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Crustacean resources are vulnerable to serial depletion – the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska

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Abstract

The seas around Alaska support (or have supported) some of the most commercially significant crustacean stocks in the world, spread over an overwhelming array of extensive and diverse coastal and open shelf areas. Major resources include three species of king crab (*Paralithodes* spp. and *Lithodes aequispina*), Tanner and snow crab (*Chionoecetes* spp.), Dungeness crab (*Cancer magister*), and five species of pandalid shrimp (*Pandalus* spp. and *Pandalopsis dispar*). Excluding the Bering Sea, the resources from the Greater Gulf of Alaska (ranging from the Aleutian Chain to the state's south-eastern panhandle contiguous with British Columbia) supported rapid expansion of several crab and shrimp fisheries during the 20 year period 1960–1980. Since then, most of those fisheries have collapsed. While some of the stock declines have been well documented and discussed (most prominently the 'dethroning' of red king crab on the shelf around Kodiak Island), it has been less apparent that the demise of Alaskan crustacean stocks is a process on a much larger scale, and is still unfolding. Here we examine trends in catch, recruitment and abundance (when possible) and discuss existing evidence of overfishing and management options. We emphasize the importance of recognizing the multi-scale spatial structure of crustacean stocks, and suggest the need to consider spatially explicit strategies, particularly the creation of reproductive refugia.

Keywords: collapse, crab, Crustacea, fisheries, metapopulations, overfishing, recruitment, refugia, serial depletion, shrimp.

Introduction

'Collapse' is one of the most frequently used words in the current debate concerning how fisheries should be managed, and ultimately whether they can be sustainably exploited. Fishery collapses have motivated scientific scrutiny of various hypotheses (e.g. climate vs. overfishing), examination of the eventual failure of the management systems involved, cross-incrimination among the various sectors in those systems (fishers, scientists, managers, politicians), exposés by the press, outrage by the public, and finger-pointing by the conservation movement. In 1995 *The National Geographic* and *The Ecologist* dedicated full issues to the overfishing problem (Fairlie, 1995; Parfit, 1995), a subject that the public rarely heard about until not too long ago. Fifteen years earlier, a comparable Special Issue published by *BioScience* sounded far more optimistic; only one essay addressed (among other subjects) the economics of overfishing (Clark, in Steele, 1981).

Impetus for increased focus on fishery collapses is a natural extension of growing emphasis on the conservation aspect of fishery management which, while having originated from the agenda of conservationist non-governmental organizations, has gained its own momentum over the last decade or so. Perhaps the most recent catalyst has been the commercial extinction of northern cod off Newfoundland and Labrador (eastern Canada) by 1992 (Hutchings and Myers, 1994). This was not the most spectacular collapse in recent memory: it is dwarfed by the mega-collapse of the Peruvian anchoveta twenty years earlier, the effects of which resounded for years along the Humboldt Current ecosystem and across Peruvian society (Clark, in Steele, 1981). But the cod crisis came at a time when sensitivity was high, and it occurred in a developed country with the best standards of scientific expertise, managerial skills, and political openness to be found, one that invests substantially in the monitoring of its fisheries. In the wake of the collapse of the cod fishery, many were left with the impression that the ultimate debacle was that of fishery science and management as we have known them. In this context it has become urgent to define, identify, document, compare and explain fishery collapses worldwide, and to draw the appropriate lessons (Walters and Maguire, 1996).

The crustacean fisheries of Alaska provide notable examples of fishery collapses, those of the red king crab, *Paralithodes camtschaticus*, from the eastern Bering Sea (1980/1982) and the Gulf of Alaska (1966/1968 and 1981/1983) being the best known among them (Wooster, 1992). Before 1982, red king crab had become the second most valuable seafood industry in the State, second only to the combined six salmonid species. It boosted the economy to the point that the small port of Dutch Harbor received landings the value of which was higher than that of the most important ports of the West Coast of the United States combined; by 1983, however, Dutch Harbor looked like a "ghost town" (Wooster, 1992). Emphasis on those selected, spectacular study cases conceals the fact that they are part of a more general phenomenon, which has not run its historical course but is still unfolding.

Several commercially valuable crustaceans have supported fisheries around Alaska, including lithodid, majid and cancrid crabs, and five species of pandalid shrimp (Table 1). Those fisheries are spread over an extensive and diverse array of coastal and open shelf areas: the eastern Bering Sea (including Bristol Bay), the Aleutian Chain, the continental shelf adjacent to the Gulf of Alaska, extensive closed areas such as Cook Inlet and Prince William Sound, and the inner passages and fjords of the State's south-east panhandle (Fig. 1). This review is concerned with the crustacean fisheries from the Greater Gulf of Alaska and adjacent areas including the south-east and the Aleutians. The eastern Bering Sea has been excluded because it constitutes a distinct, self-contained geographical unit, and its crustacean fisheries have been profusely documented and reviewed (Otto, 1982, 1986, 1990).

Because market value varies substantially among species, the best way to portray an aggregated picture of Alaska's crustacean fisheries from the Greater Gulf of Alaska is as ex-vessel value of the catches during the 40 year period 1955–1995, adjusted for inflation. Red king crab comprised the largest fraction (42%) of the aggregated historical value of the catch, followed by Tanner crab (23%; *Chionoecetes bairdi*),

Table 1. Commercially important crustaceans from the Greater Gulf of Alaska. Sources: [1] Hart (1982), [2] Garth (1958), [3] Hosie and Gaumer (1974), [4] Jensen and Armstrong (1987), [5] Armetta and Stevens (1987), [6] Somerton (1985), [7] Butler (1980)

Classification	Common name	Geographic range
Section Brachyura	True crabs	
Family Majidae		
Chionoecetes opilio	Snow crab	Arctic, circumboreal; SE Bering Sea[1]
Chionoecetes bairdi	Tanner crab	SE Bering Sea – Oregon[2,3]
Family Cancridae		
Cancer magister	Dungeness crab	Pribilof Is. – Monterey Bay, California[4]
Family Cheiragonidae		
Erimacrus isenbeckii	Korean hair crab	Pribilof Is. – Unimak Pass[5]
Section Anomura	Anomuran crabs	
Family Lithodidae		
Paralithodes camtschaticus	Red king crab	Chukchi Sea – N. British Columbia[1]
Paralithodes platypus	Blue king crab	Chukchi Sea – SE Alaska[6]
Lithodes aequispina	Brown king crab	Bering Sea – S. British Columbia[1]
Section Caridea		
Family Pandalidae	Pandalid shrimp	
Pandalus borealis eos	Pink shrimp	Point Barrow – Columbia River estuary[7]
Pandalus goniurus	Humpy shrimp	Chukchi and Bering Seas – Puget Sound[7]
Pandalus hypsinotus	Coonstripe shrimp	W. Bering Sea – Puget Sound[7]
Pandalus platyceros	Spot prawn	East Aleutians – Southern California[7]
Pandalopsis dispar	Sidestripe shrimp	Pribilof Is. (Bering Sea) – Oregon[7]

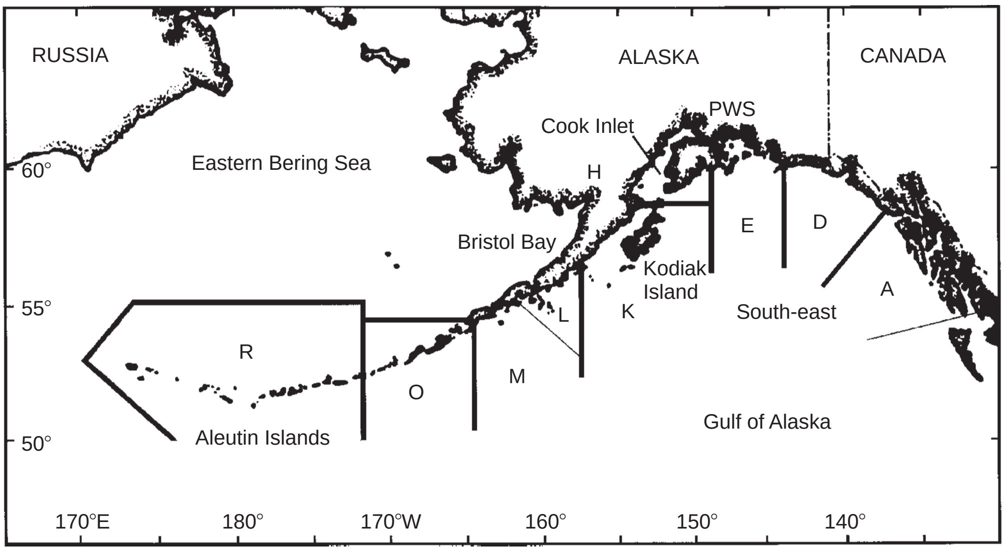


Fig. 1. The Greater Gulf of Alaska, with indication of management areas. A, South-east; D, Yakutat; E, Prince William Sound (PWS); H, Cook Inlet; K, Kodiak; L, Chignik (defined only for some resources, for others pooled with M); M, Peninsula; O, East Aleutians; R, West Aleutians.

brown king crab (13%; *Lithodes aequispina*), pink shrimp (12%; *Pandalus borealis eos*), and Dungeness crab (10%; *Cancer magister*). The contribution of other species including blue king crab (*Paralithodes platypus*), hairy crab (*Erimacrus isenbeckii*), spot prawn (*Pandalus platyceros*), and other shrimp species (Table 1) is negligible, although the relative significance of some of them has increased in recent years. The spot prawn fishery from SE Alaska, for example, was worth $2.1 million in 1991/92, making this the fourth most valuable fishery for the region. The value of the aggregated catch derived from the crustacean stocks of Alaskan waters exclusive of the Bering Sea grew steadily during the 1960s and 1970s, peaked during the early 1980s (at about 200 million 1995 US$), and has dropped since to slightly more than 20% of the historical maximum. Because the price of some important items (king and Tanner crab) has increased in real terms (Fig. 2, middle field), this collective decline is even more dramatic when portrayed as catch of the individual resources (Fig. 2, left field).

