

## Effort Dynamics of the Northern California Dungeness Crab (*Cancer magister*) Fishery

LOUIS W. BOTSFORD

*Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA*

RICHARD D. METHOT JR.<sup>1</sup>

*Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, USA*

AND WARREN E. JOHNSTON

*Department of Agricultural Economics, University of California, Davis, CA 95616, USA*

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Knowledge of the dynamic response of fishing effort to abundance is essential to a complete understanding of the cycles in catch in the northern California Dungeness crab fishery. In this fishery there is a lagged response of harvest rate to changes in abundance that is caused either by a time lag in fishermen entering and leaving the fishery following changes in abundance, a lag in market expansion and contraction following changes in abundance, or a combination of both. The time lag in this response appears to have decreased over the past 30 yr. This lagged response is a potential cause of the cycles. However, neither of the two potential cyclic mechanisms examined here, a predator–prey mechanism (with man as the predator) and a price-dependent escapement mechanism (with price dependent on past catch), is a cause of these cycles. Although time-varying effort does not cause the cycles, it does have a substantial effect on the resulting catch record and population dynamics. If there is a density-dependent recruitment mechanism in this population as proposed earlier, the presence of this lagged response would cause the period of observed cycles to be longer than would be expected on the basis of population dynamics alone. Hence, previous estimates of the expected period of cycles from various population mechanisms are low. Removal of this response is a potential means of stabilizing this fishery.

*Key words:* effort, Dungeness crab, harvest rate, predator–prey, price, stability, age, cycles

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Une connaissance de la réponse dynamique de l'effort de pêche par rapport à l'abondance est essentielle à la compréhension complète des cycles de capture du crabe dormeur dans la Californie septentrionale. Dans cette pêche, il y a un décalage entre les variations de l'abondance et le taux de capture, probablement attribuable soit à un décalage entre le temps que les pêcheurs commencent et finissent la pêche après les changements dans l'abondance, ou soit à un décalage dans l'expansion et le resserrement du marché après les changements dans l'abondance, soit à une combinaison des deux facteurs. Le retard de la réaction semble avoir diminué au cours des 30 dernières années. Cette réaction décalée est une cause potentielle de ces cycles. Toutefois, ni l'un ni l'autre des deux processus cycliques potentiels, soit une relation prédateur–proie (où l'homme est le prédateur) et une relation d'écoulement dépendante du prix (où le prix dépend des prises antérieures) n'est la cause de ces cycles. Quoique l'effort variant avec le temps ne cause pas ces cycles, il a une incidence importante sur le total des prises et la dynamique des populations. Si un processus de recrutement dépendant de la densité existe dans cette population, comme il a déjà été suggéré, la réaction décalée ferait que la période des cycles observés serait plus longue que ne le portait à croire

<sup>1</sup>Current address (R.D.M.): National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

la seule dynamique de la population. Donc, les évaluations antérieures de la période attendue des cycles d'après les divers processus relatifs aux populations sont faibles. L'élimination de la réaction est un moyen potentiel de stabiliser la pêche.

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THE catch record of the northern California Dungeness crab (*Cancer magister*) fishery is composed of cyclic fluctuations whose cause is not known. Although previous studies have focused on density-dependent (Botsford and Wickham 1978; McKelvey et al. 1980; Botsford 1981; McKelvey and Hankin 1981) and environmental (Peterson 1973; Botsford and Wickham 1975) phenomena as potential causes, little attention has been paid to changes in effort as a possible underlying mechanism. Methot and Botsford (1982) have recently shown that fishing mortality varies in a regular pattern with regard to catch. Fluctuations in effort are of interest not only because they are a potential cause of cyclic fluctuations in catch, but also because knowledge of the factors that determine effort each year (i.e. the dynamic behavior of fishermen, processors, and markets) is required to understand population dynamics adequately and to formulate fishery management policy.

The analysis described here was undertaken to (a) describe the dynamic response of effort to abundance and (b) determine the effect of that response on the fishery. First, the behavior of this fishery and the available data are described. Then possible mechanisms underlying the dynamic response of harvest to abundance are inferred by comparing actual behavior with expected behavior from proposed likely mechanisms. The possible effects of this response on population stability are then evaluated for several different assumed descriptions of population dynamics. In this context, the effect of the harvest response on the previously developed model with density-dependent recruitment is determined.

### The Fishery

While the general behavior of the northern California Dungeness crab fishery can be readily described, the mechanisms that actually determine effort in the fishery are poorly known. The fishing season extends from December through June or July and only males larger than 159-mm carapace width can be landed. In most years more than 70% of the legal crabs are landed (Methot and Botsford 1982). Most of the landings are made in the first few months of each season. This is especially true in more recent years. As abundance has fluctuated there have also been fluctuations in price, number of boats, and actual harvest rates. The factors that govern the entry and exit of boats in the fishery during each season govern the fraction of crabs harvested each year.

There are a number of economic factors that could affect the number of crabs landed each year. The price at the beginning of the season is based on negotiations between fishermen and processors, and prices also change during the season. Processors have limited the number of boats and their landings during the recent periods of high abundance and the period of high abundance in the 1960s (D. Gotshall, P.O. Box 98, Avila Beach, CA 93424, personal communication). Aver-

age seasonal price generally varies inversely with catch and has increased over the past 30 yr, even when deflated to 1967 dollars by the consumer price index (Fig. 1).

The total number of boats landing crabs each season varies positively with catch with a small lag and has also increased over the past 30 yr (Fig. 2). However, this lag appears to have decreased in recent years. The fluctuation in number of boats in the fishery is related to the high mobility of the fleet; most of these boats also fish salmon and albacore. The number of boats in the fishery unfortunately is not necessarily a direct indication of annual fishing mortality. The actual pattern of harvest rate [based on annual catch and estimates of preseason legal abundance (Methot and Botsford 1982)] is also shown in Fig. 2.

