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DID TRAWLING ON THE BROOD STOCK CONTRIBUTE TO THE COLLAPSE OF ALASKA'S KING CRAB?

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Abstract. The 1976 U.S. Magnuson-Stevens Fishery Conservation and Management Act effectively eliminated the no-trawl zone known as the Bristol Bay Pot Sanctuary, located in the southeastern Bering Sea, Alaska. Implemented by the Japanese in 1959, the boundaries of the Pot Sanctuary closely matched the well-defined distribution of the red king crab (*Paralithodes camtschaticus*) population's mature-female brood stock, thus affording a measure of protection to the reproductive potential of the stock. In 1980, the point at which the commercial harvest of Bristol Bay legal-male red king crab reached an all-time high after a decade-long increase, domestic bottom trawling in the brood-stock sanctuary began in earnest with the advent of a U.S.–Soviet, joint-venture, yellowfin sole fishery. In the first year of trawling in the Pot Sanctuary, the Bering Sea/Aleutian Islands (BSAI) red king crab bycatch increased by 371% over the 1977–1979 average; in 1981 the BSAI bycatch increased another 235% over that in 1980, most of which were mature females. As the number of unmonitored domestic trawls in the brood-stock area increased rapidly after 1979 and anecdotal reports of ''red bags'' (trawl cod-ends plugged with red king crab) began to circulate, the proportion of males in the mature population (0.25 in 1981 and 0.16 in 1982) jumped to 0.54 in 1985 and 0.65 in 1986. It is unlikely that normal demographics caused this sudden reversal in sex ratio. Our hypothesis is that sequential, sex-specific sources of fishing mortality were at work. Initially there were ten years (1970–1980) of increasing, male-only exploitation in the directed pot fishery, followed by a drastic reduction in the male harvest after 1980 (to zero in 1983). Then, beginning around 1980, there was an increase in bottom trawling among the highly aggregated, sexually mature female brood stock concentrated near the western end of the Alaska Peninsula, an area documented by previous investigators to be the most productive spawning, incubation, and hatching ground for Bristol Bay red king crab. There has been considerable discussion about possible natural causes (e.g., meteorological regime shifts, increased groundfish predation, epizootic diseases) of the abrupt collapse of the Bristol Bay red king crab population in the early 1980s. The purpose of our study was to conduct a rigorous examination of existing data in order to evaluate the relative likelihood that the collapse was caused by human fishing instead of natural mortality. Our discussion focuses on the association between record harvests of male crab in the directed fishery, the onset of large-scale commercial trawling within the population's primary reproductive refuge, and the population's collapse.

Key words: Alaska red king crab; Bering Sea; bottom trawling; brood-stock habitat; fisheries management; larval transport; meteorological regime shift; overfishing; Paralithodes camtschaticus; *podding behavior; population collapse; reproductive refuge.*

INTRODUCTION

The abrupt collapse of Alaska's Bristol Bay red king crab (*Paralithodes camtschaticus*) population was one of the more spectacular crashes in the history of U.S. fisheries management. For about a decade during the 1970s the Bristol Bay red king crab fishery was the crown jewel of Alaska's fishery resources, second in value only to the five Pacific salmon species combined. Red king crab represented Alaska's most valuable single-species fishery until 1980, but by 1983 the catch had dropped to zero and the small Aleutian fishing port of Dutch Harbor, elevated to national preeminence by red king crab dollars, looked like a ''ghost town'' (Wooster 1992:16).

Despite the precipitous nature of the crash and the substantial economic and social impacts resulting from it, there has been little scientific analysis or documentation of factors that might have led to the population's collapse. Orensanz et al. (1998) wrote at length about the serial depletion of crustacean fisheries in Alaska but excluded from their analysis the collapse of Bristol Bay red king crab, noting that it had been well documented by Otto (1986). Otto (1986:105) concluded that:

> . . . *directed or undirected fishing has not been a major cause of population decline in Bristol Bay red*

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> *king crab. . . . . . Management measures failed to prevent recent declines in landings because causes of declines in abundance are not related to fishing, and hence largely beyond control.*

This conclusion is consistent with the position of U.S. and Alaskan crab managers and modelers (e.g., NPFMC 2000, Zheng and Kruse 2002) that the crash of the Bristol Bay red king crab stock was not related to fishing but was due entirely to natural mortality associated with a recurrent meteorological regime shift called the Pacific Decadal Oscillation (Mantua et al. 1997). The consensus hypothesis that Alaska's red king crab stocks were catastrophically affected by a regime shift and unaffected by record levels of fishing mortality contrasts sharply with the position of Orensanz et al. (1998:151), who stated:

> *From a managerial perspective, the pattern and magnitude of the collective rise and fall of the crustacean fisheries of Alaska are such that overfishing has to be considered as the default working scenario, even before being tested as a scientific hypothesis.*

The positions of Otto (1986) and Orensanz et al. (1998) are incompatible; yet, more than 20 years after the collapse, each has staunch proponents among the management and scientific communities, suggesting that the story of the Bristol Bay red king crab has been told in a way that fails to resolve the issues surrounding the collapse.

The world's largest population of red king crab resides on the west coast of Kamchatka in the Sea of Okhotsk (Rodin 1989). The second-largest population is located in Bristol Bay, Alaska, in the southeastern Bering Sea. Elements common to both populations are a broad, unbroken coastal shelf and a longshore current for larval transport. The shelf must be sufficiently long (>200 km) so that recently hatched crab larvae remain on nearshore grounds suitable for settlement, after drifting downcurrent as plankters for 3–4 months. The shelf must be continuous and broad enough for the upcurrent, return migration of the population's breeders to the region where they themselves were hatched (Rodin 1989). This ''endless-belt'' reproductive strategy, common to many aquatic invertebrates with an extended planktonic life stage, was pieced together for Kamchatka king crab by Russian and Japanese scientists (e.g., Marukawa 1933, Galkin 1960) after years of research (Vinogradov 1969). A critical factor in the endless-belt strategy is the location, near the upcurrent end of the shelf, of the brood stock that annually replenishes the population. The reproductive center for the entire Kamchatka population is located in the Khairyuzov region around latitude 56° to 60° N (Rodin 1989). Understanding the importance of minimizing any disturbance to the seminal brood stock, managers of the Kamchatka population implemented in 1969 a coastal refuge between 56.3° N and 57.0° N, where trawling and other fishing was prohibited out to a depth of 400 m (Vinogradov 1969, Thomson 1989).

Using their own scientists' findings for Kamchatka, the Japanese government in 1959 prohibited trawling by its domestic fleet in a 67 000-km^2 area of Bristol Bay known as the Pot Sanctuary (Fig. 1). Because the Japanese fishing fleet was the only fleet trawling in the eastern Bering Sea during the 1950s (Kasahara 1972, Witherell and Pautzke 1997), the ban on Japanese trawling effectively eliminated most of the trawling within the Pot Sanctuary during the 1960s. The stated purpose of the Pot Sanctuary was to avoid gear conflicts between Japan's trawl fleets and its red king crab pot and tangle-net fisheries (Fredin 1987, Ackley and Witherell 1999), but clearly the closure made sense ecologically as well as administratively. A key feature of the Pot Sanctuary was that, after four years of fine-tuning (1959–1963), its final boundaries closely conformed to the spatial distribution of mature female red king crab (e.g., Fig. 2), suggesting that the no-trawl zone was designed, in part, as a reproductive refuge for the population's brood stock.

As U.S. fishermen entered the Bristol Bay crab-pot fishery in greater numbers during the 1960s, bilateral agreements were negotiated between the United States and Japan, and separately between the United States and the USSR, with the objective of reinforcing the self-imposed Japanese trawling prohibition in the Pot Sanctuary (Naab 1968*a*, *b*, 1971). These agreements, renegotiated every two years during 1964–1968, established a special sanctuary on the nearshore grounds north of Unimak Island and Black Hill (Fig. 1), where trawling and tangle-net fishing for red king crab were prohibited, with the objectives of protecting the emerging U.S. king crab fishery and safeguarding the king crab resource (Naab 1968*a*). The diplomatic focus on obtaining special-sanctuary status for an area within the Pot Sanctuary already protected by the Japanese trawling prohibition, emphasizes the area's particular value with regard to red king crab. Research conducted over the next 30 years confirmed the area's importance as the population's most productive spawning, incubation, and hatching ground (Haynes 1974, Fukuhara 1985, Armstrong et al. 1986, 1993, McMurray et al. 1986, Hsu 1987, Loher 2001). However, after enactment of the U.S. Magnuson-Stevens Fishery Conservation and Management Act of 1976 (MSFCMA),[2] this same Unimak-Port Moller area, once recognized by negotiating governments, scientists, and fishermen as habitat essential to Bristol Bay red king crab, became the most heavily trawled region in the eastern Bering Sea (Fig. 3).

By 1970, it was clear that a key element in the management of the world's largest red king crab populations was the establishment of sanctuaries that, in effect

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[2] 13 April 1976, and as amended. U.S. code title 14, sections 1801–1882.

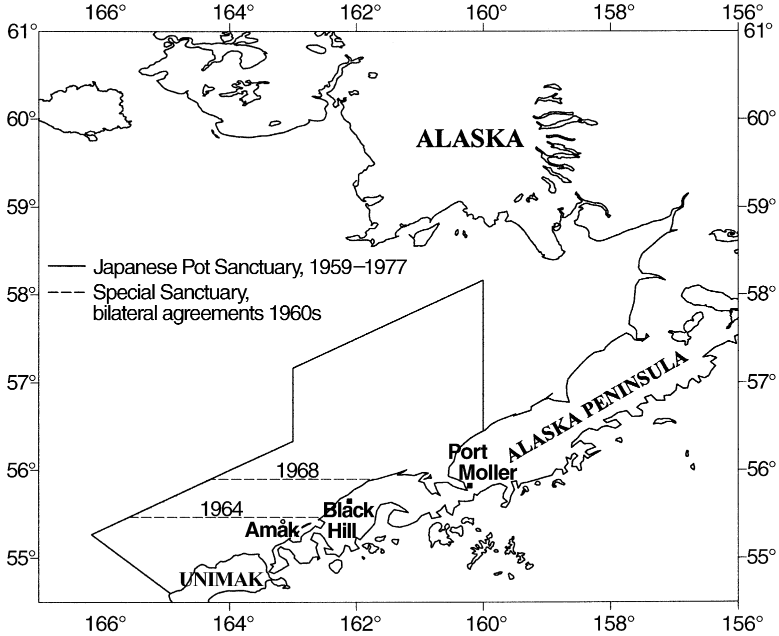

FIG. 1. The Japanese Pot Sanctuary, a 67 000 km^2 area of Bristol Bay, Alaska, USA (Southeast Bering Sea), showing the ''special sanctuary'' (Naab 1968*a*) off Unimak-Amak-Black Hill, where both trawling and tangle-net fishing were prohibited.

