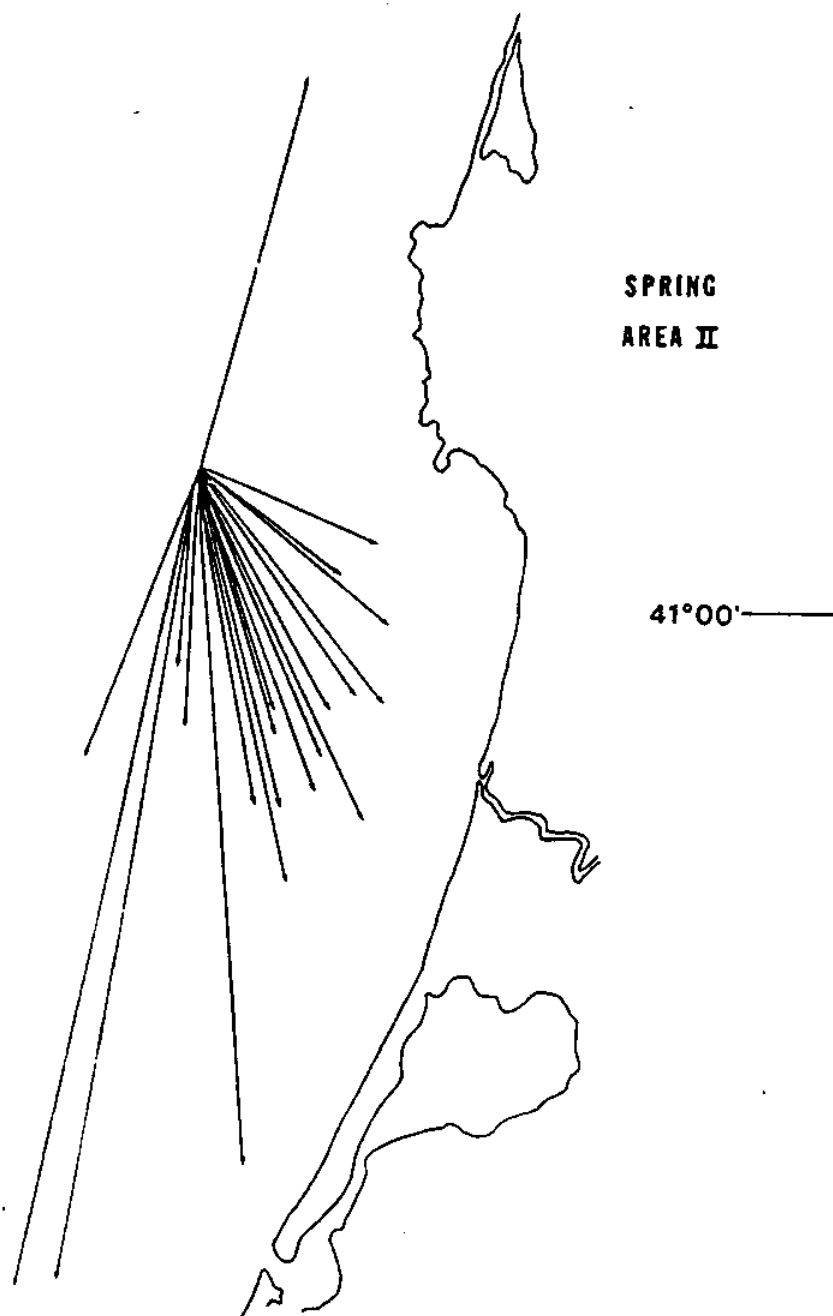


Figure 4. Individual spring movement vectors for adult female Dungeness crabs tagged and released in Area II (see Figure 1). Note that all but one of the vectors have an either south or inshore direction. However, recovery locations for these tagged crab also corresponded with locations of most concentrated fishing effort during the spring months. Vectors are drawn to scale of coastline.