### Response of Harvest Rate to Abundance

The way in which harvest rate responds to changes in abundance can have a profound effect on the population. To interpret this response better, we first review the expected effects of the several different bioeconomic mechanisms known to be operating in the fishery, then compare the actual harvest rate record to these theoretical possibilities. From this comparison we can infer the possible mechanisms operating in this fishery.

Behavior of the fishery can be viewed in terms of a static relationship that changes only very slowly (e.g. with long-term changes in price) and a dynamic relationship that reflects the way in which the static "equilibrium" is reached after rapid changes in abundance. If the fishery were given enough time (i.e. a long enough season), the static equilibrium would be approached. At that time, a reasonable model would be that the value of a day's catch would equal the cost of obtaining that catch. Remaining abundance (escapement) would then be inversely proportional to price. From Fig. 1 price varies inversely with abundance. Hence escapement would increase with increasing abundance. The change in harvest rate with abundance would be

$$(1) \quad H = 1 - E(A)/A$$

where  $H$  = harvest rate,  $A$  = abundance,  $E(A)$  = escapement at abundance  $A$ . The form of this static, equilibrium relationship between harvest and abundance is determined by the relationship between price, abundance, and escapement. For example, if the inverse relationship between price and abundance caused escapement to increase linearly with abundance, harvest rate would be constant. This relationship will change with long-term changes in price. If real price increases more rapidly than operating costs, escapement levels will decrease; hence harvest rates will increase.

Although this static equilibrium can be at least conceptually defined, it may rarely actually be reached because seasons are

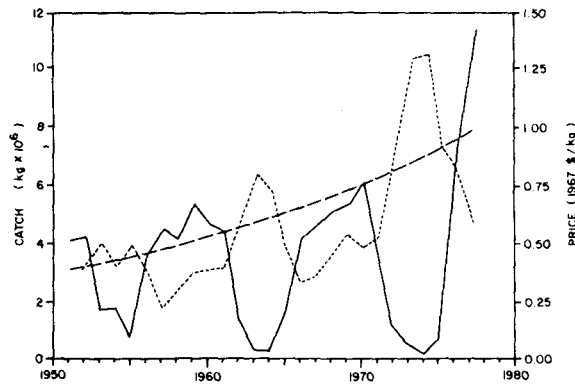


FIG. 1. Annual catch (—) and price (---) scaled for inflation (i.e. 1967 U.S. dollars). The exponential trend that was fit through these data and used to compute adjusted price is also shown (-----).

not infinitely long, and fishing capacity and market capacity can limit removal rates. In brief, there may not be enough effort to reach equilibrium before the season closes. If there is not enough fishing capacity (i.e. total boats or total crab pots), rapid increase in abundance will result in initial low annual harvest rates that increase as more boats enter the fishery. Conversely, a rapid decrease in abundance will produce an initial increase in annual harvest rate followed by a decline. The overall effect would be counterclockwise rotation of the plot of harvest rate and abundance as shown in Fig. 3.

The precise dynamic behavior of this mechanism depends on such factors as price, opportunities in other fisheries, and the capacities of boats in the fleet. If price is high, one would expect that fishermen would maintain the ability to enter the fishery rapidly when abundance increases. Hence a long-term increase in mean price would be expected to result in less dynamic variation about the static equilibrium (i.e. less lag).

In addition to the influence of a lagged response of fishing capacity, a lagged market capacity can affect the harvest rate response in a similar way. As described earlier, processors change prices within seasons and also limit landings directly. During most years there are very few processors buying crab in each port. Few buyers operating under imperfectly competitive conditions characterize an oligopsonistic market. Each is keenly aware of the actions and reaction of the other buyers in the industry. Processing firms can expand and contract their activities in selected fisheries depending on potential profitabilities. Thus, they may respond to available abundance (supplies) in ways to maximize profits, entering a fishery when attracted by high profits, and vice versa. This behavior affects the effort response of the fishery. Suppose that the demand for crab by processing firms in an industry can be represented by the lower-most demand curve (identified as  $D_{normal}$ ) shown in Fig. 4. If abundance (supply) is relatively low, price will be higher and quantity demanded lower, than under conditions of high abundance. Thus, if abundance has been low and then increases, processors will offer lower prices and purchase larger quantities. Other firms may then be attracted by the profitability of processing crab; their entry essentially shifts the demand curve to the right,

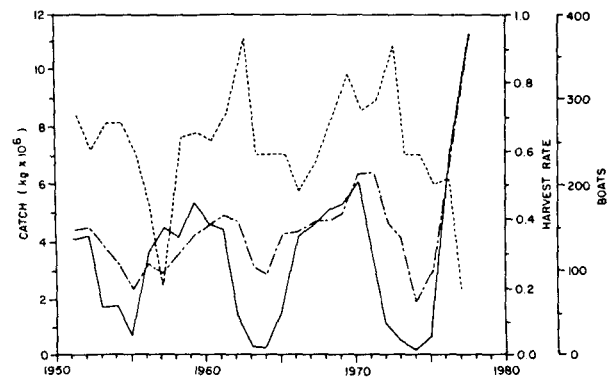


FIG. 2. Annual catch (—), total number of boats making deliveries (-----), and harvest rate (---) computed from independent estimates of preseason abundance for the northern California crab fishery (Methot and Botsford 1982). (Note: abundance estimates for several years of high abundance (1957, 1966, 1977) were not significant. Hence, although abundance in these years is known to be very high and the values of harvest rate therefore low, the exact values of harvest rate used here are somewhat arbitrary.)

increasing price paid to fishermen who respond to the price incentive by harvesting increased quantities. When abundance declines, the supply curves may shift leftward from  $S_{high\ abundance}$  to  $S_{low\ abundance}$ , along the same demand curve. Prices continue to increase until enhanced profitability is exhausted, the marginal firms or plants exit the industry, and the demand for crab from the fishery shifts back to  $D_{normal}$  from  $D_{expanded}$ . The market contracts, and both prices paid to fishermen and quantity purchased by processors, fall. The dotted time path within Fig. 4 approximates the locus of prices and quantities over time caused by changes in abundance and the behavior of processors.