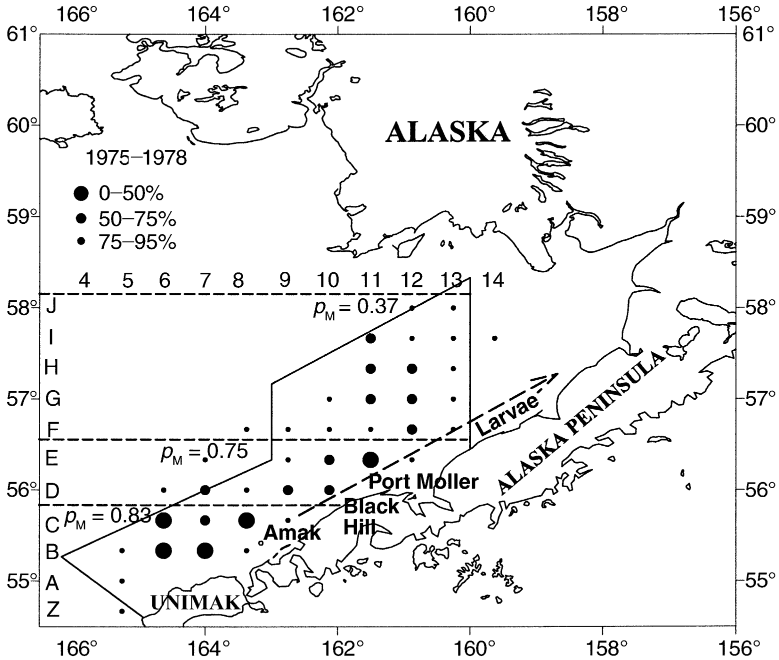

FIG. 2. The crab-weighted spatial distribution of egg-bearing females collected in the NMFS survey during 1975–1978, before trawling began in the Pot Sanctuary. The Pot Sanctuary protected from trawling all but a small fraction of the brood stock (symbols represent 95% of the total brood stock). The five largest symbols represent ~50% of the brood stock, the bulk of which is off Unimak and Amak Islands. The ranges (percentage of total brood stock) are approximate and may overlap. The proportion of multiparous females (p_M) increased from northeast to southwest. The northeast to southwest movement of the maturing brood stock complements the southwest to northeast drift of larvae.

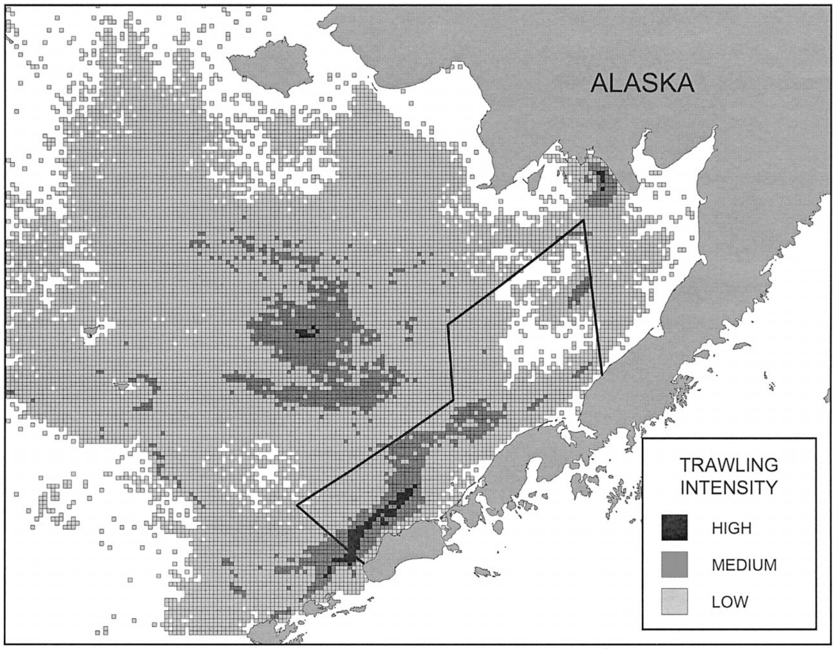

FIG. 3. The trawl-density distribution of observed tows and observed joint-venture deliveries within 25-km^2 grid squares during 1973–2001. The old Pot Sanctuary (black boundary line) no longer exists. Trawling intensity is highest (darkest squares) in the Unimak area and low (lightest) in the more offshore area of the old Pot Sanctuary, where the present-day brood stock remains.

or by design, protected the brood stock from trawling. Despite this, it was not long before the sanctuary strategy was abandoned by U.S. fisheries managers, largely because of incentives provided by the MSFCMA. Under the MSFCMA the level of foreign fishing was limited to that portion of the allowable catch not harvested by U.S. fishermen (Fredin 1987). This arrangement spurred the rapid development of a domestic groundfish trawl industry in the eastern Bering Sea, and the Pot Sanctuary was formally opened to year-round domestic trawling via Amendment 1 to the Bering Sea-Aleutian Islands Groundfish Fishery Management Plan (e.g., NPFMC 2002). However, by the time Amendment 1 took effect in January 1984, at least 5,000 domestic commercial groundfish tows, each covering 0.3–0.4 km^2 (74–99 acres), had already had been conducted within the boundaries of the Pot Sanctuary. In 1980, the year trawling began in earnest in the Sanctuary (Fisher 1980), crab-pot fishermen landed a record 59 $\times$ 10^6 kg (130 million pounds) of Bristol Bay male red king crab. Three years later, in 1983, the spawning-stock abundance had plummeted by 90–95% and the red king crab season was closed.

For the Bristol Bay red king crab population, 1980 was a turning point with regard to fishing mortality, which now included not only the retained catch from the directed pot fishery, with its discarded bycatch of female and sub-legal crab, but also the bycatch from a burgeoning domestic groundfish trawl fishery. After a decade of annually increasing red king crab harvests, the percentage of the legal-male (carapace length [CL] $\geq$ 135 mm) population taken by the pot fishery reached an all-time high in 1980 of greater than 60% (Table 1). Then, in concert with the push to Americanize the groundfish fishery, domestic trawlers in 1980 began bottom trawling within the Pot Sanctuary. We believe that the role of fishing has been understated in published accounts of the collapse of the Bristol Bay red king crab population. Moreover, we believe that management's failure to act to prevent the breaching of the Pot Sanctuary with year-round bottom trawling put the brood stock at risk and compromised the reproductive potential of the population. We hypothesize further that the population's endless-belt reproductive strategy was thwarted by the loss of the most productive segment of the brood stock from the western end of the Alaska Peninsula, a region that evolved from a 1960s special sanctuary for red king crab to a heavily trawled area known as ''Cod Alley.'' Our hypothesis includes the premise that what was once a successful reproductive strategy is now simply a migration of the population's most fecund females into the most heavily trawled region of the eastern Bering Sea. It is possible that this is one of the mechanisms that has kept the population at depressed levels for the past 20 years.

METHODS

We compiled information on red king crab behavior from two sources. The first is the indirect information on the behavior and spatial distribution of red king crab

TABLE 1. Bristol Bay (Alaska, USA) red king crab harvest (C, retained catch), the utilization of harvest rate (U_t), and fishing mortality (F), 1975–1981, under a regime of constant natural mortality ($M = 0.2$) for legal males.

Year	Legal population N_0 ($t = 0$)	 N_t ($t = 4/12$ yr)	Retained catch C	U_t†	F‡
1975	21 000 000	19 645 647	8 745 294	0.45	0.59
1976	32 700 000	30 591 078	10 603 367	0.35	0.43
1977	37 600 000	35 175 063	11 733 101	0.33	0.41
1978	46 600 000	43 594 626	14 745 709	0.34	0.41
1979	43 900 000	41 068 757	16 808 605	0.41	0.53
1980	36 100 000	33 771 802	20 845 350	0.62	0.96
1981	11 300 000	10 571 229	5 307 947	0.50	0.70

Notes: Legal population and retained catch data are from NPFMC (2001); a legal-male red king crab has carapace length ≥135 mm. At $M = 0.2$ for legal males, the retained catch is equivalent to a 1975–1981 average fishing mortality of $F = 0.57$. Sources for $M = 0.2$: Balsiger (1974), NOAA (1998*a*), Stevens et al. (2000: Appendix C).

† $U_t = C/N_t$.

‡ $F = -\ln(1 - U_t)$.

based on analysis of data from the annual Bristol Bay bottom-trawl survey conducted by the U.S. National Marine Fisheries Service (NMFS) since 1975. These data, part of the NMFS Alaska Fisheries Science Center's shellfish assessment program, reside at the Kodiak Fisheries Research Center, Kodiak, Alaska, USA. The second source of information is the direct, in situ observation from underwater investigations conducted in waters near Kodiak, Alaska, during 1984–1997 (e.g., Dew 1990, 1991, Dew et al. 1992). A NMFS trawl sample provides ''indirect'' information because it is a composite distribution collected from an area of 40 000–50 000 m^2; a trawl sample cannot reveal the fine-scale distribution readily apparent from direct, in situ observation (e.g., Figs. 4 and 5).

Data on the intensity of commercial bottom trawling in Bristol Bay during 1973–2001, estimated from the number of observed tows plus the number of joint-venture deliveries within 25-km^2 grid-squares (Fig. 3), were obtained from the north Pacific (NORPAC) fishery-observer database maintained at the Alaska Fisheries Science Center, NMFS, Seattle, Washington, USA. A joint-venture fishery is one where the unmonitored domestic trawler fleet delivers its catches directly to foreign processor vessels, some of which have observers on them. The NORPAC counts do not include tows that were unobserved because of partial observer coverage. For example, observers were present during only 29% of the joint-venture fishing effort in 1980 and 22% in 1981 (Nelson et al. 1981, 1982). Thus the NORPAC counts underestimate the actual number of commercial tows conducted in Bristol Bay during the 1980s. Prior to 1990 there was little or no observer coverage on the domestic vessels doing the fishing. Since 1990, observer coverage on domestic vessels has been 100% for vessels >38 m (125 feet) long, 30% for vessels 18–38 m (60–125 feet), and 0% for vessels <18 m (60 feet) (Megrey and Wespestad 1990, NMFS/OST 2000). Here ''coverage'' refers to the percentage of vessel fishing days during which an observer was on board. The actual percentage of tows inspected by a single observer on a continuously fishing vessel >38 m would be substantially less than 100%.