The dynamics and management of crustacean stocks exploited in Alaska have been traditionally considered from a resource-by-resource, area-by-area perspective (but see Kruse, 1993, for an exception). Simultaneous examination of historical data reveals a pattern that repeats itself at all spatial scales: *serial depletion of resources*. Historically fisheries were first developed to target the most lucrative species, then switched to others after the former showed signs of depletion. At the mega-scale of the entire region of interest, this serial depletion becomes clear in sequential patterns of rise–peak–demise in total catch shown by the red king crab, shrimp, Tanner crab and brown king crab fisheries, in that order (Fig. 2, left field; the aggregated Dungeness crab fishery has been comparatively stable.) A similar pattern unfolds when individual management areas are examined, as illustrated in Fig. 3 for Prince William Sound. Fisheries boomed and busted serially, starting with the most valuable and plentiful resources (red king crab, Tanner crab, pink shrimp, in that order), then switched to less significant ones (spot prawn, brown king crab, sidestripe shrimp, in that order).

Much of the information on Alaskan crustacean fisheries has been collected, analysed and published by the staff of the Alaska Department of Fish and Game (ADF&G). We based our inquiry on publicly available data and published documents, and conducted the analyses at the level allowed by the grain of those data; constraints of confidentiality often impose a limit on the level of aggregation in the analyses. In that sense, our essay can be viewed as an outsider's perspective. Whenever possible, we used simple population models to bring together various pieces of information. We were most interested in unveiling trends, particularly their correspondence (or lack of it) across different management areas, and in making interspecific comparisons of patterns.

We close our overview with a discussion of problems that we perceive as central to the assessment and management of the crustacean stocks of Alaska and which apply as well, we believe, to high-latitude, cold-water decapod species worldwide. We emphasize specific ways of assessing the occurrence of recruitment overfishing, and the importance of acknowledging the hierarchical spatial structure of shellfish stocks. Consequently, we stress the need to design management strategies around the theme of spatial controls, as opposed to the traditional emphasis on quotas, threshold levels and reference points associated with management under the unit stock paradigm and the dynamic pool assumption.

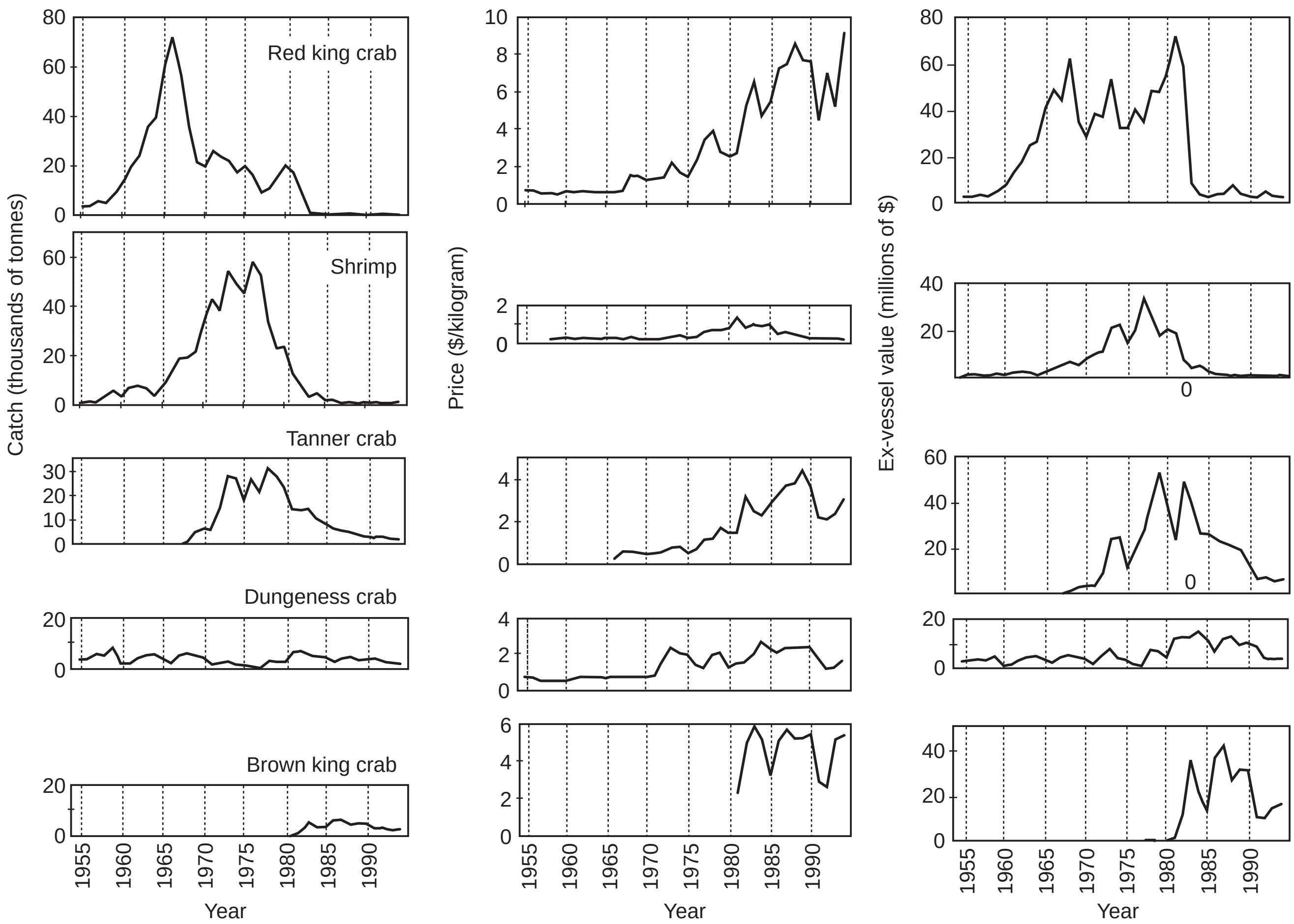


Fig. 2. Historical trends of landings of major crustacean resources from the Greater Gulf of Alaska. Left, catch; middle, unit ex-vessel price; right, ex-vessel value of the catch. Values standardized to 1983 US$; the 'all items' (CPI-U) index was used in the adjustment (USA, 1995).

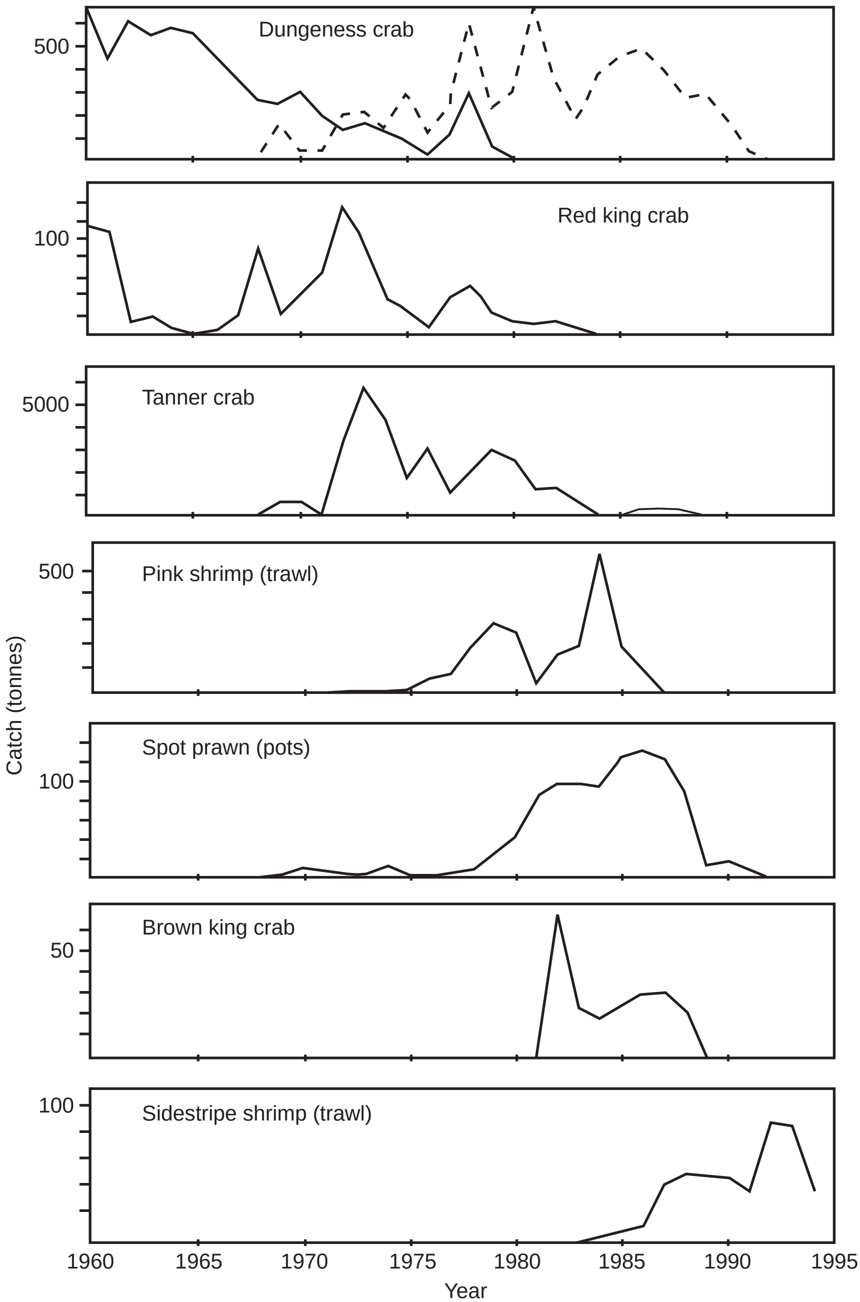


Fig. 3. Historical trends in landings from the Prince William Sound (PWS) management area. In the case of Dungeness crab, the solid and dashed lines correspond to the Orca Inlet and Copper River fisheries, respectively.