The effect of this mechanism on the harvest rate dynamics is a decrease in harvest rate following a rapid increase in abundance. As abundance remains high, catch increases because of market development, and harvest rate increases. When abundance decreases rapidly, catch decreases and harvest rate and price increase. As abundance remains low, price gradually decreases as the initial demand curve is approached, and harvest rate decreases. Thus the effect of this mechanism on the harvest rate versus abundance plot is indistinguishable from the response that resulted from a lagged fishing response. (The effect of a processor-imposed limit on landings is essentially the same as that of limited fishing capacity.) It can be distinguished, however, on the basis of the required increase and decrease in price within the high and low abundance periods, respectively. This pattern appears to be present in the high catch periods in the late fifties and sixties and the low catch periods in the early sixties and seventies (Fig. 1).

A third potential dynamic mechanism is of a completely different nature. It would occur under conditions such that fishing capacity was high enough to fish the legal population down each year to the price-determined level of escapement. However, a lag in the response of price to abundance would prevent the simple, static equilibrium described earlier. If price did not respond immediately to abundance, the response

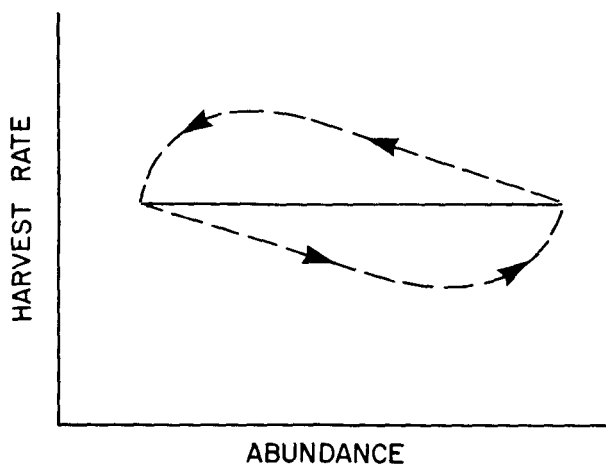


FIG. 3. A typical example of the static, equilibrium relationship between harvest rate and abundance (—) and the path that a fishery with a lagged effort response would follow (---).

of harvest rate to changes in abundance would be altered in a way that differs from those described previously. The response of price to changes in abundance could be delayed for reasons such as large stocks of frozen crabs held over from previous years.

A rapid increase in abundance with no change (or a slow change) in escapement (because of the slowly changing price) would lead to an initial increase in harvest rate followed by a decline to equilibrium as price decreased. The converse would occur following a rapid decrease in price, resulting in the clockwise rotation of the harvest rate, abundance plot shown in Fig. 5.

#### MECHANISMS PRESENT IN THE FISHERY

The plot of observed harvest rate and abundance (Fig. 6) does not follow a line of constant harvest rate but rather appears to rotate in a counterclockwise direction. Rapid increases in abundance (e.g. 1957, 1966) lead to low harvest rates, and rapid decreases in abundance lead to high harvest rates (e.g. 1962, 1972). As stated earlier, it is difficult to discern between a lag in fishing capacity and a lag in market capacity as the underlying cause of this behavior. However, the increase in price during periods of high abundance and decrease in price during periods of low abundance is commensurate with a lagged market response. As the observed behavior may be caused by either mechanism, they will be referred to collectively as a lagged effort response in the remainder of this paper.

The higher than usual value of the 1976 harvest rate is commensurate with the increase in real price of crabs. This could have resulted from a more rapid response of effort to increasing abundance because crabs were more valuable.

Any effect of lagged price on escapement is not significant enough to be apparent. The presence of a lagged response of price can be tested for in the price and catch data in Fig. 1. The correlation between adjusted price (1967 dollars with exponential trend removed, Fig. 1) and crab catch in previous years is significant at the 0.05 level at lags of zero and 1 yr

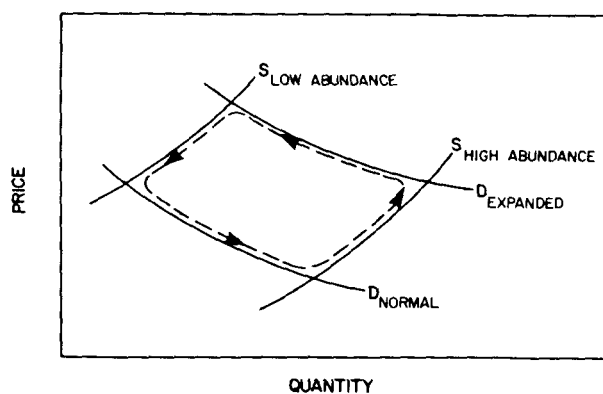


FIG. 4. Proposed changes in supply and demand curves with abundance. When moving between low and high equilibria the system moves initially along the appropriate demand curve (---). This curve shifts as high or low abundance is maintained.

but not at 2 yr ( $-0.739$  and  $-0.453$  and  $0.063$  at lags of zero, 1, and 2 yr, respectively). However, this correlation could stem from a negative correlation coefficient in year zero and highly autocorrelated catch. The partial correlation coefficient implies that the latter is the case. The partial correlation between price at time  $t$  and catch at time  $t$  given catch at time  $t - 1$  is significant but the partial correlation between price at time  $t$  and catch at time  $t - 1$  given catch at time  $t$  is not significant ( $-0.590$  and  $-0.085$ , respectively).

#### Effect of Harvest Response on Fishery Behavior

The description of the response of harvest rate to changes in abundance can now be combined with descriptions of possible population behavior to determine the effect of harvest response on population level and the fishery as a whole. We will determine whether the harvest response is the cause of the observed cycles through either a predator-prey mechanism or price-dependent escapement with a lagged response of price to abundance, then evaluate the effect of harvest response on a population with density-dependent recruitment.