In this analysis we defined the proportion of sexually mature males in the mature population as $m/(m + f)$, where m = the number of males ≥120 mm CL and f = the number of females ≥90 mm CL caught in the NMFS trawl survey. For purposes of converting between m/f and $m/(m + f)$, $m/f = [m/(m + f)]/[1 - m/(m + f)]$ and $m/(m + f) = 1 - [1/(m/f + 1)]$. The size at maturity for Bristol Bay females (≥90 mm CL) is the size at which approximately 50% are carrying egg clutches (Otto et al. 1989, Pengilly et al. 2001). The size at maturity for males (≥120 mm CL) is unconfirmed for Bristol Bay; it is based on the in situ observation at Kodiak that the smallest male capable of grasping and holding on to a female was 123 mm CL (Powell et al. 1973). These are the sizes at maturity used to manage the Bristol Bay fishery (Zheng et al. 1997). The sex ratio for each year's trawl survey was calculated by summing the sexes across all tows rather than obtaining the average sex ratio per tow. The ratio of the sums ensured that each catch was weighted according to its size.

The NMFS annual trawl survey in Bristol Bay often collects multiple samples at various station locations on an ad hoc basis, thus unbalancing the distribution of trawling effort across a grid of stations designed for systematic sampling (e.g., Zheng et al. 1995). Because adult male and female red king crab tend to occupy separate regions of Bristol Bay (Korolev 1964, Chebanov 1965, Rodin 1970, 1989, Takeshita et al. 1989), spatial imbalances in sampling effort over the years have resulted in biased estimates of sex ratio, which may have masked real changes. A random resampling of the original data would simply replicate the sex-ratio bias of an unbalanced sampling design. To retain all of the catch information and to ensure that the resamples were unbiased, we rescaled the original sample-data vector so that the probability of randomly se-

FIG. 4. A resting pod of some 9000 adult and subadult red king crab, forming a pile ~2.4 m high at a water depth of 23 m near Kodiak, Alaska, September 1993. This aggregation represents a local density of >500 individuals/m^2. (Photo by C. B. Dew.)

lecting sex-ratio data from a station location using bootstrap resampling was equal for all stations. We used the method shown in Table 2, where seven hypothetical samples are shown for station A, three for station B, and one for station C. Using the original, unadjusted data, the probability of randomly selecting a male-female number pair from station A was 2.3 times that of station B and 7 times that of station C. Using the rescaled data, the probability of randomly selecting a number pair from a particular station is equal for all stations. Because a station's scaling factor was a multiple of the number of samples collected at each of the other stations (e.g., $7 \times 3 = 21$ for station C, Table 2), some rescaled data vectors were quite large (>10 000).

The red king crab brood stock comprises two classes of sexually mature females, most of which are carrying egg clutches: primiparous females, carrying their first clutch, and multiparous females, carrying other than their first clutch. All females ≥100 mm CL carrying uneyed-egg clutches, as well as those carrying eyed-egg clutches or egg cases, were designated as multiparous. Because the fecundity of a population is ultimately limited by the number of females in the population (Ricklefs 1973), the size of the brood stock is an important population characteristic. The multiparous portion of the brood stock, composed of several age groups of relatively high-fecundity females (Otto et al. 1989, Johnson et al. 2002), represents that fraction of the stock with the greatest reproductive value.

To examine the impact of commercial trawling on brood-stock density we used a power curve, linearized by a (base 10) log–log transformation of the data (+1 to enable log transformation of 0-values) as follows:

FIG. 5. A red king crab pod alternates, approximately diurnally, between resting and foraging. This foraging pod, photographed (by C. B. Dew) in August 1993, is part of the same aggregation seen in Fig. 4. The crabs forage in a single layer, staying together and moving as a group, similar to the podding behavior documented for juveniles (Dew 1990).

$$d_t = a(c_t + 1)^b - 1$$

$$\log(d_t + 1) = \log(a) + b\log(c_t + 1)$$

where d_t = the average brood-stock density (no. crabs/km^2) from the annual trawl survey in year t, c_t = cumulative number of commercial tows during the five-year period from year $(t - 4)$ through year t, a = brood-stock density at $c_{75} = 0$; i.e., the antilog of the intercept of the regression of $\log(d_t + 1)$ vs. $\log(c_t + 1)$, and b = the slope of the regression of $\log(d_t + 1)$ vs. $\log(c_t + 1)$.

RESULTS

Between 1977 and 1983, after a period of successive record harvests and harvest rates that eventually exceeded 60% (Table 1), and after bottom trawling began in the Pot Sanctuary, the Bristol Bay spawning stock of Alaska red king crab declined in abundance by an

TABLE 2. Illustration of method for rescaling a geographically biased sample vector to an equally weighted vector from which bootstrap resampling will select a random sample.

Illustrative data

		Selection probability				
Station	No. samples per station	Station	Sample	Joint	LCM†	Scaling factor‡
A	7	1/3	1/7	1/21	63	3
B	3	1/3	1/3	1/9	63	7
C	1	1/3	1/1	1/3	63	21

Rescaling illustration

Original sample vector (n = 11)	→	Rescaled sample vector (n = 63)
$\{a_1,a_2,a_3,a_4,a_5,a_6,a_7,b_1,b_2,b_3,c_1\}$	→	$\{a_1,a_2,a_3,a_4,a_5,a_6,a_7,a_1,a_2,a_3,a_4,a_5,a_6,a_7,a_1,a_2,a_3,a_4,a_5,a_6,a_7,$ $b_1,b_2,b_3,b_1,b_2,b_3,b_1,b_2,b_3,b_1,b_2,b_3,b_1,b_2,b_3,b_1,b_2,b_3,b_1,b_2,b_3,$ $c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1,c_1\}$

Note: Lowercase letters with subscripts denote samples from their respective (uppercase letter) stations; e.g., a_6 is the sixth sample from Station A and is represented three times in the rescaled sample vector. The repetition is the result of rebalancing the sample vector so that each station (A, B, C) has an equal chance of being included in a random, computerized, bootstrap selection of samples. The probability of including Station C before rescaling was 1/11 = 0.091 vs. 21/63 = 0.333 after rescaling.

† Least common multiple of the joint-probability denominators.

‡ Scaling factor = LCM × joint probability.

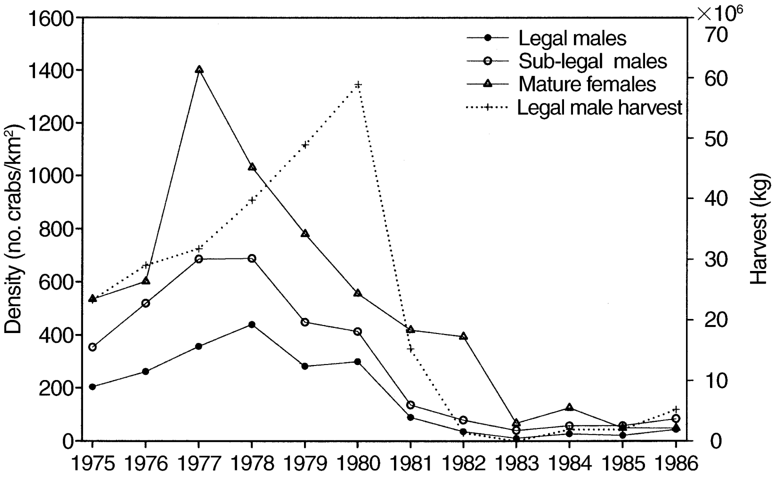

FIG. 6. Trends in density and catch over time, showing the decline of nontargeted components of the stock as well as legal male red king crabs, Bristol Bay, Alaska, USA. Record harvests were taken in 1979 and 1980, after the targeted legal population had begun its decline. Increasing harvests from a declining stock resulted in high bycatch of nontargeted red king crab.

alarming 90–95%. The decline was not limited to the relatively small fraction of the population directly targeted by the fishery (legal males ≥135 mm CL), but included sub-legal, mature males (120–134 mm CL) and mature females (≥90 mm CL) (Fig. 6).

Crab behavior and vulnerability

Red king crab may be particularly vulnerable to trawling because of their unique podding behavior, as revealed by in situ investigations at Kodiak (Dew 1990, 1991, Dew et al. 1992) and southeast Alaska (Stone et al. 1992, 1993). Unlike Tanner crab mounds, which are transitory mating aggregations consisting primarily of mature females with eyed-egg clutches (Stevens et al. 1994), podding is the persistent, year-round, day-to-day, social functioning of cohesive, identifiable population units composed of juvenile, sub-adult, and adult red king crab of both sexes. Podding behavior causes red king crab to be spatially distributed within their preferred habitat as extremely dense aggregations, and this is true whether the crab are resting (Fig. 4) or foraging (Fig. 5). Such behavior increases the fraction of the total population that can occupy the volume (or area) swept by a single unit of fishing effort. This behavior, while lowering the probability of capturing crab in a given tow, increases the probability of local extinction and thereby increases the vulnerability of red king crab to trawling within the species' preferred habitat.

The impact of trawling on red king crab is typically evaluated as the proportion of the total population killed by trawling. Such accounting fails to include the impact of persistent disruption to the social organization and spatial structure of this intensely gregarious species. To those familiar with the podding behavior of adult red king crab and the unfortunate history of trawling as a fishing method for red king crab (outlawed in all Alaskan waters by 1960), it would have been evident that large-scale, commercial bottom trawling in the primary brood-stock habitat would result in large, wasteful catches of red king crab, as was confirmed in early (1981) reports provided to managers by observers (e.g., Fig. 7). Catches such as that in Fig. 7 were known as ''red bags'' during the early years of joint-venture trawling in the Pot Sanctuary. Consistent with observer-sampling protocol at the time, none of the several thousand crab in this or other red-bag deliveries to Soviet processors in 1981 were counted or measured before being discarded (Doug Smith [former NMFS observer], *personal communication*). However, a composite sample of 1,929 crab selected from retained, non-red-bag catches during July–September 1981 (Fig. 8) indicates that the trawl bycatch of mature red king crab in the Pot Sanctuary was 88% female. Of these, 59% were the multiparous (>100 mm CL) breeders that dominated the population's egg production before the 1980–1983 collapse (e.g., Fig. 2).

Female distribution

Analysis of the geographical distribution of the Bristol Bay spawning stock before and after the collapse suggests that there was a spatially explicit component to the mortality that drove the stock to near extinction during the early 1980s. Before the population collapse, and before substantive trawling began in the Pot Sanctuary, egg-bearing females tended to congregate in nearshore waters off Unimak and Amak Islands (Fig. 2), upcurrent from the shallow-water juvenile habitat ranging along the coast of the Alaska Peninsula. Based on NMFS survey data, the 1975–1978 brood stock was distributed so that the bulk of the larval supply emanated from the Unimak–Amak region, 100–200 km up-

FIG. 7. Contents of a ''red bag'' delivered by a domestic trawler to the Soviet processor *Chasovoy* in late August 1981. According to the observer's logbook, this catch and several more like it were taken from a water depth of 55–75 m during August–September off Black Hill in the Pot Sanctuary (Bristol Bay, Alaska, USA). As was typical of red bags in the early 1980s, none of the several thousand red king crab shown here was counted or measured before being discarded. Catches such as this, omitted from extrapolations to total-fleet bycatch, suggest how the reproductive capacity of Bristol Bay red king crab might have been eroded while observer-estimated bycatch numbers remained low (photo by Doug Smith, former NMFS observer).

current from prime juvenile habitat in the coastal region of Black Hill and Port Moller (Fig. 2). This information is generally consistent with the findings and conclusions of other Bristol Bay investigators (e.g., Haynes 1974, Fukuhara 1985, Armstrong et al. 1986, 1993, McMurray et al. 1986, Hsu 1987, Loher 2001). Moreover, the Bristol Bay red king crab reproductive strategy of releasing planktonic larvae in areas optimally distant from downcurrent juvenile habitats is analogous to the strategy reported for red king crab of Kamchatka. (Vinogradov 1969, Rodin 1989).