The data

SOURCES

The main source of data was ADF&G's fishing ticket database (ADF&G, 1992), which contains information on catch (in weight and numbers), gear and effort (permits, landings, potlifts). For each species, data from the ticket files were aggregated at the level of management area and by year. Some of the ADF&G reports summarize recent data by fishing season (overlapping consecutive years); differences in the results obtained by using data grouped by calendar year or fishing season proved negligible for the purpose of our analyses. Attempts to examine data at geographic scales finer than management areas were unsuccessful owing to confidentiality restrictions. We aggregated data for analysis and presentation at the level of management areas as defined in ADF&G (1992; Fig. 1), with one exception discussed below. The ticket database (ADF&G, 1992) lists four areas within the SE Alaska Region: Juneau (A), Ketchikan (B), Petersburg (C) and Sitka (D). For management purposes, however, the SE Alaska Region is divided into two areas: South-east (A) and Yakutat (D), which do not match the areas recorded in the ticket file. Data were pooled for the entire South-eastern Region in our analyses. Data on red king crab made available from the ticket database contained little information corresponding to the Kodiak, Peninsula and Cook Inlet management areas, and so data on catch and effort for the first two areas were extracted from tables in Spalinger and Jackson (1994). Data on catch for the Cook Inlet management area were obtained from tables in Kimker *et al.* (1993), but effort data were not available. With regards to Prince William Sound, excerpts from the ticket database contained catch and effort data for the period 1979–1984 only. Data on catch in weight for pooled king crab species for the period 1960–1978 were obtained from tables in Trowbridge (1994a,b).

Every effort was made to compare data extracted from the ticket database with those published in technical reports; discrepancy often led to new data requests, and in a few cases to disregarding an entire data set. Species of king crab and shrimp were not differentiated before 1976. This did not pose a major difficulty in the case of king crabs because blue king crab catches are relatively insignificant in most areas, and brown king crab became significant only in the Aleutian Islands during more recent years. Therefore, pre-1976 landings of 'king crab' were considered as red king crab.

Another substantial data set corresponds to pot surveys of king crab conducted in the Kodiak area between 1973 and 1986 (Blau, 1985, 1986), which are publicly available (Denby and Tukey, 1990; Tukey, 1990).

FISHING EFFORT AND *CPUE*

Pot fisheries

ADF&G's ticket files and *Regional Information Reports* contain data on three correlates of fishing effort: *permits*, which correspond to the number of vessels participating in the fishery, *landings*, and *potlifts*, which in the case of trap gear correspond to individual pots lifted. We chose to use catch/potlift as our index of *CPUE* (catch per unit effort) in the case of the king crab, Tanner crab, and spot prawn fisheries. While presumably a better correlate of abundance than either catch/landing or catch/permit, catch/potlift may be biased as an index of abundance owing to gear saturation and to non-random allocation of effort by the fleet. Abundance estimates based on catch/potlift data may be biased downwards when abundance is high owing to gear saturation, and upwards when abundance is low as the fleet tends to concentrate on pockets of high density. Johnson (1991) found that commercial *CPUE* was proportional to abundance in the Kodiak Area, except in 1982 (the last year of the fishery) when it was higher than expected. This was partly explained by the public dissemination of pre-season survey data for the first time, that increased the fishing power of the fleet. Johnson (1991) also investigated the effect of changes in the Kodiak fleet on catch/potlift. Although length or gross tonnage of the vessels had a significant effect on catch rate, standardization of effort had very little effect on average *CPUE*.

The ticket files contain catch data on Dungeness crab starting in 1960 (SE Alaska) or 1963 (Prince William Sound, Cook Inlet, Kodiak), and effort (landings) in 1969 (all areas). The best series corresponds to the Kodiak area. All the correlates of effort are linearly related to each other. The relation between catch/potlift and catch/landing is also linear, with the exception of 1977; the biennium 1976–1977 was peculiar in having the lowest historical levels of effort. The pattern seems to indicate that the composition and behaviour of the fleet have changed little since 1969. Data for other areas are less consistent, but permits and landings are linearly related to each other in all the areas. Potlift data for areas other than Kodiak are either available for a shorter period than landings, completely missing, or inconsistent. For that reason, and considering the linear relation observed between the different correlates of effort, we decided to use catch/landing as our standard measure of *CPUE* in the case of Dungeness crab fisheries.

Trawl fisheries

Trawl shrimp fisheries are multispecific because of overlapping distribution of pink, humpy (*Pandalus goniurus*), coonstripe (*P. hypsinotus*), and sidestripe shrimp (*Pandalopsis dispar*). Before 1976, catch statistics were lumped into a single category, 'general shrimp', which corresponds almost exclusively to pink shrimp. In addition, multiple types of gear and a wide range of vessel sizes complicate analyses of fishing effort and *CPUE*. Beam and small otter trawls are fished in open waters on open mud–sand substrate. Larger vessels (50 to 100 feet; 15–30 m) rigged with one or two otter trawls fish farther offshore, while smaller beam trawlers (20 to 40 feet; 6–12 m) ply coastal grounds (Gaffney, 1981). The major portion of the total catch has been taken by double and single otter trawlers. Often data were censored in certain years owing to few participants for a category in a given statistical area. Number of potlifts is also recorded in the case of trawl gear, but meaning is not clear in that case and so was not used. Exploration of the data indicates inconsistencies with the notion of a haul:pot analogy. Landings may be inappropriate as a basis to calculate *CPUE* because vessels may stay at sea until they reach their holding capacity. No *CPUE* was calculated in the case of the trawl fisheries.

Biological background

Salient features of the life history of commercially valuable crustacean species from Alaska are summarized in Tables 2 and 3. Three aspects addressed below are most important from the viewpoints of assessment and management.

Table 2. Life history characteristics of commercially important crab species from the Greater Gulf of Alaska. Sources: [1] Schmidt and Pengilly (1990), [2] Otto (1985), [3] Jewett *et al*. (1985), [4] Stevens *et al*. (1993), [5] Butler (1961), [6] McCaughran and Powell (1977), [7] Donaldson *et al*. (1981), [8] Kondzela (1986), [9] Powell (1967), [10] Cleaver (1949), [11] Shirley *et al*. (1989), [12] Jensen and Armstrong (1989), [13] Wolotira *et al*. (1984), [14] Paul (1984), [15] Matsuura and Takeshita (1990), [16] Somerton and MacIntosh (1985), [17] Hankin *et al*. (1985), [18] Otto *et al*. (1990), [19] Somerton and MacIntosh (1983), [20] Butler (1960), [21] Hart (1982), [22] Marukawa (1933), [23] Hoffman (1968), [24] Bartlett (1976a), [25] Somerton (1981), [26] Shirley *et al*. (1987), [27] Kondzela (1987), [28] Haynes (1982), [29] Reilly (1983), [30] Powell and Nickerson (1965). Abbreviations: CL, carapace length; CW, carapace width; TL, total length

Trait	Red king crab	Blue king crab	Brown king crab	Tanner crab	Dungeness crab
Males					
Size at functional maturity	130 mm CL[1] (Kodiak)	70–110 mm CL[2]	92–130 mm CL[3] (varies with lat.)	119 mm CW[4] (Kodiak)	140 mm CW[5] (Br. Columbia)
Mean age at maturity	7 years (Kodiak)[6]	Unknown	Unknown	6–7 years (Kodiak)[4,7]	3 years (Kodiak)[8]
Morphologically distinct terminal instar	No	No	No	Yes	No
Maximum size	227 mm CL[9]	190 mm CL[2]	220 mm CL[2]	200 mm CW[7]	254 mm CW[10]
Mean age of recruitment to the fishery	8–9 years (Kodiak)[6]	Unknown	Unknown	7–8 years (Kodiak)[7]	5 years (Kodiak)[8]
Females					
Size at functional maturity	89 mm CL[19] (Bristol Bay)	70–110 mm CL[2]	98–110 mm CL[3]	83 mm CW (Kodiak)[7]	100 mm CW[20] (Br. Columbia)
Maximum size	195 mm CL[21]	170 mm CL[2]	192 mm CL[2]	110 mm CW[2]	170 mm CW[21]
Ability to retain sperm	No[9]	No[9]	No[9]	Yes[14]	Yes[17]
Larval duration	1.5–3 months[22]	2 months[23]	Unknown	4 months[24,25]	5 months[26,27] (SE Alaska)