#### PREDATOR-PREY CYCLES

Predator-prey cycles with man as the predator involve the following sequence of events: abundance increases, effort increases after a certain lag, abundance then decreases as a result of increased effort, effort decreases in response to decreased abundance after a time lag, and finally, because of decreased effort, abundance increases to begin the next cycle. Both a lagged response of effort to abundance and a lagged response of abundance to effort are required. Mechanisms of this kind have been associated with cyclic behavior in other exploited populations [e.g. Gulland (1974), p. 17; Wilen (1976); Bell et al. (1977)].

Because a lagged response of effort to abundance has been shown to exist, we shall evaluate whether that mechanism can cause the observed cycles in a predator-prey fashion. Abundance each year will be the sum of recruitment and the result of escapement in the previous year. This can be represented by:

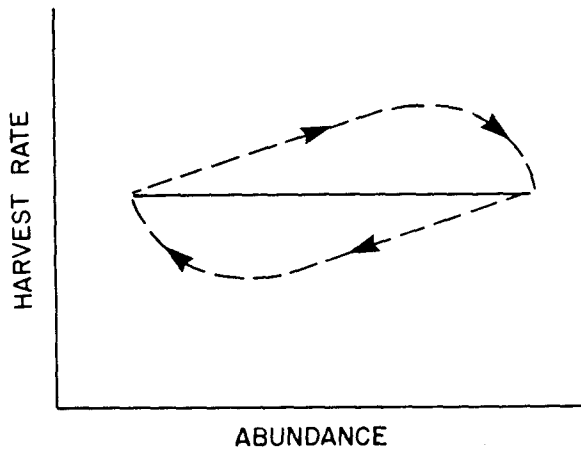


FIG. 5. The static, equilibrium relationship between harvest rate and abundance (—) and the path that a fishery with price-dependent escapement with price dependent on past catch would follow (---).

$$(2) \quad A_t = A_{t-1}(1 - H_{t-1})G + R_t$$

where  $A_t$  = abundance in year  $t$

$H_t$  = harvest rate in year  $t$

$G$  = total change in biomass during a year (includes natural mortality and growth)

$R_t$  = recruitment to legal size during the year prior to fishing season  $t$ .

For this simple representation, age structure is not included. Thus the major simplification of the model is that  $G$  is assumed constant when it would in general change with age structure.

This equation can be written in terms of the rate of increase

$$(3) \quad r = A_t/A_{t-1} = (1 - H_{t-1})G + R_t/A_{t-1}$$

In a cyclic population, changes in the values of  $H_t$  and  $R_t$  must cause the population to shift repeatedly between increasing and decreasing population size ( $r > 1$ ,  $r < 1$ ). Thus, whether this population is cyclic depends on the dependence of harvest rate on past abundance (described earlier) and the dependence of recruitment on abundance. We now evaluate the combination of harvest rate behavior described earlier with two different assumptions regarding recruitment: constant recruitment rate and recruitment rate proportional to abundance. (Density-dependent recruitment is evaluated in the next section.)

If recruitment rate is proportional to population size, in predator-prey cycles the population will increase from low levels because decreasing harvest rate is allowing a larger population to build up. If this were happening, there would be greater escapement at lower abundance. From Fig. 7 this is not the case. Higher escapement occurs at higher abundance.

If recruitment rate is constant in predator-prey cycles, the change in harvest rate itself must cause the shift between an increasing and a decreasing population. This does not appear to be the case because of the way that abundance changes. At low levels harvest rate drops from near 0.9 to near 0.5 with no change in abundance, then abundance suddenly increases.

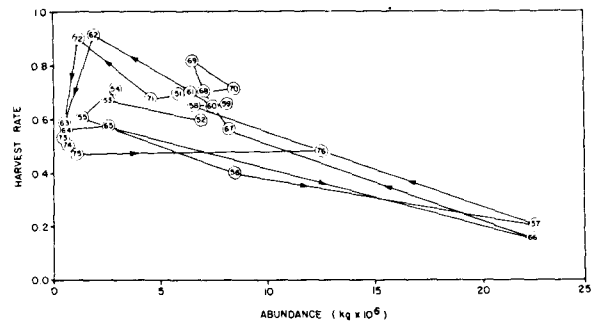


FIG. 6. Actual annual harvest rates plotted versus actual abundance for the northern California Dungeness crab fishery. (Because abundance estimates for 1957 and 1966 were not significant, the exact position of these points is somewhat arbitrary. However, abundance was unusually high and harvest rate was unusually low.)

There is again no gradual increase in abundance evident in the escapement at low levels.

The only remaining alternative is that recruitment is higher at low population levels and vice versa (i.e. density-dependent). Again the lack of gradual increase in population level (escapement) at low levels implies that for this mechanism to be significant a lagged response of recruitment to abundance is required. However, even if that were the case, it does not seem likely that the slight changes in harvest rate seen here are enough to be controlling abundance. The changes in harvest rate at high abundance levels are not large enough to cause the observed declines in abundance. Thus, even though a lagged recruitment response may be present, it does not appear to interact with harvest rate to cause predator-prey cycles.

From these considerations we can conclude that changes in harvest rate in response to abundance are not the primary cause of fluctuations in abundance in a predator-prey fashion. However, we have not discounted the possibility that they may influence population behavior significantly by exacerbating instability caused by other mechanisms.

#### PRICE-DEPENDENT ESCAPEMENT WITH LAGGED PRICE RESPONSE

Though there was little evidence for a lagged response of price to past catch or abundance and the behavior of price-dependent escapement with a lagged price response did not appear to be dominant in Fig. 6, analysis of stability of this mechanism is presented briefly because it may apply to this fishery in the future or to others. If escapement depended inversely on price, as described earlier, and price was influenced by previous catch (e.g. due to storage of past catch by processors and marketers), then catch could be cyclic. As abundance increased, high catch would lead to low prices which would result in high escapement and low catch. When abundance decreased, low catch would eventually lead to high prices which would result in low escapement and high catch, and the cycle would then repeat.