The brood-stock distribution that existed after the population collapse was substantially different from the pre-collapse distribution. The Unimak–Amak females of 1975–1978 were not present in 1983–1986, and the brood stock, now reduced to less than 10% of its previous abundance, was concentrated some 250 km to the northeast, well offshore of Port Moller (Fig. 9). More specifically, during the 1975–1978 pre-trawling period, 55% of the total Bristol Bay brood stock was

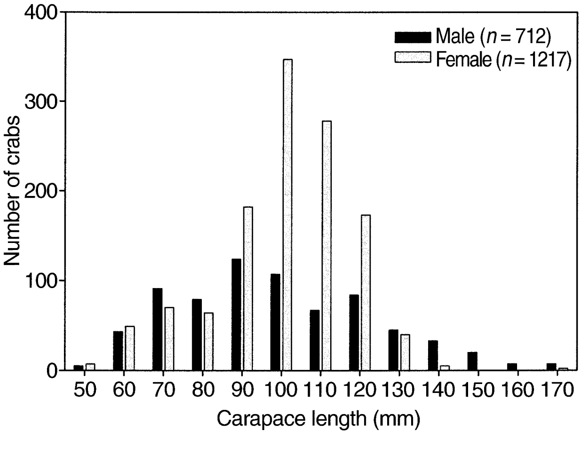

FIG. 8. Size and sex of the sampled, non-red-bag bycatch delivered to the *Chasovoy* and the *Prokofyeva* from trawl catches in the Pot Sanctuary during July–September 1981. Of the mature red king crab, 88% were females, of which 59% were multiparous (carapace length ≥ 100 mm).

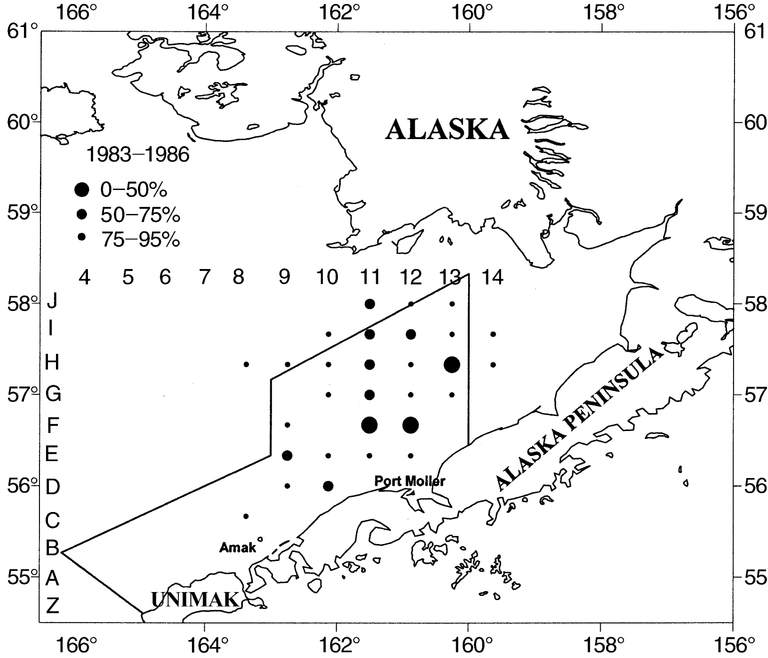

FIG. 9. The crab-weighted spatial distribution of egg-bearing females collected in the NMFS survey during 1983–1986. After several years of trawling in the Pot Sanctuary, the multiparous egg-bearing females of 1975–1978 (Fig. 2) were gone from the Unimak-Amak region, and 50% of the total brood stock (largest symbols) was concentrated at three stations well offshore of Port Moller, where commercial trawling is lightest (Fig. 3).

concentrated at 10 stations (rows Z–C [Figs. 2 and 9]) near Unimak and Amak Islands and 83% of these crab were multiparous (Fig. 2). By 1983–1986, after several years of trawling in the Pot Sanctuary, the congregations of egg-bearing females were gone from the Unimak–Amak region and 50% of the total brood stock was concentrated at three stations 70–100 km offshore of Port Moller on the Alaska Peninsula (Fig. 9). Larvae hatched in this offshore region are unlikely to be transported to nursery habitat along the coast of the Alaska Peninsula (Loher 2001).

The loss of brood stock from the Unimak–Amak region was primarily a loss of multiparous crab. Prior to the collapse, and before the advent of trawling in the Pot Sanctuary, there was evidence of a southwest-northeast multiparity gradient in which 83% of the females in the Unimak–Amak region (rows Z–C) were multiparous, 75% in the more northeasterly rows D–E were multiparous, and 37% in rows F–J were multiparous (Fig. 2). The implied northeast to southwest ontogenetic movement of the maturing brood stock is counter to the southwest to northeast nearshore larval drift along the Alaska Peninsula, suggesting an endless-belt reproductive strategy whereby female red king crab, over a period of several years, tend to return to the area where they themselves were hatched. Prior to the 1980–1983 collapse of the population, the Bristol Bay brood stock was 66% multiparous and 34% primiparous; conversely the 1983–1986 post-collapse brood stock was 37% multiparous and 63% primiparous (Table 3). That is, by 1983–1986, less fecund, first-time spawners were contributing most of the spawning production to a population normally sustained by several age groups of relatively more fecund, multiparous crab. The abrupt change from a relatively stable, multiple-age brood stock to one that was largely dependent on the annual recruitment of pubescent females, a phenomenon corroborated by Hsu (1987), demonstrates that the Unimak multiparous crab, rather than simply moving to a different area, were lost to the population.

Male distribution

Similar to females, the collapse of the mature male population was characterized by a spatially explicit loss of animals from the southwest sector of the Bristol Bay range, suggesting a common cause for the disappearance of males and females (Fig.10). Unlike females, about half of the male population was distributed outside the Pot Sanctuary during both the pre- and post-collapse periods. The reason for this is that in any given year only about 50% of the reproductively mature males in Bristol Bay participate in the mating migration to nearshore spawning grounds within the Pot Sanctuary. The other 50%, recently molted and incapable of mating, remain offshore on overwintering and foraging grounds northwest of the Pot Sanctuary until the next spawning season (Rodin 1970, 1989). This difference in the behavioral ecology of mature males and females caused a marked difference in their spatial distributions. Using the Pot Sanctuary boundary for ref-

TABLE 3. The number and proportion of primiparous and multiparous female red king crab in the Bristol Bay brood stock.

Year and region	Number		Proportion	
	Primip.	Multip.	Primip.	Multip.
Unimak-Amak region, rows Z, A, B, C				
1975	258	869	0.23	0.77
1976	360	3459	0.09	0.91
1977	54	492	0.10	0.90
1978	499	1350	0.27	0.73
Average			0.17	0.83
Nearshore Port Moller (rows D, E)				
1975	113	336	0.25	0.75
1976	203	410	0.33	0.67
1977	157	562	0.22	0.78
1978	86	318	0.21	0.79
Average			0.25	0.75
Offshore Port Moller (rows F, G, H, I, J)				
1975	435	118	0.79	0.21
1976	401	72	0.85	0.15
1977	685	577	0.54	0.46
1978	508	1029	0.33	0.67
Average			0.63	0.37

Notes: The proportion of multiparous females in the Bristol Bay brood stock generally decreased from southwest (Unimak-Amak) to northeast (offshore Port Moller). See Fig. 2 or Fig. 9 for alphabetic row locations.

erence, 49% of the males and 91% of the females were within the Pot Sanctuary during 1975–1978. Similarly, during 1983–1986 after the population collapse, 49% of the males and 93% of the females were within the Pot Sanctuary. Thus, regardless of population density, only about 50% of the population's mature males are available for mating in any given year. This fact, based on Japanese tagging studies during the 1960s (Fujita et al. 1973, Takeshita et al. 1989) and supported by NMFS survey data from the 1970s and 1980s, is not accounted for in the management of Bristol Bay red king crab. The length-based assessment model used to manage the red king crab fishery since 1995 assumes that all mature males are available to mate one or more times each year (Zheng et al. 1997), thereby substantially overstating the Bristol Bay male reproductive potential and understating the impact of harvesting the largest males.

Fishing pressure

Any evaluation of the position of State and Federal fishery managers that the Bristol Bay red king crab collapse was caused by a ''drastic increase in natural mortality'' (Otto 1986:104) must be accompanied by a reasonable accounting of the fishing mortality imposed on the stock around the time of the collapse. According to Ricker (1975), the retained catch (C), expressed as a proportion of the target population at the time of the fishery (N_t), is the rate of utilization ($U_t = C/N_t$). The red king crab fishery occurs approximately four months after the NMFS trawl-survey estimate of the legal-male target population (N_0). Therefore, because natural mortality (M) operates within the population for four months before the fishery begins each year, N_t is always less than N_0 and is calculated as $N_t = N_0e^{-Mt}$, where $t = 4/12$. From U_t, the rate of fishing mortality (F) is calculated as $-\log_e(1 - U_t)$. Managers have decided that the average mature biomass over the post-collapse period of 1983–1997 should be used to define the baseline Bristol Bay red king crab stock (e.g., Rugolo et al. 2001: Appendix C). The average rate of fishing mortality imposed on legal males during this 15-year baseline period is $F = 0.24$ (range: 0.00–0.48), not counting any bycatch mortality. We used $F = 0.24$ to evaluate management's position that fishing played only a negligible role in the decline of Bristol Bay red king crab. During 1975–1981, the F imposed on legal males (ig-