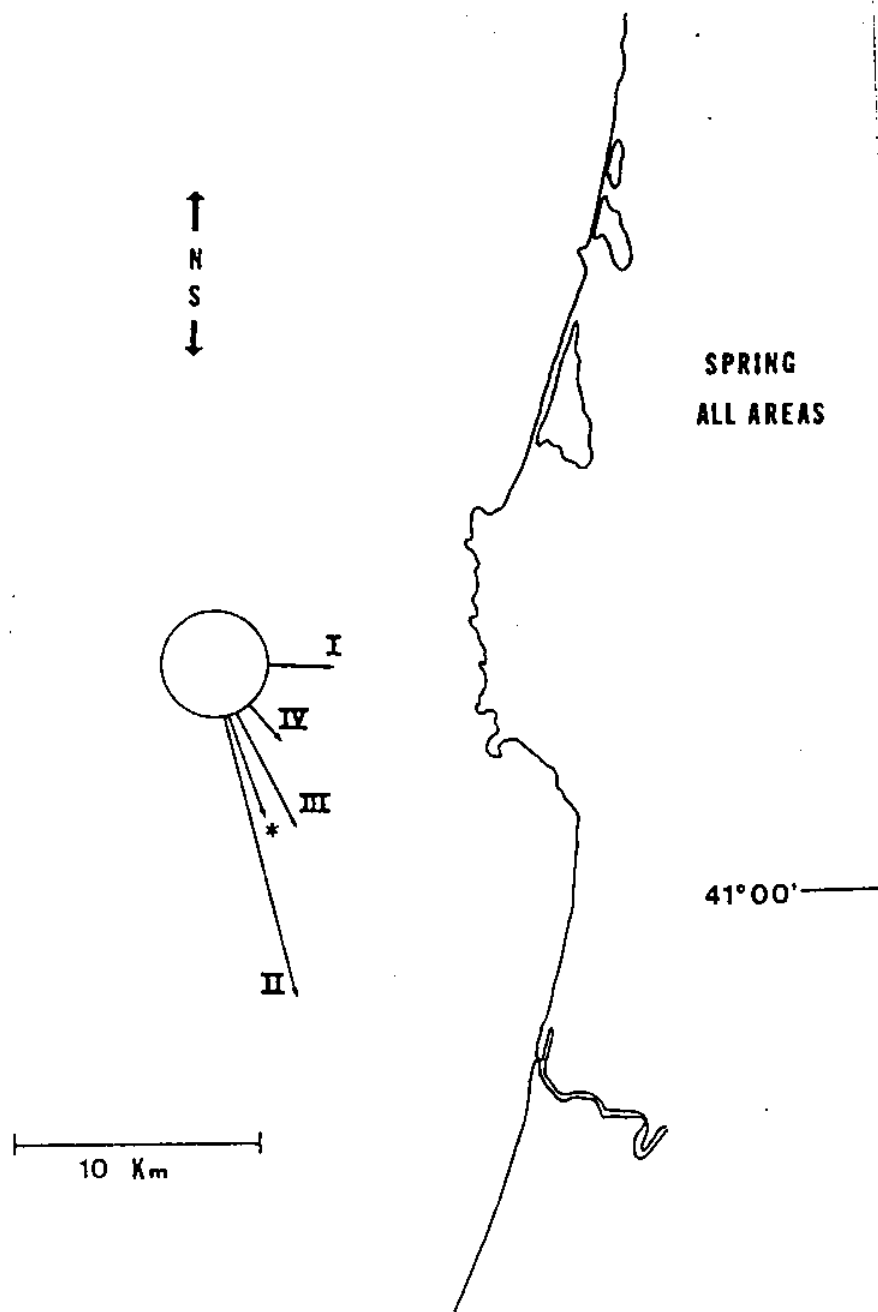


Figure 5. Summed resultant vectors for movements of crabs in areas I-IV and for all areas combined (asterisk) during spring months. Note that, three out of the four summed vectors for distinct release locations suggest movement south and inshore, and that the summed vector for all areas combined is also in a south and inshore direction. Movement vectors in areas II and III were significant, as was the movement vector for all areas combined. However, recovery locations for crabs generally corresponded to areas of concentrated fishing effort, thus invalidating an implicit assumption that fishing effort is randomly distributed. Vectors are drawn to scale of coastline.

Annual molting probabilities

Commercial gear selection. A comparison between numbers of adult females retained at size in commercial traps and in nonselective traps dramatically illustrated the potential significance of gear selection bias in tag recovery data. This comparison is best reflected in the generated commercial gear selection curve (Figure 6). For the open port commercial trap gear, 50% retention was achieved at 153 mm, and 100% retention began at 155 mm; this is essentially a "knife-edge" selection curve. Below 134 mm carapace width, retention was effectively zero. As an illustration of the potential magnitude of commercial trap size selection bias which could result, consider recovery of two crabs each tagged at 140 mm, one of which molted to 153 mm before recovery. The molted crab would have a commercial gear retention rate of 50%, whereas the nonmolted crab would have a retention rate of about 0.3%; the ratio of these retention rates is about 150:1. However, as previously mentioned, the above calculation assumes that all traps were fished for two days or longer before being pulled. The alternative method which we used to calculate relative recovery rates (based on empirical recovery data, not the generated selection curve) showed that the crab that molted to 153 mm would have been about 6 times more likely to be recovered than the crab that had remained at 140 mm.