To analyze stability of this mechanism, we assume that escapement each year depends (possibly in a nonlinear fashion) on a weighted sum of total catch in previous years.

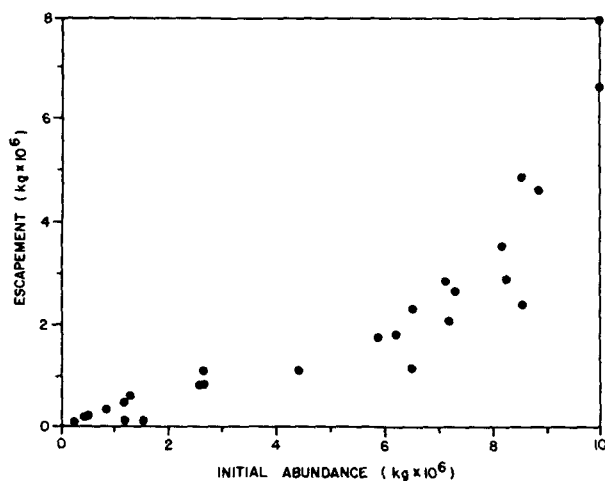


FIG. 7. Annual escapement and initial abundance estimates for the years 1955 through 1976 in the northern California Dungeness crab fishery.

$$(4) \quad (1 - H_t) A_t = g \left[ \sum_{s=1}^T k_s H_{t-s} A_{t-s} \right]$$

where  $k_s$  = a constant specifying the relative effect of catch in the  $s$ th previous year on escapement in the current year ( $s = 1, 2, \dots, T$ ). In the crab fishery, for example,  $g$  would be an increasing function of its argument (i.e. as catch in previous years increases, market price is depressed and escapement increases).

By defining catch to be

$$(5) \quad C_t = A_t H_t,$$

we can express the equations (2) and (4) as

$$(6) \quad C_t = Gg \left[ \sum_{s=1}^T k_s C_{t-1-s} \right] - g \left[ \sum_{s=1}^T k_s C_{t-s} \right] + R_t.$$

This expression has the intuitively satisfying interpretation that catch is growth per unit biomass ( $G$ ) times last year's escapement minus this year's escapement plus this year's recruitment ( $R_t$ ). The fact that catch is the weighted difference between two lagged escapements critically affects dynamic behavior of this system.

The derivation of the conditions under which this model would be unstable and the catch record that would result are in the Appendix. The relevant result here is that for a wide range of reasonable forms of the dependence of price on past catch, any unstable cycles produced will be of period two. Intuitive support for this result can be gained from equation (6). Catch depends on the difference between a function ( $g$ ) of past catches at different time lags (time lags in the first term are shifted backward in time by 1 yr with respect to time lags in the second term). Because of this, in the dynamic behavior of this system each lagged catch is approximately cancelled by its corresponding component in the other term. There is only one term left uncanceled, the term involving catch at a lag of 1 yr. Only cycles of period two can result

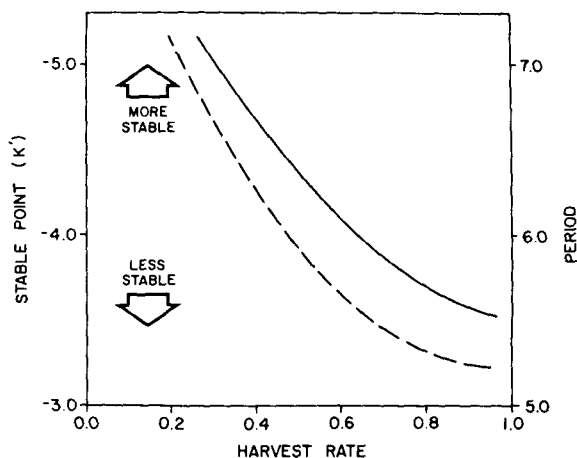


FIG. 8. The stable point  $K'$  (---) and the period of cycles produced (—) for a discrete time model with density-dependent recruitment as the (constant) annual harvest rate is varied.

from a lagged response at 1-yr lag.

A second result of this analysis is that if price depends significantly on the present value of catch in addition to past values of catch, the system becomes much more stable. Because of these two results, it is not likely that this mechanism is causing the observed periodic fluctuations in catch.

#### DENSITY-DEPENDENT RECRUITMENT

Density-dependent recruitment is one of the possible causes of the observed cycles in the northern California crab population. The stability and behavior of an age-specific model with density-dependent recruitment and constant effort were analyzed by Botsford and Wickham (1978) in relation to this population. However, the results obtained by them assumed constant effort, hence, do not hold for the time-varying effort identified here. To determine whether the density-dependent recruitment mechanism is present in this population, the behavior of a model that includes the dynamic response of effort to abundance must be known.

The results obtained by Botsford and Wickham (1978) were in terms of (a) the stability inherent in the age structure of the population and (b) the period of cycles produced. In their model recruitment was the product of total reproduction and a recruitment survival function that depended on effective population size. Stability depended on the relative values of the normalized slope of the density-dependent recruitment function (i.e. the amount that the recruitment survival function changed with a change in population size) and the inherent stability of the population age structure. The general result was that a population with a greater number of age-classes was usually more stable (i.e. could tolerate a steeper slope of the recruitment survival function) than a population with fewer age-classes. The period of the cycles was shown to be roughly twice the mean lag between the age at which the inter-age, density-dependent effect acts on younger animals and the age at which older animals cause this effect (i.e. approximately the mean age of those individuals causing

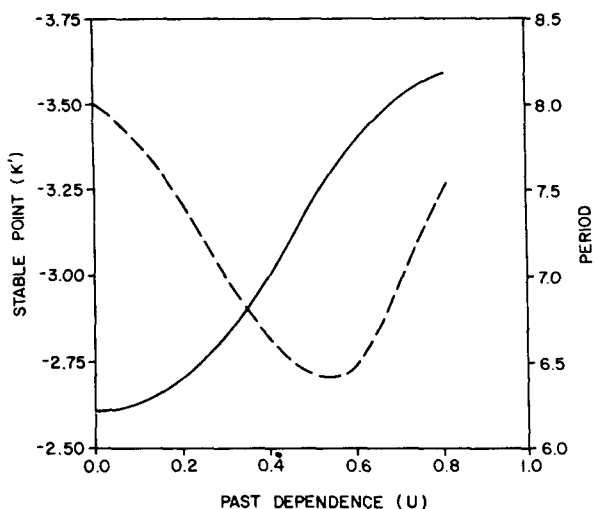


FIG. 9. The behavior of the stable point  $K'$  (---) and the period of cycles produced (—) by the discrete time model with density-dependent recruitment with constant effort replaced by a lagged response of harvest to abundance as the degree of lagged response is varied from  $U = 0$  (constant effort) to higher values.

density-dependent recruitment).