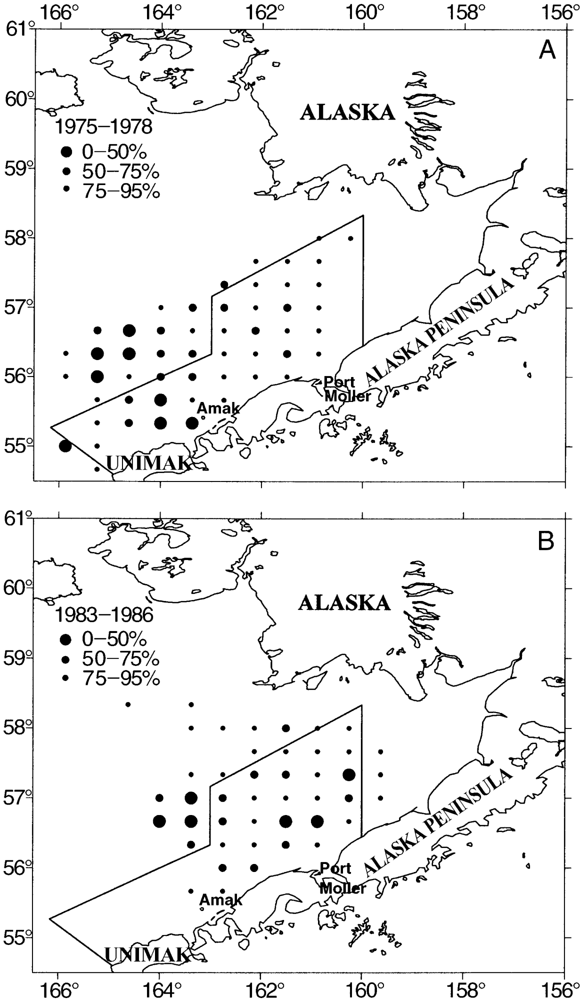

FIG. 10. The distribution of mature male red king crab (A) before and (B) after the population's collapse. Similar to multiparous females, mature males disappeared from the Unimak–Amak spawning grounds after several years of trawling in the Pot Sanctuary. Both before and after the collapse, a substantial proportion of the mature-male population was located on male molting grounds to the northwest, outside the Pot Sanctuary, >100 km from nearshore spawning grounds.

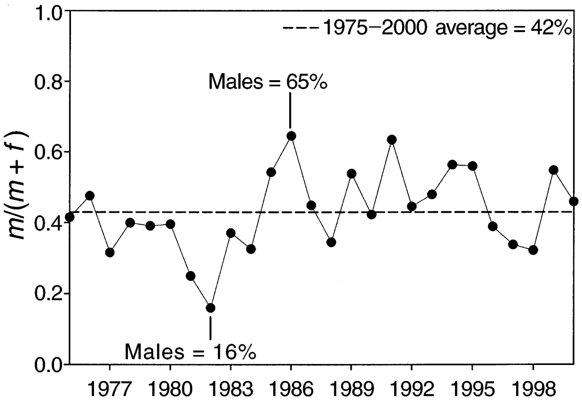

FIG. 11. Mature red king crab males as a proportion of the total mature population (*m*, number of males; *f*, number of females), 1975–2000. The reversal in sex ratio from female dominance (84%) in 1982 to male dominance (65%) in 1986 suggests that the mortality of females during this time was greater than that of males, even though the red king crab fishery was directed to males only.

noring bycatch mortality) varied between 0.41 and 0.96 (average $F = 0.57$) and peaked in the record-harvest year of 1980 (Table 1), two years after the target population began its decline (Fig. 6). That is, using a constant natural mortalty of $M = 0.2$, consistent with Balsiger (1974) and Rugolo et al. (2001: Appendix C) and believed to be a conservative estimate of natural mortality for king crab (e.g., Federal Register 1998*a*), the fishing-induced mortality rate exceeded the 1983–1997 baseline average of $F = 0.24$ by 69–300% during the seven years leading up to the collapse of the resource. Thus, fishing rates considered high by today's baseline standards were the norm in the directed red king crab pot fishery of Bristol Bay during 1975–1981.

Sex ratio

In a male-only fishery such as the Bristol Bay red king crab fishery, the sex ratio of the mature stock can be used as an indicator of fishing impact. The sex-ratio trend in Fig. 11 shows that the proportion of males in the adult population dropped to its lowest levels of 0.25 (0.22 to 0.29) in 1981 and 0.16 (0.11 to 0.22) in 1982 (ranges are 95% bootstrap confidence limits). This decline in the proportion of males occurred after a decade-long, 15-fold increase in the commercial harvest of male crab to an all-time record in 1980. The 1982 low point of males in the mature population, perhaps the result of past fishing pressure, was followed by a reversal in sex ratio, with the proportion of males in the adult population increasing from a 1982 low of 0.16 to a 1986 high of 0.65 (0.51 to 0.78) (Fig. 11). This reversal can be interpreted as: (1) a 306% increase in the relative abundance of adult males, possibly due to a sharp reduction in the commercial harvest (to zero in 1983), or (2) a 58% decrease in the relative abundance of adult females. To examine which was more likely, we analyzed absolute abundance trends in males and females estimated by the NMFS trawl survey and found that the sex-ratio reversal was caused by a decline in the abundance of females rather than a resurgence of males. That is, from 1982 to 1986, male abundance remained essentially unchanged (+5%), while female abundance decreased by 88% (Fig. 6). By 1986 the Bristol Bay red king crab population was beset by two factors: high pre-collapse utilization rates (average $U_t = 0.43$), which rose to a maximum of $U_t = 0.62$ in 1980 as the population was collapsing (Table 1), and increasing mortality of mature females after 1982. Both of these factors appeared as trends in the annual sex-ratio data.

Trawling vs. brood-stock abundance

We examined the relationship between trawling and brood-stock abundance by separating the Bristol Bay brood stock into two components, each with different trawling histories: (1) the nearshore, Unimak-Amak-Black Hill component and (2) the offshore component north of Port Moller (Fig. 12). During 1980–1981, while the population was collapsing, the cumulative number of commercial tows in the Unimak area was 4.7 to 6.5 times the number in the offshore area. By 1996–1998, cumulative trawling in the Unimak area exceeded by 8–10 times that in the offshore area (Table 4).

We used the cumulative number of commercial tows (c_t) during the previous five-year period from year ($t - 4$) through year t to predict brood-stock density in year t (d_t). In the heavily trawled Unimak area, the relationship between density and cumulative trawling was estimated as follows:

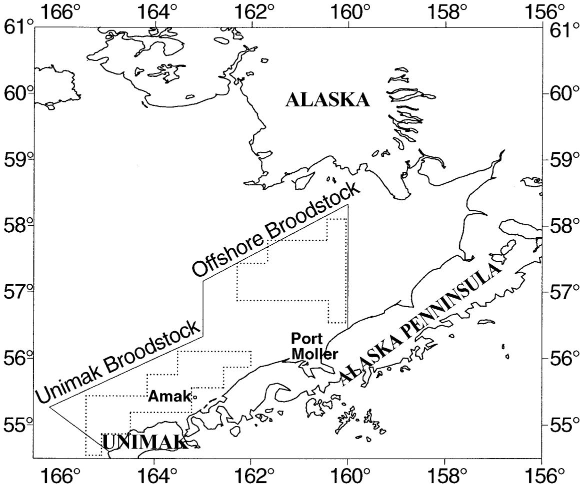

FIG. 12. Two 17 836-km^2 areas within the Pot Sanctuary with different trawling histories (Table 4) were used to compare brood-stock trajectories. By 1982 the Unimak brood stock had been subjected to 2.7 times more trawling than the offshore brood stock.

TABLE 4. A minimum estimate of the annual number, the cumulative total number, and the five-year moving cumulative total number (c_t) of commercial tows in two areas with different trawling histories.

	Unimak				Offshore			
Year	No. tows/yr	Cumulative total no. tows	c_t	Brood-stock density	No. tows/yr	Cumulative total no. tows	c_t	Brood-stock density
1975	0	0	0	1924.3	0	0	0	431.7
1976	0	0	0	2260.6	0	0	0	665.5
1977	2	2	2	3416.9	0	0	0	2178.7
1978	20	22	22	2855.3	0	0	0	2227.7
1979	22	44	44	1232.4	0	0	0	1522.5
1980	249	293	293	433.2	45	45	45	1016.2
1981	503	796	796	110.8	124	169	169	1531.3
1982	504	1300	1298	187.4	314	483	483	1308.6
1983	1052	2352	2330	16.6	788	1271	1271	168.2
1984	676	3028	2984	125.0	1271	2542	2542	458.2
1985	1387	4415	4122	66.6	2039	4581	4536	190.5
1986	1896	6311	5515	138.4	384	4965	4796	146.7
1987	1269	7580	6280	189.2	299	5264	4781	249.0
1988	3337	10 917	8565	275.7	523	5787	4516	43.9
1989	2981	13 898	10 870	90.7	5	5792	3250	181.1
1990	5825	19 723	15 308	532.1	46	5838	1257	147.1
1991	5220	24 943	18 632	31.6	383	6221	1256	174.7
1992	4216	29 159	21 579	2.0	217	6438	1174	327.1
1993	5053	34 212	23 295	58.4	18	6456	669	335.5
1994	6393	40 605	26 707	0.0	3	6459	667	261.2
1995	7134	47 739	28 016	63.3	1	6460	622	311.0
1996	6905	54 644	29 701	16.0	2	6462	241	324.3
1997	6989	61 633	32 474	14.4	20	6482	44	1062.0
1998	3717	65 350	31 138	159.1	0	6482	26	1223.7
Total	65 350				6482			

Note: Data for number of tows per year are from NORPAC; see *Methods.*

$$d_t = 4414.75(c_t + 1)^{-0.476} - 1$$

$$(r = -0.772;\ \mathrm{df} = 22).$$

In the lightly trawled offshore area it was estimated as

$$d_t = 1567.37(c_t + 1)^{-0.246} - 1$$

$$(r = -0.747;\ \mathrm{df} = 22).$$

A comparison of the linearized power relationships (Fig. 13) demonstrates that: (1) the initial density in the Unimak area was 2.8 times that of the offshore area (4415/1567 = 2.8); (2) the rate of decline of brood-stock density with trawling in the Unimak area was 1.9 times that of the offshore area (−0.476/−0.246 = 1.9), and these rates of decline were significantly different ($P < 0.05$); and (3) cumulative tows explained 60% (r^2) of the variation in brood-stock density in the Unimak area and 56% in the offshore area. During the time of peak trawling within the lightly trawled offshore area, c_{86} = 4,796 tows and the 1986 brood-stock density was predicted to be 194 crab/km^2, for a decrease of 88% from a 1975 initial level of 1,567 crab/km^2. In the heavily trawled Unimak area, c_{97} = 32 474 tows and the brood-stock density was predicted to decrease 99% from 4,415 crab/km^2 in 1975 to 30 crab/km^2 in 1997. The 1997 density in the Unimak area was predicted to be less than the 1997 density in the offshore area by a factor of 20. After a period of 24 years and 10 times as much trawling, the Unimak brood stock, initially 2.8 times more abundant than the offshore brood stock, fell to less than 1% of its 1975 abundance and remained about 5% as abundant as the offshore brood stock in 1998. Given the rate and magnitude of these declines, and considering that two different levels of trawling

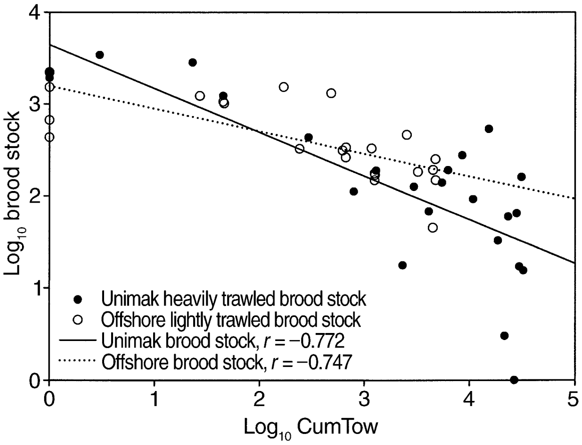

FIG. 13. The log–log relationship between brood-stock density and cumulative trawling (CumTow, c_t) in two areas, the lightly trawled offshore area and the heavily trawled Unimak area. The rates of brood-stock decline (slopes) are significantly different ($P < 0.05$).