Number of larval stages	4 zoeae + 1 glaucothoe[22]	4 zoeae + 1 glaucothoe[23]	4 zoeae + 1 glaucothoe[28]	2 zoeae + 1 megalops[24]	5 zoeae + 1 megalops[29]
Egg bearing period	11–13 months[30,11]	14–15 months[16,12] (biannual spawn.)	1 year[2]	1 year[25]	8 months[26]
Larval hatching	February–June[2]	April–July[2]	Unknown	March–July[13]	August–October[26] (Alaska)
Size at settlement	0.5 mm CL[22]	2.6 mm CL[23]	5–6 mm TL[28]	3.4 mm TL[24]	11 mm TL[29]
Maximum age	>20 years[15] (Japan)	17 years[16]	Unknown	12–15 years[5] (Kodiak)	8 years[18] (Br. Columbia)

Table 3. Life history characteristics of commercially important shrimp species from the Greater Gulf of Alaska. Sources: [1] Ivanov (1969), [2] Berkeley (1930), [3] Butler (1964), [4] Butler (1980), [5] Armstrong *et al*. (1995), [6] Chew *et al*. (1974), [7] Balsiger (1981), [8] Kurata (1981), [9] Kimker and Donaldson (1987), [10] Shumway *et al*. (1985), [11] Price and Chew (1972), [12] Haynes (1979), [13] Haynes (1976), [14] Anderson (1991), [15] Bartlett (1976b), [16] Baik *et al*. (1991). Abbreviations: AK, Alaska; BC, British Columbia; BS, Bering Sea; GOA, Gulf of Alaska; PWS, Prince William Sound; SE AK, South-east Alaska; WA, Washington state; others as in Table 2

Trait	Pink shrimp	Sidestripe shrimp	Coonstripe shrimp	Spot prawn
Males				
Size at functional maturity (CL)	19 mm (GOA); 22 mm (BS)[1,2]	22 mm (BC)[2]	24 mm (BC)[3]	13–28 mm (BC)[4]
Mean age at maturity	2 years (GOA); 3.5 years (BS)[1,2]	1.5 years (BC)[2]	1.5 years (BC)[3]	1.5 years (BC); 2.0–2.5 years (PWS)[4,5]
Maximum size (CL)	17 mm (PWS); 24–25 mm (BS)[2,5]	31 mm (BC)[4]	30 mm (BC)[4]	50 mm (BC); 45 mm (PWS)[4,5]
Females				
Primary females	Yes[4]	No[4]	Yes[4]	No[5]
Size at functional maturity	27 mm (GOA)[1]	29 mm (BC)[2,3]	25–29 mm (PWS)[5]	31–33 mm (WA); 38–42 mm (PWS)[5,6]
Mean age at maturity	4.5 years (GOA)[1]; 5.5 years (BS)[2]	2.5 years (BC)[3]	2.5–3.5 years (BC and PWS)[3,5]	2.5–3.5 years (WA); 4 years (PWS)[5,6]
Maximum size (CL)	25 mm (BC)[3]	39 mm (AK)[7]	51 mm (BC, Japan)[4,8]	62.5 mm (BC)[4]
Egg bearing period	7–8 months (BS)[10]	5.5 months (BC)[3]	6–11 months (Japan)[8]	4–5.5 months (BC)[4]
Larval hatching	March–May (GOA)[14,10]	March–April (BC, SE, AK)[4]	March–June (Japan)[8]	March–April (BC)[2,3]
Size at hatch (TL)	5–6.5 mm[15]	9.3 mm[2]	2.5–3.5 mm[16]	8.1 mm[6]
Larval duration	4 months (BC)[10]	5–6 months (BC)[3]	1–2 months (Japan)[8]	<3 months[11]
Number of larval stages	6 (GOA)[12]	5–6[2]	6[13]	4[11]
Size at settlement (TL)	15–21 mm (AK)[12]	30 mm (BC)[3]	14 mm (AK)[13]	12–13 mm (WA)[6]
Maximum age	5–7 years (AK)[3]	4 years[4]	4 years (BC, PWS)[4,5,8]	10 years (PWS)[5,9]

GROWTH

Crustacean growth is episodic; individuals do not have permanent hard structures that can be used to estimate age. Stock assessment and modelling must rely on size data, and on indices of shell condition assumed to be correlated with shell age (i.e. time lapsed since the most recent moult event). We compiled growth parameters estimated by previous authors for the main commercial crab species, and made use of them in simple population models, as described in the Appendix.

MATING SYSTEMS

Alaskan crab and shrimp fisheries are sex selective, albeit in radically different ways: male selective in crab fisheries, female selective in shrimp fisheries. This defines different problems from the viewpoint of recruitment overfishing.

Sexually mature crabs are easy to sex and usually highly size dimorphic, which creates the opportunity for sex-selective harvest strategies. As is also the case for many other crab fisheries, only males can be legally harvested in Alaska. Males of all Alaskan commercial species are polygynic, and females of true crabs (e.g. Dungeness and Tanner crabs) can store sperm across years and reproductive seasons. Legal size is set above minimum male mating size, so that males have the opportunity to mate at least during one mating season before becoming vulnerable to the fishery. For those reasons it has long been assumed that male escapement can effectively fertilize the reproductive female stock; even if not, long-term sperm retention could possibly mitigate the effects of variable sex ratio. Under such conditions, a harvested stock should be safe from recruitment overfishing. Such optimism, however, is being increasingly challenged because of complexities in male mating behaviour (unsuspected until recently), limits to effective male polygyny, and decay over time of the viability of stored sperm (Paul, 1984; Elner and Beninger, 1992; Paul and Paul, 1992).

All the pandalid shrimp species harvested in Alaska are protandric hermaphrodites, maturing first as males and changing sex later in their life history. Large, commercially valuable shrimp are female. Female-biased selection by the fishery has attracted considerable theoretical attention, as data have been presented that are consistent with the hypothesis that fishing has induced changes in the size at which sex-change occurs in some stocks (Charnov, 1979, 1981; Charnov and Anderson, 1989). If there is some room for optimism regarding recruitment overfishing in crab fisheries, the prospects for its occurrence could not be worse among pandalid shrimps. In the case of the comparatively small pink shrimp, smaller females may escape the fishery. In the large and highly priced spot prawn, however, the catch includes the entire female size range and the largest males.

SPATIAL STRUCTURE OF POPULATIONS

Mark–recapture and radiotracking studies indicate that, while being highly motile, the adults of spot prawn and Dungeness, Tanner and king crabs are remarkably sedentary, remaining on average confined to restricted geographic regions (Donaldson, 1980; Merritt, 1985; Kimker and Donaldson, 1987; Kimker, 1989; Stone *et al*., 1992). Adults of all species show gregarious reproductive behaviour. Adult king crab, for example, form pods (Dew and Cumminskey, 1995), a behaviour previously known only for juveniles (Powell and Nickerson, 1965). Tanner crab converge seasonally on some locations during the mating season (Stevens *et al*., 1994). Empirical evidence indicates that, in spite of their potential mobility, adults of commercial crustaceans do not show long-range dispersal during their lifetimes, or that they move back and forth (e.g. onshore–offshore) along paths determined by gradients in the near-bottom environment. Adult stocks have strong and persistent spatial structure.

The duration of larval stages is in the order of 2–3 months for most commercial Alaskan species (Tables 2 and 3). During that period, larvae may be transported over distances of the order of hundreds of km between points of hatch and settlement (Incze *et al*., 1982, 1984, for Tanner crab, and Kurata, 1959; Haynes, 1974; Shirley and Shirley, 1989, for red king crab). It should be noticed, however, that when the requisite benthic habitat to which larvae settle is restricted (e.g. island or narrow coastal shelves; *sensu* McConnaughey *et al*., 1992, 1994), larvae often have a suite of behaviours which provide for 'directional' dispersal, or minimize it altogether (Sulkin, 1984). Many bays and fjords along the coastal zone of Alaska have circulation patterns that may provide for adequate mechanisms of larval retention. In any case, the spatial scale of potential larval dispersal is always much larger than that of potential adult movements and migrations. Such geographically structured adult stocks with geographic segments of the adult population interconnected by larval dispersal conform generally to the meta-population conceptual model (Orensanz *et al*., 1990; Botsford *et al*., 1994).

Density-dependent mechanisms (compensatory or depensatory) that control recruitment to benthic stocks have small operational spatial scales, but their effects may be felt at varying spatial scales depending on whether density dependence occurs before or after larval dispersal (Botsford and Hobbs, 1995). The effects of *pre-dispersal* density dependence are felt at the macroscale determined by larval dispersal. Pre-dispersal compensatory or overcompensatory mechanisms include infection by nemertean worms and other egg predators, and low fecundity because of competition for food or prime habitat. Pre-dispersal depensation is expected to occur mostly as a result of a reduction in the chance of encountering male mates when concentration of the population is low. The effects of *post-dispersal* density-dependence are more site specific; cannibalism of new settlers by juveniles of the same age class (Fernandez *et al*., 1993) or by resident adults is an example. Given this multiplicity in the operating scale of regulatory mechanisms, and the fact that all the regions occupied by a metapopulation are open, to some extent, to settlement by larvae originating in other regions, conventional (aggregated) stock-recruitment analysis is not adequate in this context.

Resource-by-resource overview

In the Appendix we present a brief overview of methods and models used to assess crab stocks in Alaskan waters; we introduce a simple model that integrates data on *CPUE*, mean size in the catch, and various types of data on shell condition, and makes use of pre-existing knowledge about growth. The trends in abundance and recruitment of king and Tanner crab stocks discussed below were primarily investigated with that model.