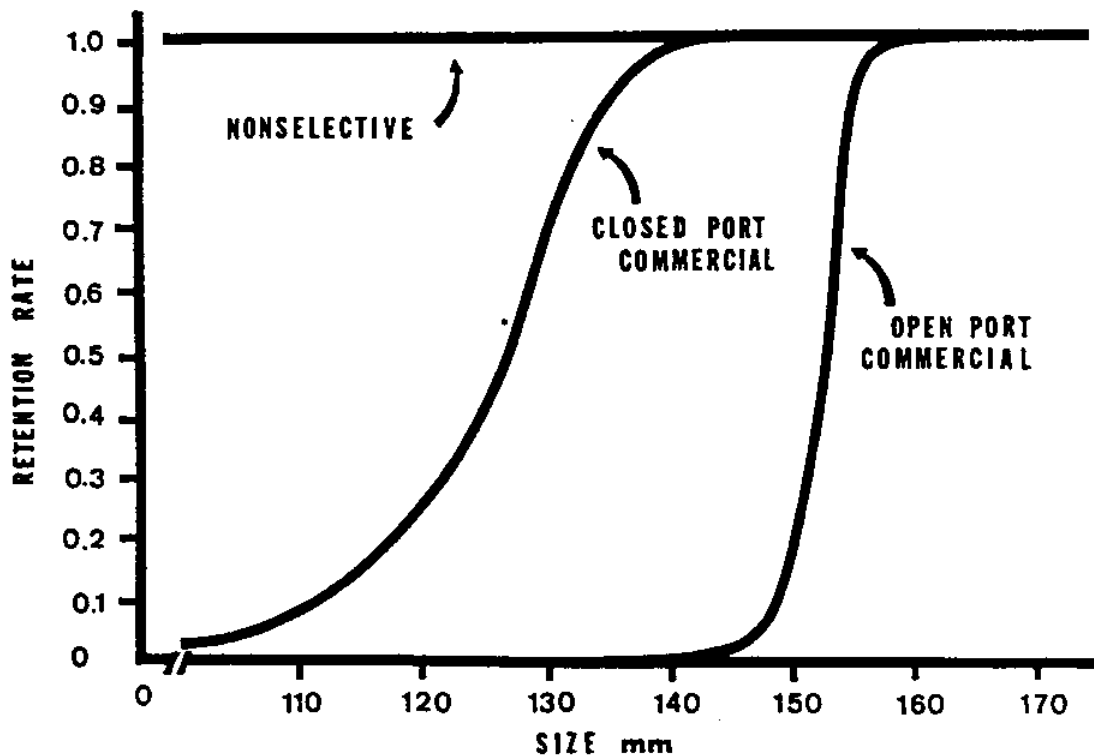


Figure 6. Selection curves for female Dungeness crabs captured by open port commercial crab traps, closed port commercial traps, and nonselective experimental traps (modified as described in text). Size is carapace width, excluding tenth anterolateral spines. Note that selection curves for males would not be the same as for females because of different width/depth relation.

Tag retention. The text table below presents tag loss data for female crabs that molted in the absence and in the presence of adult male crabs. Tag loss through molting was not significantly different between the two groups. Laboratory tag retention rates averaged about 0.90 for both groups combined and 95% confidence limits for tag retention rates were from 0.84 to 0.96. However, because the period from tagging to molting was so brief in the laboratory, these figures should probably be regarded as upper limits for tag retention rates.

	<u># Tagged</u>	<u># Retained Tag</u>	<u>Retention Rate</u>
Male Present	42	37	0.881
Male Absent	48	44	0.917
Pooled	90	81	0.900

An estimator for annual molting probabilities. An estimator that attempts to account and adjust for the biases of gear selection and tag loss was developed in Diamond (1983) and is presented below:

$$\hat{P}(x) = \frac{1}{1 + \frac{N(x) \cdot F(x+\delta) \cdot \hat{T}}{M(x) \cdot F(x)}} \quad (1)$$

where:

- $P(x)$ = annual probability of molting from size x ;
- $N(x)$ = number of crabs recovered after one molting season at large that were tagged at size x and had not molted ;
- $M(x)$ = number of crabs recovered after one molting season at large that were tagged at size x and had molted ;
- $\delta = \delta(x)$ = (expected) molt increment for a crab tagged at size x ;
- $F(x)$ = recovery rate for crabs of size x ;
- $F(x+\delta)$ = recovery rate for crabs at size $x+\delta$ (i.e. for crabs that molted to size $x+\delta$ from size x);
- \hat{T} = (estimated) tag retention rate through one molt.