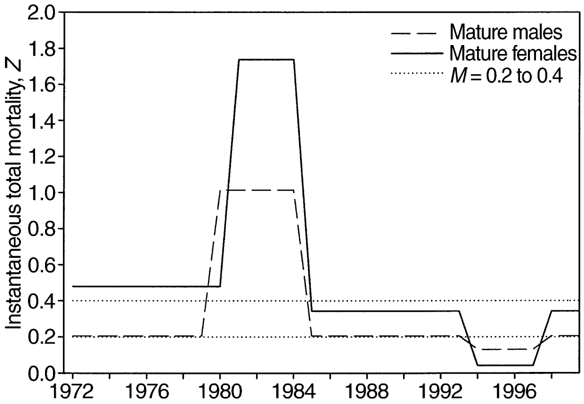

FIG. 14. Total (Z) vs. nautral (M) mortality for male and female red king crabs, Bristol Bay, Alaska, USA. Fishing mortality (F), is equal to $Z - M$.

activity in the Unimak and offshore areas each moved the local population quickly toward extinction, it is apparent that the survival of discarded, trawl-caught crab is negligible. That is, the long-term survival of red king crab affected by commercial trawling is insufficient to offset the mortality and social disruption caused by past and present levels of trawling within the Pot Sanctuary.

Fishing vs. natural mortality

Fishing mortality (F) can be separated from natural mortality (M) by partitioning total mortality ($Z = F + M$) (Ricker 1975). In a male-only fishery, female red king crab die either from natural mortality or as bycatch. Using the total mortality (Z) estimated for female red king crab in the length-based assessment model (NPFMC 2000, Zheng and Kruse 2002), we evaluated the relative magnitude of bycatch based on natural mortality values of $M = 0.2$ and $M = 0.4$, a range likely to include the true M for female red king crab, which is assumed to be equal to or slightly greater than that for males ($M = 0.2$). For the period 1981–1984 during which $Z = 1.738$ (Fig. 14), $F = Z - M$ was 1.338 to 1.538, and the rate of bycatch ($b = 1 - e^{-F}$) ranged from 0.7376 to 0.7852. Thus, assuming M varied between 0.2 and 0.4 during 1981–1984, 73.8 to 78.5% of all the mature females in Bristol Bay were estimated to die each year from fishing-bycatch mortality, and $(1 - e^{-Z}) - b$, or 3.9 to 8.7%, were estimated to die from natural mortality. That is, of the mature females dying each year, an estimated 89.5–95.3% were dying as bycatch and 4.7–10.5% from natural causes.

DISCUSSION

Endless-belt reproductive strategy

The significance of the Unimak brood stock may best be understood by considering its role in the downcurrent–upcurrent life-cycle strategy of Bristol Bay red king crab. Red king crab eggs hatch at the bottom of the water column and the planktonic larvae drift passively with water currents for 350–460 degree-days (Nakanishi 1987, Kurata 1960, 1961) until they settle to the bottom as very small crab to begin their lifelong epibenthic existence. At temperatures typical of nearshore Bristol Bay from Unimak to Port Moller during April–July (3–5°C), 350–460 degree-days translates to a drifting, planktonic phase of 2–5 months. Such an extended larval-drift period means that the larvae may settle to the bottom far from where they were hatched. It follows that optimum hatching locations are those that are an optimum distance upcurrent from optimum juvenile habitats. Historically the most productive red king crab spawning, incubation, and hatching grounds were located near and shoreward of the 50-m isobath of Bristol Bay, from western Unimak Island to Black Hill and Port Moller (Haynes 1974, Fukuhara 1985, Armstrong et al. 1986, 1993, McMurray et al. 1986, Hsu 1987, Loher 2001). Red king crab larvae hatched in these waters remain in suitable habitat during their larval-drift period by virtue of the nearshore current that flows to the northeast at about 2–3 cm/s from Unimak Pass along the Alaska Peninsula, toward the head of Bristol Bay (Schumacher and Kinder 1983, Loher 2001). Researchers believe that red king crab larvae hatched on these historically important grounds near the west end of the Alaska Peninsula have a better chance of remaining in good habitat and surviving to adulthood than do larvae hatched in central Bristol Bay (Armstrong et al. 1993), where most of the hatching occurs today.

According to Loher (2001), the loss of the Unimak–Amak multiparous females has decoupled Bristol Bay's largest expanse of prime nursery habitat from its larval supply. As a result, the highly productive nursery areas along the Alaska Peninsula near Port Moller and Black Hill have contributed only minimally to recruitment since the mid-1980s (Loher 2001). The historical migration of increasingly fecund females from northeast to southwest within the Pot Sanctuary, a migration implied by the 1975–1978 multiparity gradient (Fig. 2), is consistent with the basic endless-belt life-cycle strategy common among benthic invertebrates with planktonic larvae (e.g., Incze and Naimie 2000, Groeneveld and Branch 2002). It is possible that an evolutionary strategy to concentrate the brood stock's productivity at the upcurrent end of the coastal shelf in the Unimak–Amak region, a strategy successful over past ages, is now largely a dead-end migration into the densely trawled region of Cod Alley.

Regime-shift hypothesis

After the Bristol Bay red king crab population collapsed to less than 10% of its 1975–1980 abundance, theories abounded as to possible causes. The preeminent hypothesis with regard to the sudden collapse is the regime-shift hypothesis. Some regime-shift proponents believe that a 1977 climate change caused a catastrophic, three- to six-fold increase in the mortality of adult red king crab in the early 1980s (Zheng et al. 1995), and eliminated a spatially explicit, highly productive component of the Bristol Bay brood stock. Others (e.g., Tyler and Kruse 1996) theorize that the regime shift disrupted the historical stock–recruitment relationship between parents and progeny, effecting a series of recruitment failures that only became apparent in the early 1980s.

The mechanisms through which the meteorological regime shift is proposed to have acted on the adult stock are disease and increased groundfish predation by yellowfin sole (*Limanda aspera*) and Pacific cod (*Gadus macrocephalus*). The theory that groundfish predation caused the decline in crab abundance is unsupported by available data and was rejected by Kruse and Zheng (1999). Existing data indicate that yellowfin sole eat only the larvae of red king crab (Haflinger and McRoy 1983). Bakkala (1981) cited several food-habit studies showing that 50 different taxa were found in yellowfin sole stomachs throughout a broad area of the eastern Bering Sea, with no mention of red king crab as a prey item. Haflinger and McRoy (1983) characterized their yellowfin sole stomach-content data as ''uncertain'' because the estimated consumption of red king crab larvae was extrapolated largely from a single yellowfin sole (of 1,239 examined) that had eaten an extraordinary number of larval red king crab. Using Haflinger and McRoy's data, Jewett and Onuf (1988) calculated that the extrapolated number of red king crab larvae consumed by all the yellowfin sole in the southeastern Bering Sea may have represented 5% of the larvae available that year. If we account for the low reproductive value of an individual larva in terms of the estimated number of offspring it will likely contribute to the next generation, the population-level impact of larval losses on the order of 5–10% is negligible (e.g., Slobodkin 1970).

Similarly, extensive data on the food habits of Pacific cod in the eastern Bering Sea demonstrate that cod predation, which accounted for an estimated loss to the mature female red king crab population of 1–4% during 1981–1985 (Livingston 1989), was not a significant factor in the mature-female decline of 85–90% during the same 1981–1985 time period. Moreover, Livingston (1989) found that Bering Sea cod ate less red king crab as the abundance of crab declined, a density-dependent pattern common among predators with a wide spectrum of prey species. Thus, the mortality arising from cod predation on red king crab is compensatory. Unlike the depensatory effect of predation in a single-prey system, compensatory predation tends to stabilize a prey population, not drive it toward extinction (e.g., Whittaker 1975).

Separately, speculation persists that the regime shift resulted in environmental conditions that optimized the spread of an unspecified, epizootic disease instumental in the decline of the population (Otto 1985, 1986, 1989, Otto et al. 1989). Data and observations supporting the epizootic scenario are lacking, and it is difficult to envision tens of millions of diseased adult red king crab dying within 1 or 2 years without corroborating observations from scientists annually examining crab in the field or from fishermen transporting hundreds of thousands of live crab to market. Red king crab deadloss, i.e., the weight of crab dying on the way to the processors, ranged between 1.0% and 3.3% (average 2.0%) of the harvest during 1975–1980 (ADFG 2001). During 1981–1986, when the hypothesized epizootic would have been at its peak, the average deadloss decreased to 1.8%, with a range of 0.2% to 3.2%. Information published during the 20–25 years that have elapsed since the 1980–1983 Bristol Bay stock collapse does not support the premise that a regime-shift-mediated spike in the rates of predation and disease caused an increase in the natural mortality of adult red king crab.

At the other end of the life-history spectrum, Tyler and Kruse (1996) postulated that a mid-1970s regime shift toward lower barometric pressure in the Pacific Ocean may have caused a localized reproductive failure of red king crab in Bristol Bay, which materialized as a recruitment failure in the early 1980s. However, the correlation between barometric pressure and red king crab recruitment was significant only if Tyler and Kruse (1996) arbitrarily rejected the strong-recruitment data of 1970. The Tyler-Kruse (1996) recruitment-failure scenario is not consistent with the length-based assessment (LBA) model, used since 1995 to manage the Bristol Bay red king crab stock (Zheng et al. 1995, Zheng and Kruse 2002). Instead of a recruitment failure, the LBA model, which includes the 1970 recruitment data rejected by Tyler and Kruse (1996), indicates that year-class recruitment during the early 1980s was ''average'' and that it was the adult crab which suddenly disappeared. In fitting the LBA model to the NMFS survey data, Zheng et al. (1995) found it necessary to invoke an unidentified source of natural mortality to remove nearly 85% of the entire adult population in two years (1981–1982). It is unlikely that a somewhat subtle and recurrent, decadal, meteorological phenomenon could so abruptly exert this degree of direct mortality on a healthy population of adult crab.