These characteristics are reflected in the values of period and stable point obtained through simulation of a discrete-age version of the baseline model (with reproduction) presented in Botsford and Wickham (1978) (Fig. 8). The stable point  $K'$  is the minimum value of slope of the density-dependent recruitment function that can be tolerated before the population becomes unstable. Hence, a more negative value of  $K'$  corresponds to an inherently more stable population. As the level of constant effort increases, the relative number of age-classes decreases (i.e. older age-classes are depleted), and the population becomes less stable. Also, because the mean age of the population decreases with increased effort, the period of the cycles decreases.

Though we don't know the specific mechanism causing the response of harvest rate to abundance, we can evaluate the effect of this response on population stability through a simple model that mimics harvest rate dynamics. Define

$$(7a) \quad C'_t \equiv H_{norm} A_t (1 - U) + C_{t-1} U,$$

$$(7b) \quad \text{then let } C_t = C'_t, \quad C'_t < H_{max} \times A_t,$$

$$(7c) \quad C_t = H_{max} A_t, \quad C'_t \geq H_{max} \times A_t,$$

where  $U$  = a constant ( $0 \leq U \leq 1.0$ )

$C_t$  = catch in year  $t$

$A_t$  = abundance in year  $t$

$H_{norm}$  = equilibrium harvest rate

$H_{max}$  = maximum harvest rate.

In this model, catch is a weighted sum of abundance harvested at a rate of  $H_{norm}$  and last year's catch (7a), except that harvest rate is constrained to be less than  $H_{max}$  (7b and 7c). The constant  $U$  reflects the relative dependence of harvest rate, and therefore catch, each year on the previous year's catch

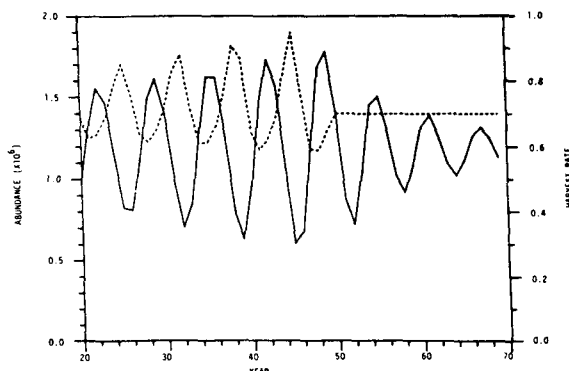


FIG. 10. An example of increased stability through removal of a lagged effort response. Catch (—) and harvest rate (---) are initially fluctuating in an unstable fashion. When harvest rate is set to a constant value for  $t > 60$  yr. the population becomes stable.

(i.e. the relative inertia or lag in the response).

For values of  $H_{norm}$  and  $H_{max}$  that produce a typical pattern of harvest rates, as the value of  $U$  is varied from 0.0 (a constant harvest rate) to higher values (greater past-dependence), the period of the cycles produced increases (Fig. 9). The inherent stability of the model also decreases up to  $U = 0.8$  at which it increases. Because it is not likely that current catch depends to such a large degree on past catch, this value is probably beyond the values that produce a reasonable model of the actual response. Thus, over the reasonable range of values, stability decreases with increased dependence of the effort response on previous catch.

### Discussion

The dominant response of effort in this fishery over the past 30 yr is one of considerable inertia or resistance to rapid change. The dramatic increases and decreases in abundance are not perfectly "tracked" by the catch record. This effect is caused by two limitations on the rate of "outflow" from the population to the consumer. The first is the limited number of boats or crab pots. Because of the limited capacity of each boat, catch cannot change dramatically until the number of boats or pots changes. The second limitation is the rate at which processors will accept crabs. This rate is prevented from changing rapidly by economic factors. The relatively small number of firms in the industry can engage in collusion to protect or increase profits by limiting quantities. As these two limiting mechanisms, fishing capacity and market capacity, operate in series, either one of them can be the "limiting factor" at different times.

The lack of significance of a price-dependent escapement mechanism with past-dependent price is somewhat unexpected. Escapement does appear to increase with the inverse of adjusted price as would be expected if the population were reduced to the zero-profit level each year. That the plot of harvest rate versus abundance (Fig. 6) does not reflect this type of fishery is primarily because of the years following a rapid increase or a rapid decline in abundance (i.e. 1956, 1966 and 1962, 1972). The dependence of price on past catch is expected because of the stores of frozen crab that are left from

year to year in processors' lockers. A possible explanation for the absence of this relationship is that a prediction of abundance (based on a preseason cruise) was available before the price negotiations that preceded each season. This could have shifted dependence on past catch to dependence on the (expected) present catch. A second possibility is the adjustments in price that are made during most seasons. They would also shift price-dependence toward the present.

The lagged effort response in this fishery appears to be less prevalent in recent years. This would be expected on the basis of the increase in real price. (The general increase in real price is not confined to this fishery but has also occurred in others in recent years.) As price increases, the lag in response of fishing capacity will decrease because of the increasing advantage of maintaining the ability to enter the fishery rapidly. The increasing value of crabs will also induce other processors to enter the fishery, thus decreasing the lag associated with market response.