RED KING CRAB

Regular commercial landings started in Kodiak in 1936, in Cook Inlet in 1937 and in Peninsula in 1947 (Kimker *et al*., 1993; Spalinger and Jackson, 1994), but it was not until 1950 that the fishery became firmly established, and catches were officially recorded. Commercial fisheries in SE Alaska and the Aleutians started a decade later, in

1960/61 (Koeneman and Botelho, 1990; Griffin and Ward, 1994). After 1960 the red king crab resource rose in significance to become the most important component of Alaskan crustacean fisheries (Bering Sea excluded), when these are put in historic perspective (Fig. 2). Total catch subsequently plummeted during the late 1960s, and continued to decline towards a terminal collapse during the early 1980s (Fig. 2). Because prices rose as catches dropped, the fishery did not lose its economic significance until its final demise (Fig. 2). The terminal decline of 1980–1983 was even more spectacular in the Bering Sea (Fig. 4) than in the Gulf of Alaska (where important stocks were already at a low level). The debacle of the Alaskan king crab fisheries and its disastrous social and economic consequences are well documented (Wooster, 1992).

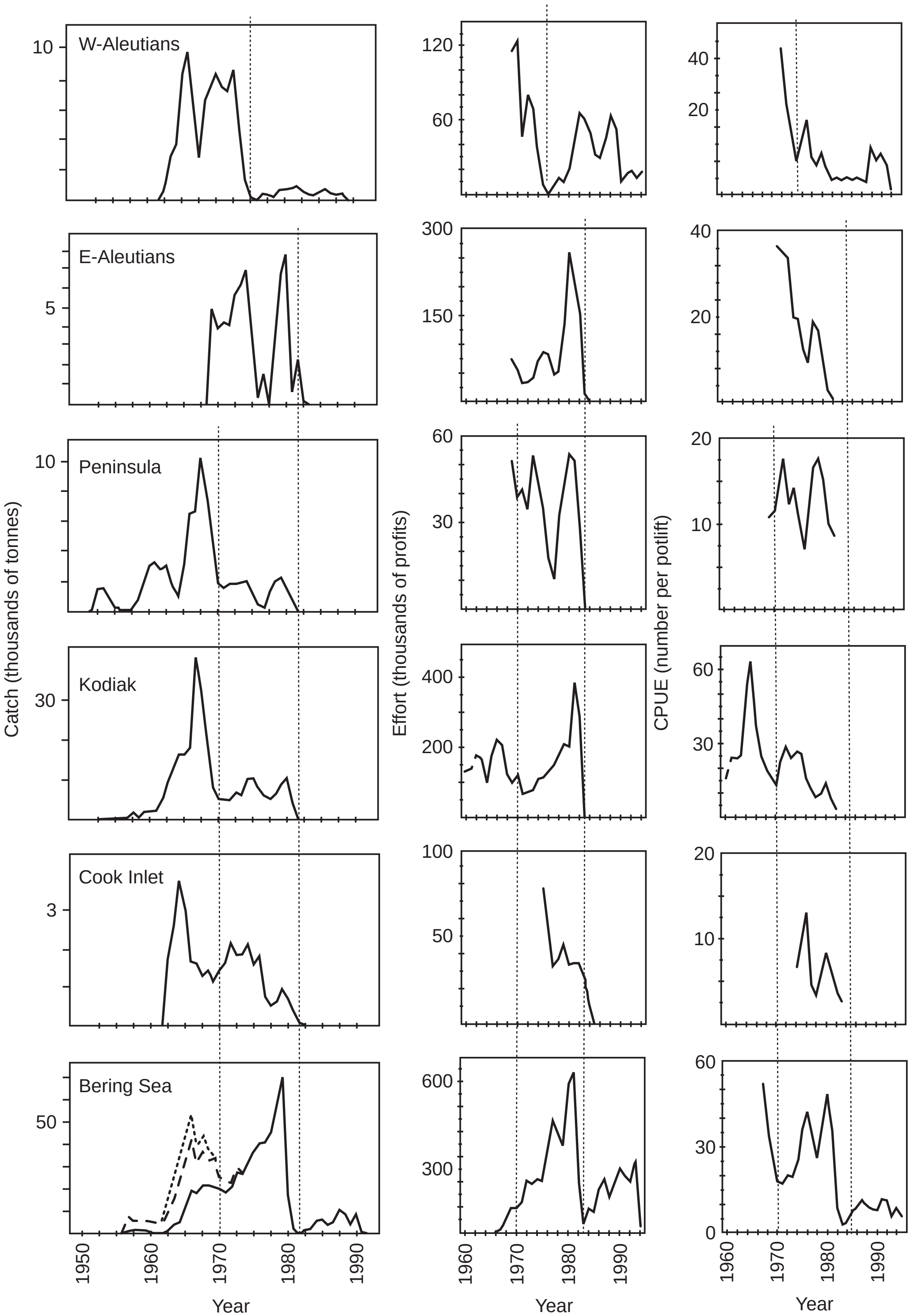
The magnitude of the collapse of the Bering Sea fishery during the early 1980s made it less evident that this was not the first, nor the last of several declines in Alaskan red king crab stocks (Fig. 4).

- During the late 1960s, catches dropped precipitously in Kodiak and Peninsula, and in the then international fishery (Soviet, Japanese and American) of the eastern Bering Sea; *CPUE* also dropped in the two areas for which data are available – Kodiak and the eastern Bering Sea. Although fragmentary, these data seem to signal a decline the geographical spread of which was perhaps comparable to the better-documented collapse of the early 1980s (see below).
- The West Aleutians fishery collapsed during the early 1970s, and has not recovered to the present.
- The widespread collapse of the early 1980s was clearly visible as a sharp decline in *CPUE* over a vast geographic region, from Kodiak to the E. Aleutians as well as in the Bering Sea.
- A little later, on a far more modest scale, the fishery of SE Alaska collapsed in 1984.

While the stocks in the eastern Bering Sea and Kodiak have been under intense scrutiny, it is intriguing that in the debate about the collapse (or collapses) of Alaskan red king crab stocks, there is little emphasis on the geographic range of the distinct episodes outlined above.

We start by re-examining the case of Kodiak, which has contributed approximately half of the accumulated catch for the 50 year period 1945–1995. The most prominent feature of reconstructed trends in recruitment and abundance for the period 1960–1983 is an apparent recruitment pulse in 1964–1965 (Fig. 5(c); see Appendix), preceded by a period (1960–1963) during which apparent recruitment was lower, close to the 1966–1980 average level. Rothschild *et al*. (1970, p. 37) observed the same pattern in catch-per-landing data for the period 1960–1969, and advanced an alternative hypothesis: "the large increases in apparent abundance during the mid-1960s might have been associated with a shift in the distribution of fishing from shallow to deeper waters. This would tend to produce, when examining each stock in its entirety, an increase in small crabs in the catch and would tend to produce an increase in recruitment and a diminution in the average size." Estimated harvest rate declined during the period 1967–1971, to a historical low (about 20% of the legal stock) in 1971–1973. It then rose continuously between 1973 and 1982 (to about 70%), while recruitment and abundance were declining, until the fishery finally collapsed and was closed in 1983.

In a most interesting monitoring routine conducted by ADF&G, the percentage of barren females was used early on to assess the possible occurrence of recruitment


W-Aleutians
E-Aleutians
Peninsula
Kodiak
Cook Inlet
Bering Sea
Catch (thousands of tonnes)
Effort (thousands of profits)
CPUE (number per potlift)
Year
Year
Year