The form of this estimator is such that, in practice, it is not necessary to separately estimate the recovery rates $F(x)$ and $F(x+\delta)$; what is required is an estimate of the ratio of the two recovery rates [i.e. $F(x+\delta)/F(x)$].

In the numerical examples which follow, we attempt to illustrate the manner in which this estimator accounts for biases of crab trap size selection and tag loss, and to show the substantial impact that failure to account for such biases could have on estimates of annual molting probabilities. All examples are based on the following hypothetical set of data:

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$$\hat{P}(x) = \frac{1}{1 + \frac{N(x) \cdot F(x+\delta) \cdot T}{M(x) \cdot F(x)}} \quad (1)$$

where:

$P(x)$ = annual probability of molting from size x ;

$N(x)$ = number of crabs recovered after one molting season at large that were tagged at size x and had not molted ;

$M(x)$ = number of crabs recovered after one molting season at large that were tagged at size x and had molted ;

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$$x = 140 \text{ mm}; N(x) = 8; M(x) = 18; x+\delta = 153 \text{ mm}.$$

Thus, 26 crabs $[N(x) + M(x)]$ were recovered that had been tagged at an initial size of 140 mm (x); of these 26 crabs, 18 $[M(x)]$ had molted to a size of 153 mm ($x+\delta$).

Example 1. No commercial gear selection.

In the absence of commercial gear selection, all molted and nonmolted crabs would be recovered at the same rates, regardless of size, so that $F(x) = F(x+\delta)$ and $F(x+\delta)/F(x) = 1$. If there is no tag loss (i.e. $T = 1$), then equation (1) reduces to the simple and intuitive estimator of annual molting probability: the ratio of the recovered crabs that molted to the total number of crabs that were recovered. (This is the "naive" estimator discussed in Hankin et al., this Symposium). That is,

$$\begin{aligned} \hat{P}(x) &= \frac{1}{1 + \frac{N(x)}{M(x)}} = \frac{M(x)}{M(x) + N(x)} \\ &= \frac{18}{18 + 8} = 0.69 . \end{aligned}$$

The effect of correcting for negative bias due to tag loss is to slightly increase the resulting estimate of annual molting probability. For example, if $T = 0.7$, then

$$\begin{aligned} \hat{P}(x) &= \frac{1}{1 + \frac{N(x) \cdot \hat{T}}{M(x)}} = \frac{M(x)}{M(x) + N(x) \cdot \hat{T}} \\ &= \frac{18}{18 + 8 \cdot (0.7)} = 0.76 . \end{aligned}$$

Example 2. Size selective commercial recovery gear.

For $x = 140$ mm and $x+\delta = 153$ mm, our empirical estimates of recovery rates gave:

$$F(x+\delta)/F(x) = 6.05 .$$

Using the same recovery data as above and assuming that there is no tag loss ($T=1$), the molting probability estimator gives:

$$P(x) = \frac{1}{1 + \frac{N(x) \cdot F(x+\delta)}{M(x) \cdot F(x)}} = \frac{1}{1 + \frac{8}{18} \cdot (6.05)} = 0.27 .$$

Thus, adjustment for size selection bias results in a substantial reduction in the estimate of annual molting probability from 0.69 (Example 1) to 0.27. Correcting for tag loss would again slightly increase the estimate of annual molting probability. For this same example, if $T = 0.7$, then the molting probability estimate would be 0.35 (which should be compared with the biased estimate of 0.76 in example 1).

Discussion

Gotshall (1978), based on visual inspection of plotted tag recovery data, proposed that adult male Dungeness crabs moved northward in northern California during winter months, and then southward and inshore during the spring. Our analyses of movement data from female Dungeness crabs in northern California suggest that the apparent trend observed by Gotshall was probably not statistically significant; winter movements of females had no statistically significant directional tendency. Regardless of the statistical conclusion regarding winter movements, however, analyses of these movements were not seriously biased by the distribution of fishing effort. With the exception of crabs that may have moved into very deep waters (> 75 m), the distribution of fishing effort during the winter was such that movements of tagged crabs in all directions should have been equally likely to have been recorded. In such a case, the use of circular statistics to evaluate the significance of possible tendencies of crabs to move in particular directions seems a substantial improvement over qualitative and subjective visual methods (as used by Gotshall).