The trend in the influence of effort response on this fishery appears to be generally toward increasing stability. Decreased lag increases stability of predator-prey mechanisms and the density-dependent recruitment mechanism. The fact that instability can arise with no lag in effort, because of the price-dependent escapement mechanism with past-dependent price, does not contradict this general trend. Instability from this mechanism is of a special kind. It occurs in what would be a stable region in continuous time and is possible only because this system is defined in terms of discrete time. This is reflected in the fact that cycles arising from this mechanism would be of period two. Thus, the overall trend is toward greater stability.

Other mechanisms may influence effort in this fishery. Botsford et al. (1982) analyze a cyclic covariation of California salmon catch with crab catch. Salmon catch peaks when crab catch is increasing. Because crab and salmon seasons do overlap, high salmon catch could contribute to low harvest rate during years of increasing crab abundance. Also, in recent years, limitations on entry into other fisheries have induced fishermen to make a couple of landings in fisheries that are not yet limited (such as the crab fishery), merely so that they can maintain the option of later participating in that fishery on a larger scale even if entry is eventually closed.

The impact of the lagged response on stability of a population with density-dependent recruitment is relevant both to the issue of the cause of the cycles and future management of the fishery. The stability results obtained seem intuitively reasonable. Earlier work using constant effort showed that stability increased as effort decreased causing the relative numbers in older age-classes to increase. The period also increased as the numbers in older age-classes increased. As one replaces constant effort with a lagged response of effort to catch, one would expect a decrease in stability because a lagged feedback system is being allowed to overshoot the equilibrium by a greater amount. Conversely, a decrease in the lagged effort response allows less overshoot, hence would be expected to stabilize the system. This reasoning holds until the lag becomes so great ( $U = 0.8$ ) that the increased overshoot allows a substantial increase in the number of older individuals in the population. From the constant effort results, we know that this acts to stabilize the population.

The results in Fig. 9 appear to be robust to variations in  $H_{max}$  and  $H_{norm}$  over ranges of values that match observed harvest rates. Slight variations in  $H_{max}$  do not substantially change results. Varying  $H_{norm}$  to 0.5 or 0.7 produces a less stable population at 0.7 and a more stable population at 0.5, as would be expected on the basis of constant effort results (Fig. 8). The pattern of changes in stability as  $U$  is varied is preserved.

The new result, that the period of cycles produced by density-dependent recruitment increases with a lagged effort response, has important implications for the determination of the cause of the cycles. Botsford and Wickham (1978) noted that the period of observed cycles was greater than the period of cycles produced by a model with constant effort, current estimates of life-history parameters, and the density-dependent recruitment effect occurring near the time of post-larval settlement. The last characteristic would be the case if cannibalism were the density-dependent mechanism. McKelvey et al. (1980) pointed out the same disparity between model periods and observed periods, using a different model with discrete time and age. They chose, however, to reject cannibalism as a potential cause of the cycles on that basis. [See Botsford (1981) and McKelvey and Hankin (1981) for further discussion.]

The fact that the observed lagged effort response can cause an increase in period of 25% (Fig. 9, constant effort versus  $U = 0.6$ ) is an example of a previously unknown mechanism that can have a significant effect on the period of observed cycles. As such, it underscores the potential hazards of rejecting mechanisms because they do not satisfy a certain model when it is not known whether the other parameters and structure of the model accurately mimic the real population (Botsford 1981). Thus, this result casts doubt on both the specific rejection of cannibalism as a cause of the cycles by McKelvey et al. (1980) and the general form of argument used in doing so.

A second feature of the stability results is their potential use in management. The fact that removal of a lagged response can make the population more stable leads directly to consideration of employment of this fact in management. If the amount of effort (or catch) could be increased over its present value during high years and possibly lowered during low years, the population could stabilize at a constant value. The increase in effort following an increase in abundance could possibly be brought about by better prediction of good years and early market development or reduction of the oligopsonistic nature of the fishery. (The latter would probably increase overall value of the fishery even if stability were not affected.)

The potential effect of this behavior can be demonstrated by simulating the fishery using a lagged effort response [equation (7)] then switching to constant effort (Fig. 10). In this example, removal of the lagged effort response caused the population to become stable. The actual change in harvest policy required to stabilize the crab fishery (if it is possible) requires further definition of the population and the fishery. The possible policies examined should not be confined to those that would return the system to constant harvest rate but rather should include schemes which go beyond that to policies that include higher harvest at high abundance and lower



harvest at low abundance. Other simulations have shown that these policies can have an even stronger stabilizing effect than just removing the lag.

This scheme would be beneficial in spite of the fact that the actual cause of the cycles is unknown. If the cycles were caused by environmental factors rather than density-dependent recruitment, long-term landings from the fishery would probably be increased even though the population would not stabilize at a constant value. A policy such as this could also serve as a test of several potential causes of the cycles. If the population were stabilized by such a policy, then density-dependent mechanisms that involve only the unfished females and mechanisms involving the environment could be rejected. A gratuitous observation on the stabilizing effects of diminished lag is that the decrease in lag that has accompanied the long-term increase in market price could possibly stabilize the fishery without actual policy changes.

The influence of a lagged fishery response on stability of models with density-dependent recruitment has shed some light on mechanisms underlying cycles and provided a potential management approach. However, both the identification of the cyclic mechanism and the eventual advisability of such a management scheme depend critically on further definition of the life history parameters of the crab and the influence of environmental variables on this population.