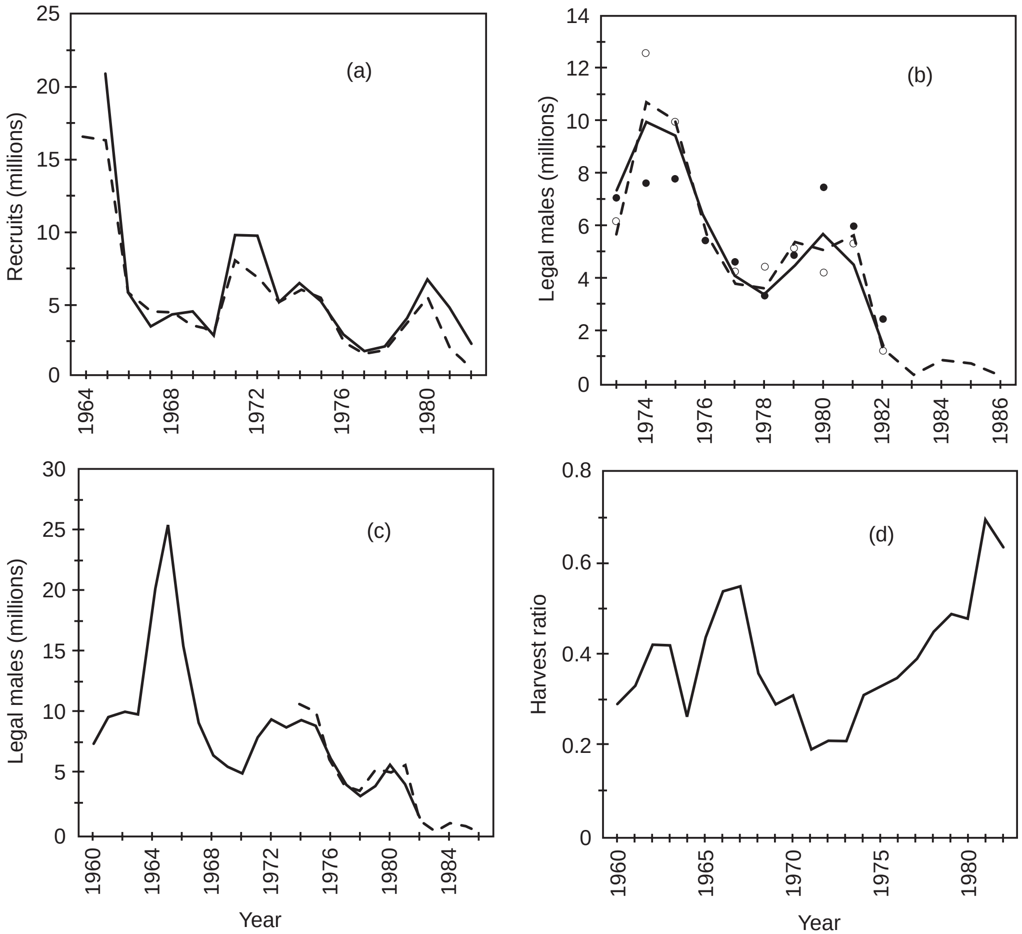


Fig. 5. Red king crab, Kodiak management area. (a) Period 1964–1982: comparison of recruitment estimates obtained by us – with data on commercial *CPUE* and mean weight in the catch ($\lambda_{CPUE} = 0.1$), and by Zheng *et al*. (1996) – based on catch-at-size analysis (equal weight given to all the components of the SS), $M = 0.4$ year^{-1}. (b) Pre-season abundance of legal-size males estimated for the period 1973–1986. Solid line: model fitted to data on *CPUE* from commercial catch and pot surveys, and mean weight in the commercial catch (1973–1982). Dashed line: model fitted to *CPUE* data from pot surveys combined with $\hat{q}_s$. Solid circles: estimated by Blau (1985) based on mark–recapture data. Open circles: estimated by Zheng *et al*. (1996) based on survey data. (c) Pre-season abundance of legal-size males estimated for the period 1960–1986. Solid line: model fitted to data on commercial *CPUE* and mean weight in the commercial catch. Dashed line: model fitted to survey *CPUE* data, combined with $\hat{q}_s$. (d) Harvest rate estimated for the period 1960–1982.

Fig. 4. Red king crab: catch, effort and annual *CPUE* during the period 1959–1995. There is no information available on number of potlifts and catch in numbers for the early years of most fisheries. In the case of catch from the Bering Sea, the dashed and dotted lines indicated the contribution from, respectively, the Japanese and Soviet fleets, added on top of the catch by the American fleet (solid line). Vertical dashed lines indicate the average timing and geographic spread of major regional-scale low-abundance years (at or above area level).

overfishing in red king crab from the Kodiak management area. Only 3–5% of 12 000 females examined in 1966 were barren, leading to the conclusion that the stock was 'biologically sound' (WRSMS, 1996). This happened in the midst of a precipitous decline of the annual catch and increasing harvest rate, which climbed to about 60% of the legal male stock during the years 1966–67 (Fig. 5(d)). The average percentage of barren females collected in several locations in 1967 was 16% (WRSMS, 1996). As catch and *CPUE* continued to drop during the 1968/69 season, up to 25% of the females sampled were barren in some locations. Powell *et al.* (1974) indicated that "recent increases in the number of adult females with broods of reduced size appear related to simultaneous increased exploitation rates" (p. 172) and "incidence of non-ovigerous adult females is lowest in areas where sub-legal sized males are abundant, but is often high in exploited areas with few adult males" (p. 179, citing unpublished ADF&G data). Pot surveys conducted by ADF&G between 1973 and 1986 (Blau, 1986; Denby and Tukey, 1990; Tukey, 1990) yield a detailed picture of the per-capita reduction in reproductive contribution by females during the period that led to the collapse of the fishery in 1983. The number of females per male increased by a factor of six as the male population was depleted by the fishery (Fig. 6(a)), while the fraction of adult females with a full clutch of eggs declined from 91–96% in 1973–1975 to an average 50% after 1978 (Fig. 6(b)). If, as it seems arguable, this reduction reflects reduced fertility caused by the scarcity of males, the fishery became *effectively* non-sex-selective during its final years. During the first trawl survey conducted throughout the management area (1987), 47% of the adult females sampled were barren, compared with 0% barren females in samples collected during the first years of the pot survey in the early 1970s.

The East Aleutians, Peninsula and Kodiak (a continuous geographical realm) yielded about 75% of the historical catch of non-Bering-Sea Alaskan red king crab. A regional-level comparison shows several regularities that were not noticed in previous studies, largely confined to the Kodiak area. The period is important because it corresponds to the decline and final collapse of stocks across the Gulf of Alaska. Trends in the three

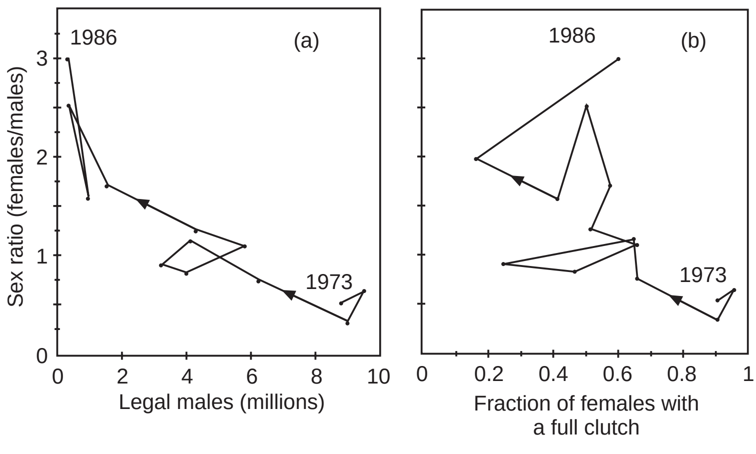


Fig. 6. Red king crab, Kodiak management area, 1973–1986. (a) Change in sex ratio (females/males) of adults in annual pot surveys as the estimated population of legal males declined. (b) Decline in the fraction of females with a full clutch of eggs as sex ratio (females/male) of adults increased.

areas show several features in common: recruitment declined in the three areas between 1972 and 1976–1977, when it reached a regional minimum, then showed a new pulse that peaked around 1979–1980, and finally declined in the three areas through 1982 (Fig. 7). The similarities in these trends suggest mechanisms that operate at a geographical scale larger than that of the individual management areas. Catch-per-pot in surveys conducted in two districts of Cook Inlet (Southern and Kamishak) between 1974 and 1985 show the same basic pattern, although the final pulse in abundance of recruits and legal males was a bit delayed (1981) in the Kamisha District (Merritt *et al*., 1988).

The development of the West Aleutians fishery was very different. Catch and *CPUE* dropped precipitously during the early 1970s (Fig. 8(a); Appendix), for unexplained reasons (NPFMC, 1976b; Phinney, 1977). The Alaska Board of Fisheries closed the fishery during the 1976/77 season; it has remained at a very low level ever since. On average, half of the post-collapse catch has been composed of recruits. Harvest rate increased after the 1976/77 closure, peaked during the 1988/89 season at about 60%, and subsequently dropped to less than 20% in 1994. Subsequent to its collapse, the red king crab fishery was in part substituted by the development of the brown king crab fishery (Fig. 8(a–d); commented below).

At the other end of the geographic range of interest, the SE Alaska fishery (Fig. 8(e)) was closed in 1984 owing to evidence of low abundance. Woodby (1994) concluded that by 1985 (closure of the fishery) the legal male stock had declined to less than 20% of the 1979 level. Harvest rates during the period 1979–1985 were high, in the range 44–61%. The stock remained at low levels of abundance during five years after the closure, but has rebounded after 1992 (Woodby, 1994); the fishery was re-opened in 1994. The SE Alaska 'stock' is composed by a number of disjoined populations often circumscribed to fjords or bays. While stocks are assessed separately (Woodby, 1994), guideline harvest rates apply to the aggregated 'stock'.

BROWN KING CRAB

Only small incidental catches were landed before the 1980/81 season. Prompted by the collapse of the red king crab fisheries, fishermen started to target brown king crab in the East and West sectors of the Aleutians during the early 1980s (Fig. 8(a–b); Benveniste, 1983; Griffin and Ward, 1994), where most of the cumulative Alaskan catch has originated (70% from the West, 22% from the East). Next in importance is SE Alaska (7%); catches in other areas have been negligible. The Bering Sea contributed only about 2% of the historical all-Alaska landings.