Fishing vs. natural mortality

Within the context of the debate as to whether it was natural mortality or fishing mortality that caused the Bristol Bay stock collapse, it is important to know what is meant by ''natural'' mortality in the LBA model. Natural mortality (M) is usually defined as deaths from all causes except man's fishing (e.g., Ricker 1975). In the LBA model (Zheng et al. 1995, 1998), man's fishing is narrowly defined to include only the retained catch of legal male red king crab; natural mortality in the model comprises deaths from all other causes, including the fishing-bycatch mortality resulting from catching and discarding (1) females and sub-legal males in the directed, male-only red king crab fishery, (2) all red king crab caught in pot fisheries targeting other species such as Tanner crab, and (3) all red king crab caught in the groundfish trawl fishery. However, bycatch often substantially exceeds the retained catch. Data from Griffin et al. (1983) and ADFG (2001), which include no trawl bycatch, show that the 1982–1983 red king crab bycatch from the Tanner and red king crab pot fisheries (6.96×10^6 legal, sub-legal, and female crab) was 12–13 times that of the retained catch (0.54×10^6 legal crab). Representing all fishing bycatch mortality as natural mortality, as is done in the LBA model, results in a 5- to 9-fold mortality spike in 1980–1981 (NPFMC 2000, Zheng and Kruse 2002), coincident with an all-time record harvest and the beginning of commercial trawling in the Pot Sanctuary (Fig. 14). We believe that this kind of accounting overstates the role of natural mortality, masks the impact of fishing, and provides the regime-shift hypothesis with unwarranted support, without which the hypothesis is moot.

Fishing and sex ratio

Further devaluing the impact of fishing is the general consensus that imbalances in sex ratio have been negligible and have placed no constraints on reproductive success (Otto 1985). Loher (2001), relying on personal communication (Bradley G. Stevens, NMFS, Kodiak, Alaska, USA), stated that the sex ratio (m/f) has remained close to 1.0 over time ($m/[m+f] = 0.50$). Larkin et al. (1990) stated that m/f never fell below 0.83 males per female ($m/[m+f] = 0.45$) from 1969 through 1983. This consensus is inconsistent with the results of our examination of the adult sex ratio around the time of the population collapse. In 1981 the proportion of adult males in Bristol Bay fell to 0.25, approaching the level of 0.17 demonstrated by Wada et al. (2000) to inhibit successful reproduction in the spiny king crab (*Paralithodes brevipes*). A year later the Bristol Bay ratio dropped to a low of 0.16, consistent with observations that a substantial proportion of mature females, particularly large females, failed to molt, mate, and spawn in 1982 (Otto et al. 1989). It is likely that sex-specific fishing mortality, rather than natural mortality, caused the observed sex-ratio changes (Fig. 11).

With respect to red king crab reproductive success, the significance of the sex-ratio imbalance observed during 1981 and 1982 is best appreciated by considering that only about half of all mature males participate in spawning each year. The management of Bristol Bay red king crab, as specified in the harvest strategy (Zheng et al. 1997), relies on the assumption that all mature males ($\geq$120 mm carapace length) are capable of mating one or more times during each spawning season. This assumption fails to account for the fact that a substantial proportion of the mature-male population molts each year during the January through June spawning season. Evidence suggests that most of these red king crab, similar to the snow crab (*Chionoecetes opilio*) of Canada (Sainte-Marie et al. 1999, 2002), do not participate in mating in the same year they molt. Takeshita et al. (1989), using the 1966 tag-recapture data of Fujita et al. (1973), reported that only about 50% of mature males, mostly skipmolts, participate in Bristol Bay mating in any given year. Newly molted (new-shell) males tend to remain offshore as nonparticipants in the migration to inshore spawning areas. The Japanese tagging studies confirmed earlier 1958–1965 reports by Soviet scientists that new-shell males of reproductive size remained offshore along the 100-m isobath off Unimak Island and did not take part in spawning (Korolev 1964, Chebanov 1965, Rodin 1970, 1989). Both the Japanese and Soviet findings are consistent with the occasional large, NMFS-survey catches of new-shell, mature males collected during the spawning season from male-only aggregations at offshore stations >100 km away from known spawning grounds.

If only one-half of mature males participate in spawning each year, the overall sex ratio of 0.16 (1 male per 6 or 7 females) observed in 1982 translates to an effective sex ratio of 0.08, or 1 male per 12 or 13 females, which is substantially less than the proportion of males needed for successful reproduction in spiny king crab (Wada et al. 2000). Annual calculations of effective spawning biomass, integral to the State of Alaska's harvest strategy (Zheng et al. 1997) and considered to be an example of conservative management (e.g., Stevens et al. 2000: Appendix C), may overstate by a factor of two the male reproductive potential of the Bristol Bay red king crab population. This life-history trait appears to have been overlooked in the management of Bristol Bay red king crab (e.g., Zheng et al. 1995, Zheng and Kruse 2003, 1997). According to Rosenberg et al. (1996), when defining overfishing in federal fishery management plans, insufficient attention is often given to the life-history characteristics of specific stocks; and a definition that fails to consider that only half of the mature male crab participate in spawning in any given year is unlikely to protect the stock from overfishing.

In view of the information presented thus far, it may be unreasonable to maintain that the collapse of the Bristol Bay red king crab population was a product of natural mortality, with only a negligible contribution from fishing mortality. Using $M = 0.2$, the 1980 record harvest of Bristol Bay legal-male red king crab imposed a utilization rate (U_t) of 0.62, with a 95% confidence interval of 0.41–1.03, where the range reflects the -40% to $+50\%$ uncertainty of the 1980 population estimate. In hindsight it appears that a precautionary management stance should have recognized the June 1981 change in the sex ratio to 0.25, from the 1975–1980 average of 0.40, as an indicator of excessive male harvests. This notwithstanding, managers set the 1981 guideline harvest level (GHL) at 11.1–15.8 $\times$ 10^6 crab (ADFG 2001) to be taken from a NMFS source-population estimate of 11.3 $\times$ 10^6 crab (Otto 1986). During a 91-day extended season (up from 40 days in 1980), fishermen in 1981 managed to harvest only 5.3 $\times$ 10^6 crab, equivalent to an utilization rate of 0.50 (95% confidence limits: 0.41–0.64). In the following year, 1982, although the estimated numbers of exploitable males had decreased each of the four years since 1978 (Otto 1986), managers set the GHL range equivalent to a bounded utilization rate of 0.30–1.22. In doing so, managers were apparently unaware (e.g., Otto 1985, Loher 2001) that the sex ratio was now at a potentially dysfunctional level of 0.16. Crab managers have maintained that the harvest as a percentage of the harvestable stock (U_t) ''never exceeded 60%'' prior to the population's collapse (Otto 1986:104). However, for the six years leading up to the population's 1981–1983 collapse, bootstrap confidence intervals around estimates of the harvestable stock were, on average, -35% to $+44\%$, which is substantially wider than the original intervals ($\pm$15–20%) provided to resource managers (Otto 1986). Therefore confidence is low that harvest rates never exceeded 60%. Without a candid appraisal of the uncertainty associated with source-population abundance estimates, as well as an accounting of the natural mortality that occurs between the survey (May–June) and the fishing season (September–October), the actual fraction of the stock taken by the fishery is likely to be underestimated. A management strategy that maintains high male-only utilization rates in the face of both drastically declining population levels and a male-depauperate sex ratio and, as the population collapses, recommends a GHL equal to or greater than the estimated size of the source population, and then extends the fishing season in an effort to obtain this harvest (all of which happened in 1981), is a markedly aggressive strategy. However, it is possible that the effects of a highly exploitive fishery directed against the largest males in the population could have been reversed if, as managers assumed, directed fishing under management control was indeed the only source of fishing mortality affecting the population. Unfortunately, the assumption that the managed fishery was the dominant source of fishing mortality became untenable after 1979, when large-scale commercial trawling began in the Pot Sanctuary, a habitat that had served as a reproductive refuge for Bristol Bay red king crab since 1959.

Trawling bycatch numbers

Because the Pot Sanctuary excluded only foreign-vessel trawling, the brood-stock protection afforded by the Pot Sanctuary was effectively removed in 1977 by virtue of the 1976 Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) stimulus to domestic fishery development. The first incursion by domestic trawlers into the Pot Sanctuary was in the form of a 1980 pilot study to determine the feasibility and profitability of a joint-venture, U.S.-USSR fishery for yellowfin sole (Fisher 1980). The fish caught in a joint venture are defined as U.S. landings; but in 1980 there was no domestic market for yellowfin sole, and the product was transported to the USSR and marketed in the USSR and Africa (Fisher 1980). In 1980, the first year of joint-venture trawling in the Pot Sanctuary, when trawl effort was low relative to that which came later, the bycatch of red king crab in the Bering Sea/Aleutian Islands (BSAI) region increased by 371% over the 1977–1979 average. In the following year, the BSAI red king crab bycatch increased by another 235% over that in 1980. The 1980–1985 average bycatch of red king crab in the BSAI region, 85–90% of which came from the previously untrawled Pot Sanctuary representing only 3% of the total BSAI area, was 9.7 times the average bycatch of 1977–1979 (e.g., Nelson et al. 1981, 1982, 1983, Berger et al. 1984, 1985, 1987). These relative comparisons show that the proportionately small Pot Sanctuary provided a disproportionately large contribution to the total BSAI red king crab bycatch. Unfortunately, because of the qualitative nature of observer-bycatch data collected during the 1980s, it is not possible to quantitatively evaluate the direct impact of Pot Sanctuary trawling on Bristol Bay red king crab.