There is no question in our minds that many adult female Dungeness crabs move inshore to molt and then mate with adult males in shallow sandy areas during the spring in northern California. However, the fraction of the female population that engages in such movements remains unknown. Because fishing effort was concentrated in shallow waters during the spring months, movements of females that had moved to deeper waters or remained offshore would not have been recorded in proportion to their frequency had they taken place. However, if substantial numbers of female crabs remained offshore during the spring, or actually moved further offshore, we are reasonably confident that they would have to be females that were not destined to molt and mate during the spring molting/mating season. Because it is not necessary for adult females to molt and mate each year in order to produce and extrude viable egg masses in the fall (Diamond 1983; Hankin et al., this Symposium), it is indeed possible that some females may remain offshore during the spring. If these females were destined to molt, one would expect aggregations of legal-sized males in offshore locations and associated concentrations of fishing effort; these are not observed in the northern California fishery. Given these considerations, we feel confident that there is indeed an inshore spring mating migration among female crabs that are destined to molt and mate. Definitive proof that such a migration of females takes place for all females, regardless of molting state, would require an expensive large-scale sampling program in which vessels were chartered to fish at all depths during the spring months so as to ensure that fishing effort (for tag recoveries) would be uniformly distributed. Although this kind of approach has been successfully applied in small-scale localized crab tag recovery projects (see Hyland et al. 1984), we are hesitant to advocate such an approach for studies of movements of Dungeness crabs in most West Coast areas.

In contrast to a relative inability to adjust for possible biases due to the distribution of fishing effort, it seems possible (theoretically at least) to attempt adjustment for biases resulting from commercial crab trap size selection and tag loss through molts. Above all else, it seems most important to fish nonselective crab traps alongside commercial crab traps so as to allow assessment of the degree of size selection bias. Several advantages result from comparisons of size frequencies of crabs captured in the two gear types. First, the minimum size of full vulnerability to the commercial crab traps can be readily established. For crabs exceeding this size of first full vulnerability to commercial gear, it is unnecessary to make any adjustments for commercial gear size selection in analysis of tag recovery data for molting probabilities (or survival rates; see Hankin et al., this Symposium). Second, use of nonselective traps ensures that significant numbers of small crabs will be captured and allows for the tagging of these small crabs. Finally, length frequency analysis of data collected from nonselective traps can lead to a meaningful assessment of stock size composition; this is virtually impossible based on size frequencies collected from commercial crab traps or from commercial crab traps with closed escape ports. Size selection curves in fixed commercial trap gear (Figure 6) have such a steep slope that collected length frequency data have little practical value for animals smaller than the legal size for male Dungeness crabs.

Although the estimator that we developed can in theory account for biases due to size selection and tag loss, there were serious practical problems involved in actual application of the estimator to collected data. First, as pointed out previously, the selective properties of fixed crab trap gear appear to sensitively depend on trap soak time. Traps exhibited their full selective properties only after having been fished for two full days or more without rebaiting. Because early season soak times in northern California were often less than two days, use of the formal fitted gear selection curve generated estimates of molting probabilities (not presented) which were probably biased at least as severely as were "naive" calculations which omitted consideration of possible size selection altogether. Our reliance instead upon empirically-derived relative recovery rates was certainly a preferable alternative to ignoring size selection bias altogether, but it too had practical problems in application. First, we implicitly assumed that recovery rates depended only on size and not on molting history or condition. It is possible that this assumption is false; freshly molted crabs may more aggressively search out food and may enter traps at higher rates than nonmolted crabs. Second, the use of early season data to estimate relative recovery rates was, in part, invalidated by the general trend of increasing soak time for traps as the commercial fishing season progressed and catch rates for legal males dropped. However, during the beach run most traps are once again fished for less than two day soaks. Because most recoveries took place during the early season and during the spring beach run, the overall effect of changing soak time is unclear.

Finally, it is likely that the tag retention rates reported in this paper are overestimates of real tag retention rates. Tagging conditions in the laboratory are obviously more favorable than on board a vessel during a winter storm at sea, and results of laboratory tagging may therefore not give an accurate reflection of tag retention in the field. For example, we observed that tags had migrated away from the

suture line on some recovered crabs that had molted; many of these crabs would probably have lost their tags if they molted a second time. In addition, the length of time from tagging to molting was far shorter for laboratory-tagged crabs than for field-tagged crabs. Tag retention may depend on the degree of development of the newly-forming exoskeleton at the time of tagging. Presumably, this new exoskeleton will be more completely formed by the time molting is imminent (when laboratory tagging took place) as opposed to several months in advance of molting (when field tagging took place). Improved field-derived estimates of tag retention rates could probably be derived from analyses of data collected from a double tagging study. If crabs were tagged with anchor tags at both the right and left sides of the posterior epimeral suture, then the relative numbers of molted and nonmolted recoveries which retained one and two tags could be used to estimate tag loss through molting and to distinguish such loss from tag loss not associated with molting. We hope to carry out such a double tagging study on adult female Dungeness crabs in the future.

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