In the earlier years of the fishery, the catch was composed of large crabs (mean weight above 2.25 kg); a rapid drop in mean weight of crabs caught commercially after 1984 reflected a reduction in legal size. With the reduction in legal size the fishery apparently changed from one based on an accumulated biomass of post-recruits to one based primarily on new recruits. An apparent increase in recruitment during the early 1980s suggested by the model (Fig. 8(c); Appendix) partially reflects the fact that a tier of the population composed of smaller individuals (1.8 to 2.3 kg) became available to the fishery following the reduction in legal size. Fishing effort and catch peaked in 1987, then dropped by about 50% between 1987 and 1994 (Fig. 8(b)). While apparent abundance and recruitment were also declining (Fig. 8(c–d)), *CPUE* fluctuated around a relatively constant long-term average of about 8 crabs/potlift. As with fishing effort,

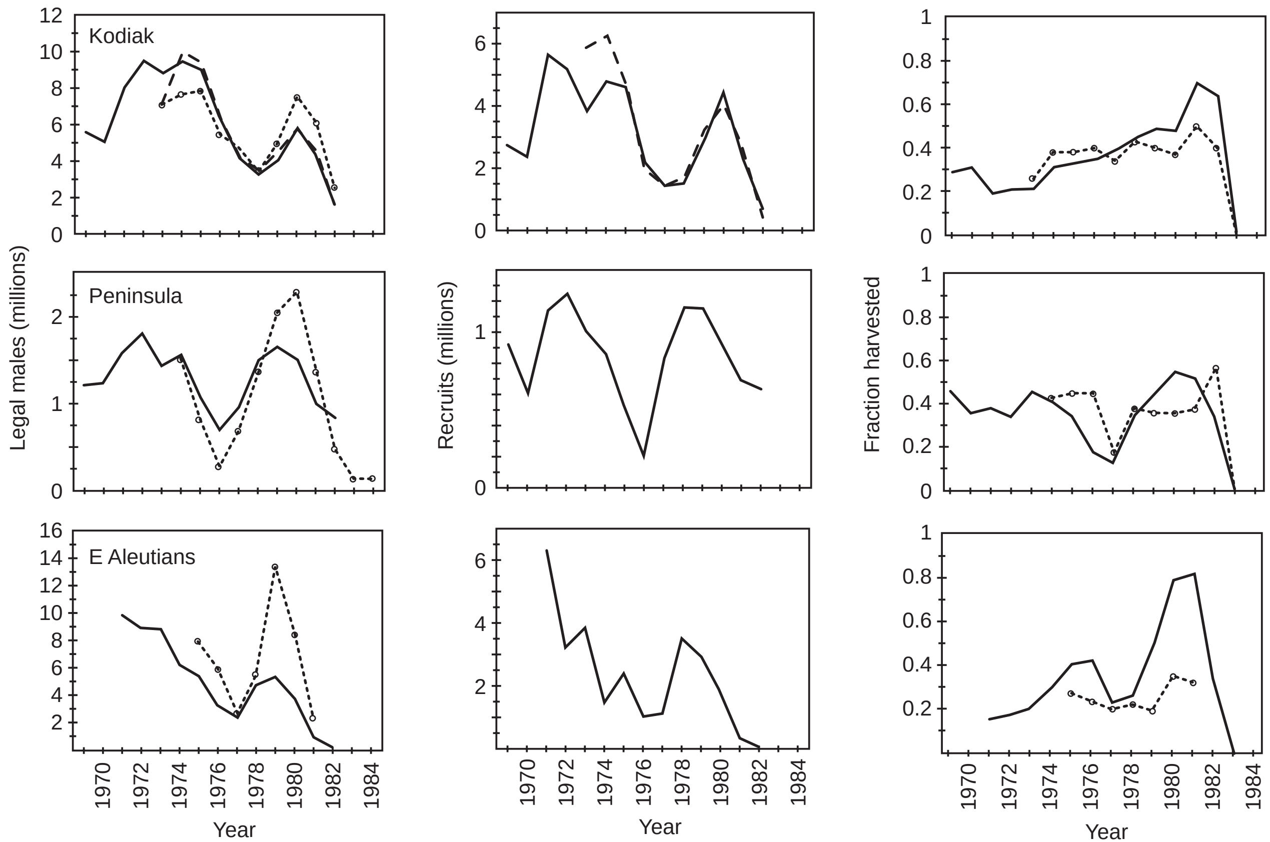


Fig. 7. Red king crab, period 1969–1984. Comparison of estimated trends of legal male abundance (left), recruitment (middle) and harvest rate (right), among three management areas: Kodiak (top), Peninsula (middle) and East Aleutians (bottom). Solid lines: model fitted to commercial *CPUE* and mean weight in the commercial catch. Dashed lines (Kodiak only): model based on *CPUE* from commercial catch and pot surveys, and mean weight in the commercial catch. Dotted lines: abundance of legal males and harvest rate estimated by Blau (1985) based on mark–recapture data.

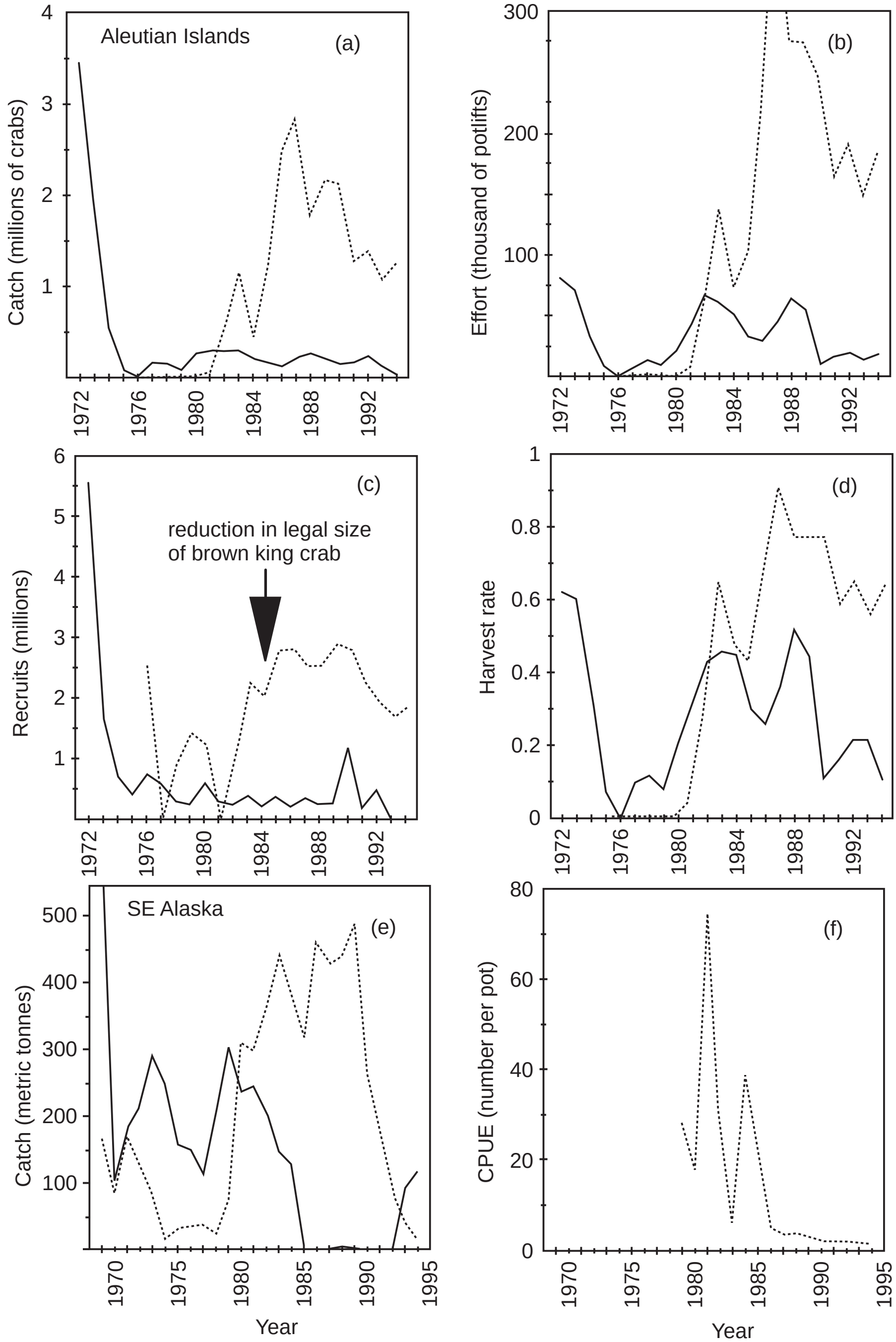


Fig. 8. Red and brown king crab (respectively solid and dashed lines) from the Aleutian Islands (East and West Aleutian management areas combined, period 1976–1994) and SE Alaska (period 1969–1994). Aleutian Islands: (a) catch, (b) effort, (c) recruits and (d) estimated harvest rate. South-east Alaska: (e) catch and (f) *CPUE* (based only on the subset of registration areas and years for which both catch in number and number of potlifts were available; no consistent *CPUE* data available for red king crab).

apparent harvest rate seems to have increased rapidly through 1987 when it may have neared 90%, and has dropped since to an apparent level of 60% of the legal male stock. These result must be taken with caution owing to the discontinuous geographic structure of brown crab stocks, which creates a scenario prone to hyperdepletion.

BLUE KING CRAB

Blue king crab occur in a number of isolated pockets in SE Alaska, Prince William Sound and Kodiak. Landings have been small and sporadic, generally associated with the red king crab fishery. Major fisheries are located in the Bering Sea. Given that stocks are composed of disjoint small populations presumably not connected through larval dispersal (Somerton, 1985), they must be considered as vulnerable to serial depletion and biological extinction.

TANNER CRAB

The domestic Tanner crab fishery began in 1967 around Kodiak and off the south coast of the Alaska Peninsula (Spalinger and Jackson, 1994). Kodiak has led in production with 46% of the landed weight during the period 1969–1994, followed by Peninsula (16%), Cook Inlet (11%), Prince William Sound (10%), Chignik and SE Alaska (~7% each). The contribution of the Aleutians has been of little significance (2%); trends in catch and effort in the Eastern Aleutians track those of the Bering Sea; they were not included in this review. Fishing effort data for SE Alaska and Prince William Sound are incomplete and/or inconsistent; abundance could not be assessed for these two areas.