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- BELL, G., P. HANFORD, AND C. DIETZ. Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*). J. Fish. Res. Board Can. 34: 942-953.
- BOTSFORD, L. W. 1981. Comment on cycles in the northern California Dungeness crab population. Can. J. Fish. Aquat. Sci. 38: 1295-1296.
- BOTSFORD, L. W., R. D. METHOT, AND J. E. WILEN. 1982. Cyclic covariation in the California king salmon (*Oncorhynchus tshawytscha*), silver salmon *O. kisutch* and Dungeness crab (*Cancer magister*) fisheries. Fish Bull. U.S. (In press)
- BOTSFORD, L. W., AND D. E. WICKHAM. 1975. Correlation of upwelling index and Dungeness Crab catch. U.S. Fish. Wildl. Serv. Fish. Bull. 73: 901-907.
1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833-843.
- CLEAVER, F. C. 1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Washington State Dep. Fish. Biol. Rep. 94A: 47-82.
- GULLAND, J. A. 1974. The management of marine fisheries. University of Washington Press, Seattle, WA.
- METHOT, R. D., AND L. W. BOTSFORD. 1982. Estimated pre-season abundance in the California Dungeness crab (*Cancer magister*) fisheries. Can. J. Fish. Aquat. Sci. 39: 1077-1083.
- MCKELVEY, R., AND D. HANKIN. 1981. Reply to comment on cycles in the northern California Dungeness crab population. Can. J. Fish. Aquat. Sci. 38: 1296-1297.
- MCKELVEY, R., D. HANKIN, K. YANOSKO, AND C. SNYGG. 1980. Stable cycles in multi-stage recruitment models: an application

to the Northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37: 2323-2345.

- PETERSON, W. T. 1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. U.S. Fish. Wildl. Serv. Fish. Bull. 71: 902-910.
- WILEN, J. E. 1976. Common property resources and the dynamics of over-exploitation: the case of the North Pacific fur seal. Resources paper No. 3, Univ. British Columbia, Vancouver, B.C.

### Appendix

The approach to stability analysis is to determine conditions for local stability of a linearized version of the model in terms of small variations about an equilibrium point. If the linearized model is stable, the model is locally stable. If the linearized model is unstable, the model is locally unstable. The condition of equilibrium, assuming recruitment, is

$$(A-1) \quad C_t = g \left[ C_t \sum_{s=1}^T k_s \right] (G - 1) + R_t$$

From the definition of a small variation in catch about equilibrium,

$$(A-2) \quad \Delta C_t = C_t - C_e$$

and from equations (6) and (A-1) the linearized model can be expressed as

$$(A-3) \quad \Delta C_t = g' \left[ C_e \sum_{s=1}^T k_s \right] \sum_{s=1}^{T+1} h_s \Delta C_{t-s}$$

where  $g'(x) = dg(x)/dx$

$$\begin{aligned} h_s &= -k_1 & s &= 1 \\ h_s &= -k_s + Gk_{s-1} & 1 < s < T \\ \text{and } h_s &= Gk_T & s &= T. \end{aligned}$$

The coefficients ( $h_s$ ) of lagged values of the variation in catch are the difference between the coefficients ( $k_s$ ) describing the influence of past values of catch on escapement and  $G$  times these same coefficients lagged by one time interval. This implies that if the values of  $k_s$  decrease by a certain fraction for each interval (i.e.  $k_{s+1} = pk_s$ ,  $0 \leq p \leq 1$ ), for values of  $p$  near the value of  $G$ ,  $h_s$  is very small for all  $s > 1$ . Stability will then be determined by  $k_1$ , and the system will behave as one that depends only on the past year's catch. Stability conditions for this simple case are similar to other familiar models (e.g. the single age-class stock-recruitment model). The system will be stable if  $g'k < 1$ , unstable if  $g'k > 1$ , and the response will be cyclic with period 2 yr.

Determination of stability for cases other than this simple case is more difficult. If escapement depends on catch up to  $n$  yr in the past, analysis of an  $n$ th order system is required. However, by assuming that the dependence of escapement on past catch decreases by a fixed proportion each year, we can simplify the analysis considerably.

We define a new variable  $S_i$  that could physically be the biomass of crabs in storage for  $i$  yr. We then assume that the amount in storage decreases by a fixed proportion each year

$$(A-4) \quad S_i = p^i C_{i-1}$$

This enables us to express the system in terms of only two variables  $S_i$  and

$$(A-5) \quad S = \sum_{i=1}^{t-1} p^i S_i$$

The equations describing the system are

$$(A-6) \quad S_i' = g[S]G - g[pS_i + pS]$$

$$(A-7) \quad S' = p(S_i + S)$$

where the primes denote values in the current year and unprimed variables refer to the values in the previous year.

From the modified Schuur-Cohn criterion (Freeman 1965), also called the Jury test (Lewis 1977), we obtain the necessary and sufficient conditions for stability.

$$(A-8) \quad g' < \frac{1-p}{-p(2p-1-G)}$$

and

$$(A-9) \quad g' < \frac{1-p}{p|2p-G|}$$

The system will be unstable if either of these is violated. Note that for  $p = G$ , the first condition reduces to  $pg' < 1$ , the same condition as arrived at above from the observation that the system would behave as if there were only a single lagged response after 1 yr. From equations (A-8) and (A-9), stability of this model depends on the relative values of  $G$ ,  $g'$ , and  $p$ . As stated earlier,  $p$ , the fraction of stored stock not sold each year, varies between 0.0 and 1.0. The value of  $g'$ , the change in escapement with a change in past catch, is positive for a compensatory relationship between escapement and past catch. The value of  $G$ , the relative growth rate of biomass from 1 yr to the next, depends on growth and survival of the species as well as fishing effort.

Stability conditions [equations (A-8) and (A-9)] were verified by simulation for a range of values of  $p$ . Values of  $G$  were computed from estimates of growth and survival rate of the crab population (Botsford and Wickham 1978). Unstable behavior was always cycles of period two. Addition of the dependence of price on current catch increased stability by a factor of two if the weighting of present dependence was equal to the weighting of catch 1 yr in the past, and by a factor of 10 when the weighting of present catch was doubled. Thus the system is much more stable when price depends on present catch.

FREEMAN, H. 1965. Discrete-time systems. John Wiley & Sons, Inc., New York, NY.

LEWIS, E. R. 1977. Network models in population biology. Springer-Verlag, Berlin-Heidelberg, New York.