The hypothesis that trawling on the spawning stock contributed to the collapse of the Bristol Bay red king crab population has been discounted by investigators (e.g., Otto 1986, Stevens 1990, Armstrong et al. 1993) who accept at face value estimates of the absolute numbers of crab caught and killed by trawling, estimates published (e.g., Nelson et al. 1981, 1982, 1983, Berger et al. 1984, 1985, 1987) with no warnings that they were biased low. However, it is important to note that the red king crab data collected by observers during the yellowfin-sole joint venture are not suitable for quantitative analysis. The observer, restricted to a foreign processor and unable to monitor the domestic vessels doing the trawling, collected data only from delivered catches that were of commercial value and placed in deck bins to await processing. At least in 1981, catches (red bags) dominated by red king crab, a prohibited species of no commercial value to the joint venture, were unloaded near the stern ramp of the processors (e.g., Fig. 7) and discarded without analysis (Doug Smith [former NMFS observer], *personal communication*). As it became obvious that such deliveries were impolitic, some catcher vessels simply jettisoned red bags at sea, using cod-end zippers or other means (Kris Poulsen, *personal communication*). Other participants in the joint venture confirmed the red-bag phenomenon but declined to be cited here. As conducted, the observer counts systematically excluded from consideration all but a biased, disproportionately small fraction of the total red king crab bycatch from trawling in the Pot Sanctuary during the 1980s. The bias results from the fact that, as the number and size of the unexamined red bags increased, the proportion of the total bycatch analyzed by an observer decreased. The relationship between an observer's daily sample and the real bycatch for that day is unknown; therefore a meaningful extrapolation from samples to total bycatch is not possible. Over the past 20 years investigators, unaware of the uncounted red bags, have provided estimates of trawling impact based on bycatch numbers that are far too low. The bias associated with the failure to account for red bags was greatest during the years surrounding the population's collapse when, because of relatively high population densities, the probability of red bags was greatest. However, observer counts tend to be biased low even today because of the removal of prohibited species from a haul prior to an observer's sampling, a scheme known as ''pre-sorting'' (NMFS/OST 2000: 327, van Zile 2002).

Regime shift vs. human fishing

Theories as to what happened to the Bristol Bay red king crab population fall into two broad categories. The regime-shift category, comprising all sources of natural mortality, holds that the abrupt stock collapse was due to factors beyond human control and was neither caused nor hastened by fishing, direct or indirect (e.g., Otto 1986, Tyler and Kruse 1996). The depletion category, comprising all sources of fishing mortality, maintains that the collapse was caused by overfishing (e.g., Kruse et al. 1996, Orensanz et al. 1998). With regard to the regime-shift category, the science of detecting large-scale, meteorological phenomena such as the Pacific decadal oscillation is relatively well developed; but the science of evaluating their microscale effects on local populations is not. After an exhaustive literature search, Paul (1985) concluded that there was virtually no existing information on the recruitment process or the factors that modify ocean survival of Alaska red king crab larvae. Ten years later Sinclair and Frank (1995) concurred, saying that even though the large-scale description of shifts in atmospheric conditions are robust, the lack of detail makes it difficult to consider the underlying processes by which the physical environment influences population responses. So little is known about population-level effects that consensus is lacking among king crab investigators as to whether the regime shift negatively affected early-life-stage recruitment (e.g., Tyler and Kruse 1996), or whether it directly killed pre-adult and adult crab, a necessary conclusion based on the LBA model (Zheng et al. 1995).

Inasmuch as estimates of early-life-stage recruitment do not exist, the linkage between environmental regime shifts and recruitment is a matter of speculation. There are no larval or early-juvenile sampling programs by which early year-class strength, or annual recruitment to the age-0 or age-1 Bristol Bay red king crab population, might be directly assessed. Instead, recruitment success for any given year is assumed to be proportional to the number of crab that appear in survey trawls 6–8 years later, at age 5–7. This assumption overlooks the possibility that unobserved fishing mortality during the intervening years might alter the relationship between year-class strength and adult abundance (thus introducing bias to the stock–recruit function as well). For example, if unobserved bycatch from the 1983 commercial-trawl fishery was substantial enough to markedly reduce the number of age 5–7 crab counted in the 1984 survey, then the low counts might be mistakenly attributed to poor recruitment during 1976–1978. As for the regime shift causing recruitment failure, the larger, older crab in the Bristol Bay stock went through their most precipitous decline in 1981 (NPFMC 2001). Assuming an age of at least eight years for a legal red king crab (Balsiger 1974), the negative effects of the regime shift on the larval recruitment of crab that became legal in 1981 would necessarily have occurred in 1972–1973, or at least four years too early for the regime shift that occurred in 1977 (Benson and Trites 2002). Such arithmetic exercises, while admittedly simplistic, are inconsistent with the scenario of a population collapse via a recruitment failure imposed by the 1977 regime shift. Moreover, it is unlikely that a large-scale, meteorological regime shift would have acted in a spatially explicit way, as described by Loher (2001), to eliminate the brood stock from the heavily trawled Unimak area where it was most abundant, while leaving the brood stock relatively unscathed in the lightly trawled, offshore area where it remains today (Figs. 2 and 9).

Management based on regime shift

Although its effects on red king crab are unknown and perhaps unknowable, the regime shift is the primary justification for the continued exploitation of a stock that has undergone one of the more dramatic collapses in the history of U.S. fisheries management and now persists at a level well below its 1975–1980, pre-collapse abundance. Managers have used the 1977 regime shift and its hypothetical effects on the environment and ecology of Bristol Bay to redefine the Bristol Bay red king crab population to be, in effect, a population with no history prior to 1983. In this way, the high-abundance years of 1975–1980, years in which the fishery extracted a total of 232 × 10^6 kg or 70–80 million legal-male red king crab from Bristol Bay, are not included in the baseline average used to evaluate whether the stock is overfished. A stock is overfished, and a rebuilding plan must be prepared for the stock, if it falls below a critical level known as the ''MSST'' (minimum stock-size threshold), defined as 50% of the baseline average (maximum sustained yield, MSY) stock size (NOAA 1998*a*, *b*). The current baseline period used by managers to calculate the MSY stock size consists of only the post-collapse years, 1983–1997 (e.g., Rugolo et al. 2001: Appendix C). Using an expanded 1975–1997 baseline, which includes the high-abundance, pre-collapse years for which we have data, results in a doubling of the legal-male MSST. Thus, the rebuilding requirement is triggered sooner, at a higher stock-size level. Using the expanded (1975–1997) baseline, the legal-male stock size falls below MSST in 4 of the 12 years between 1986 and 1997; using management's current (1983–1997) baseline, the stock does not fall below MSST in any year between 1986–1997. The use of a more conservative MSST would indicate an awareness of or concern for the fact that the stock being exploited suffered a precipitous, $>$90% decline during 1978–1983. In our opinion, resetting the historical baseline to include only the remnants of a population in the aftermath of a catastrophic collapse defeats the purpose of the guidelines under MSFCMA.

NMFS guidance as to precautionary implementation of the MSFCMA recommends caution in interpreting a long run of poor recruitment as the result of an environmentally driven change in stock productivity. In particular, for a period of declining abundance, the burden of proof rests on managers to demonstrate that it was the environment, and not fishing, that caused the abundance decline (Restrepo et al. 1998). However, for Bristol Bay red king crab it appears that this burden may not have been met. Instead, the preponderance of the evidence we have presented points not to the environment but to fishing as the cause of the decline. If the 1977 regime shift caused an abrupt discontinuity in the reproductive success of Bristol Bay red king crab, and if this discontinuity persists today as a feature of red king crab population dynamics, then the current practice of using a single stock–recruitment function to define the long-term (1968 to present) relationship between parents and progeny, as is done in the LBA model (e.g., Zheng and Kruse 2003, Zheng et al. 1995), violates the principle of stationarity (Hilborn and Walters 1992) and should be abandoned. Using the burden-of-proof recommendation by Restrepo et al. (1998) and casting aside the regime shift hypothesis as untestable, it is likely that the Bristol Bay red king crab population exists and has existed since the late 1970s in a state of chronic overexploitation.

Many fishing practices continue even when past experience and abundant scientific evidence demonstrate that these practices are ultimately destructive (Ludwig et al. 1993). In Alaska, the destructiveness of bottom trawling as a fishing method for red king crab was soon recognized by fishermen and conservationists alike, and by 1960 the practice had been made illegal in all Alaskan waters (Nickerson et al. 1966, Otto 1985). Furthermore, the lessons learned from Japanese research on the Kamchatka population stressed the importance of providing sanctuaries for newly settled juveniles and breeding adults, where fishing of any kind was prohibited (Marukawa 1933). Consistent with Marukawa's (1933) recommendation, the Japanese Pot Sanctuary boundaries in Bristol Bay were drawn in 1959 to include the mainstay of the population's brood stock (Hsu 1987, Loher 2001), the population's primary spawning grounds (Fukuhara 1985, Hsu 1987, Loher 2001), the area of greatest larval release (Haynes 1974, Fukuhara 1985, Armstrong et al. 1986), and prime juvenile habitat most likely to produce adults (McMurray et al. 1986, Armstrong et al. 1993). Despite the wisdom gained from red king crab investigations over the past 70 years, the value of the Bristol Bay Pot Sanctuary in safeguarding the population's reproductive potential was overlooked or ignored in the process that led to an expanding regime of unmonitored trawling by U.S. domestic vessels on the very brood stock that, by most accounts, contributed the bulk of the replacement numbers to the red king crab population in its ascendancy. Trawling in the high-fecundity Unimak brood-stock area began in 1977, the year the MSFCMA took effect, and expanded rapidly after 1979 (Table 4). Between 1977 and 1983 the number of trawls in the Unimak area increased by a factor of about 1200. By 2001 more than 80 000 commercial trawls had been hauled through this 17 836-km^2 area, and the once-productive Unimak brood stock had essentially disappeared.

More than 20 years after the 1980–1983 collapse of the Bristol Bay red king crab population, the stock has not recovered; nor is there a trend suggesting that recovery is imminent. This decades-long refractory period has persisted under the following management assumptions: (1) that the 1977 regime shift adversely affected the long-term productive capacity of the stock, (2) that fishing was not a major factor in the stock's decline, and (3) that the Unimak–Amak habitat essential to the population's reproductive strategy needs no protection from bottom trawling. We have presented information indicating that these assumptions are suspect. The first assumption, which allowed managers to respecify the stock as one whose history began in 1983, has enabled continued exploitation of the collapsed Bristol Bay stock without the benefit of a rebuilding plan or a defined, mandatory reduction in fishing mortality. Such respecification is consistent with NMFS guidance on National Standard 1 (NOAA 1998*b*) for a stock whose long-term productive capacity has been affected. However, implicit in management's use of a single spawner-recruit curve for the period 1968 to present (e.g., Zheng and Kruse 2003) is the assumption that recruitment from a given number of spawners has remained unchanged over the past 36 years. If it is true, as we believe, that the primary cause of the red king crab collapse was human fishing, then it is incumbent upon managers to revisit the decision to continue exploiting the stock without a formal rebuilding plan. A critique of existing management strategies via the rebuilding-plan process might lead to a better understanding of important life-history characteristics overlooked in the past. For example, it should be possible to improve estimates of male reproductive potential, effective spawning biomass, and stock–recruitment relationships by acknowledging that only about 50% of mature males are available to spawn each year. More importantly, consideration by managers of the apparent ontogenetic downcurrent–upcurrent reproductive strategy of red king crab may once again highlight the importance of the western end of the Alaska Peninsula as the driver for the endless-belt cycle common to self-sustaining populations of red king crab. At present, the relatively few multiparous females gathering to incubate and hatch their eggs in the Unimak–Amak region are exposed to an historically high probability of being dispersed, injured, or killed by trawling rather than contributing progeny to the next generation.

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