Along the shelf of the Gulf of Alaska, in Kodiak, Chignik and Peninsula (which together contributed about 70% of the historical non-Bering-Sea Alaskan harvest), catches increased faster than fishing effort during the early 1970s (Fig. 9, left); effort peaked during the early 1980s. These stocks share prominent common features in their dynamics: increased apparent abundance during the early 1970s, then a decline reflecting an apparent decline in recruitment (Fig. 9). Harvest rate, on average, increased before 1979, and declined ever since (Fig. 9, right). In Kodiak most of the legal-size male population may have been harvested after 1979 (Fig. 9); this apparently became a recruitment fishery as catches declined during the period 1980–1985. During recent years all these fisheries have been either closed or sporadically open to negligible harvests, owing to the low level of the stocks (Table 4).

The spatial dynamics of the fleet is undocumented, but it is likely that the increase in apparent abundance observed during the late 1960s and early 1970s reflects (at least in part) serial depletion rather than a pulse in recruitment, as discussed above for red king crab. At the scale of the shelf of the Gulf of Alaska, landings peaked first in Kodiak (1973/74), next in Chignik (1976), and finally in Peninsula (1978). At the much smaller scale of Prince William Sound, catches after 1976 peaked first for the Northern and Hinchinbrook Districts (1978), next in the Western District (1978/1979), and finally in the Eastern District (1979/1980), matching distance from harbour; the fishery collapsed soon afterwards (Fig. 3, post-1976 data by district in Trowbridge, 1992, 1994b).

DUNGENESS CRAB

The Dungeness crab fishery, the oldest commercial crab fishery in Alaska, began in 1916 with inshore harvests by small vessel in the South-east area. Other fisheries developed

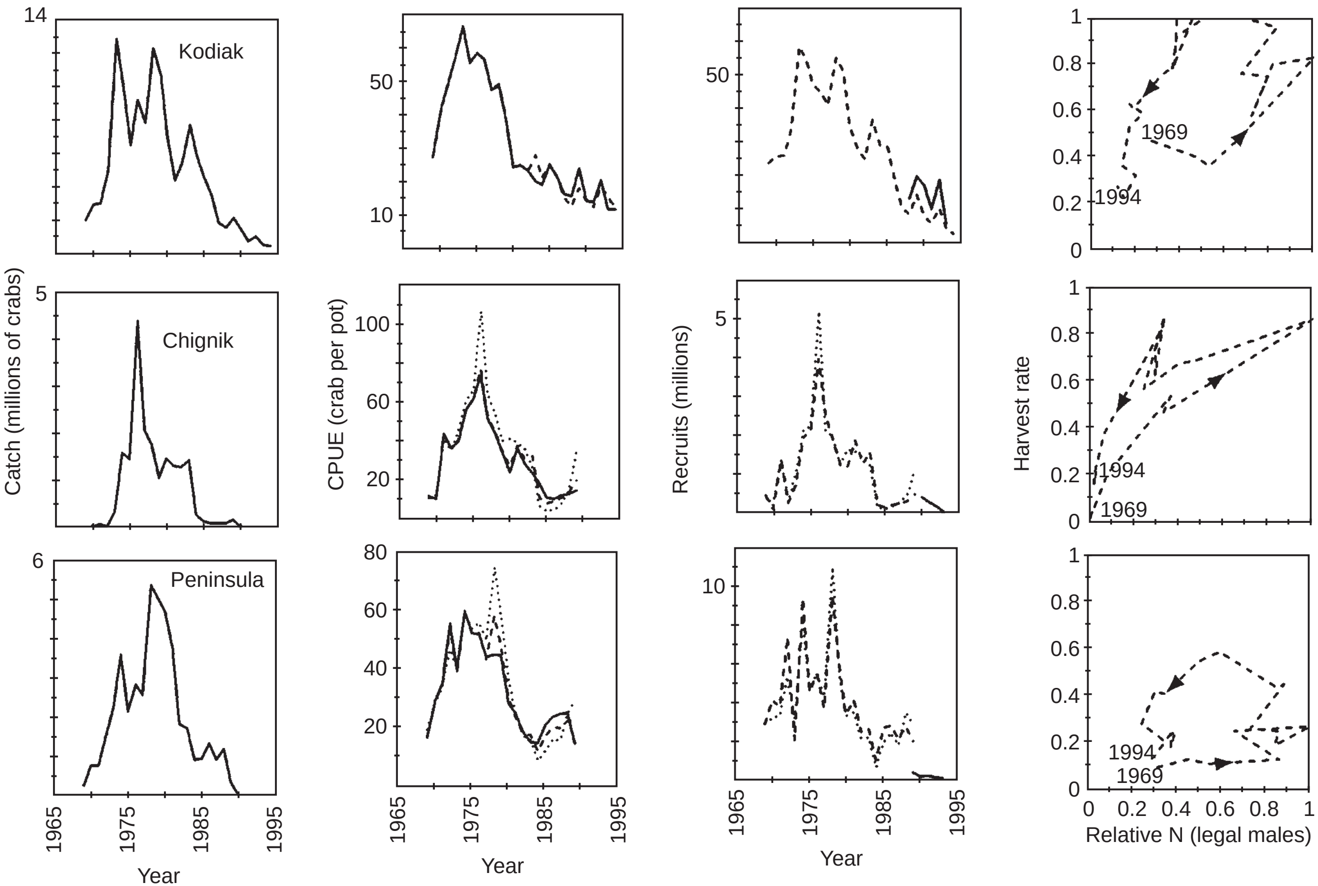


Fig. 9. Tanner crab: catch, *CPUE*, estimated number of recruits, and relation between estimated abundance of legal males and harvest rate, compared among Kodiak (top), Chignik (middle) and Peninsula (bottom). Solid lines: observations (including abundance index of recruitment based directly on trawl surveys). Dashed and dotted lines: model fits with λ_{CPUE} set equal to, respectively, 1 and 0.1.

Table 4. Management strategy and current status of major crustacean fisheries from the Greater Gulf of Alaska in terms of catch. Main sources on management regime: Kruse (1993) and ADF&G (1997). Abbreviations: ER, exploitation rate; FP, fishery performance; GHL, guideline harvest level; GHR, guideline harvest range; MT, minimum threshold; S, season; 2S, size and sex; 3S, size, sex and season

Fishery	Management strategy	Current status (1997)	Catch	
			Peak year	1994 catch as % of peak year
Red king crab				
South-east	FP, MT, GHL	Closed 1985/86, reopened 1994	1969	2.2
PWS	3S	Closed since 1984/85	1972	0
Cook Inlet	ER, GHL	Partially closed 1982 and 1983; fully closed since 1984/85	1962	0
Kodiak	ER, GHL	Closed since 1983	1965	0
Peninsula	ER, GHL	Closed since 1983/84	1966	0
Aleutians	FP	Closed since 1983/84	East: 1980	0
			West: 1972	1
Brown king crab				
South-east	FP, GHL	Open	1989	
PWS	FP	Closed 1989/90; low level	1986	1.3
Aleutians	2S	Open	1987	52
Tanner crab				
South-east	FP	Open	1982	60
PWS	FP	Closed since 1989	1978	0
Cook Inlet	ER	1994, 12 hour season; 1995 and 1996 closed	1973	3.3
Kodiak	ER	1994, 5 day season; 1995 closed	1973 and 1978	3.8
Chignik	ER	Closed since 1990	1976	0
Peninsula	ER	Closed since 1990	1978	0
E. Aleutians	FP	Emergency closure since 1995; population decline indicated by survey	1978	6

Dungeness crab				
South-east	2S	Open	Cyclic	–
Yakutat	2S	Closed in 1997	Cyclic	–
PWS	3S	Orca District, closed since 1980;	1960	0
		Copper River District, closed since 1993	1981	0
Cook Inlet	3S	Southern District closed since 1991	1979	0
Kodiak	2S	Open	1981 and 1984	16
Pink shrimp				
South-east	S, FP, GHL	Open 1992–1997 (beam trawl)	1958	36
PWS	S, FP, GHL	Open but pinks depleted; harvest mainly sidestripe shrimp	1979 and 1984	0
Cook Inlet	S	Inside Kachemak Bay, closed since 1986; outside Kachemak Bay, no catch 1989–90, closed pending approval of management plan	1978	0
Kodiak	S, ER	No catch	1971	0
Chignik	S	Stocks exhausted by 1981; no catches since 1982	1976	0
Peninsula	S	Closed in 1980 and 1981; no catches since 1982	1977–78	0
Aleutian		No significant catches since 1983		
Spot prawn				
SE	S, GHR by district	Open	1994	100
PWS	S, FP, GHL	Closed in 1992	1986	0
Cook Inlet	S, FP, GHL	Inside Kachemak Bay, closed in 1989/90;	1980–81	0
		outside Kachemak Bay, closed	1984–85	0

later in Cook Inlet and Prince William Sound (1924) and Kodiak (1942). The largest contribution to the cumulative catch for the period 1969–1994 originated in SE Alaska/Yakutat (47%), followed by Kodiak (35%), Prince William Sound (10%) and Cook Inlet (7%). The catch from other areas is negligible.

During the 15 year period 1962–1977, there was a general annual catch decline in SE Alaska and Yakutat reflecting a general decline of the stocks (NPFMC, 1976a), although extremely low catches during 1976–1977 everywhere were a function of poor markets for Alaskan Dungeness crab (Eaton, 1985; Kimker, 1985a). The strong 1978 year class apparently fuelled the fishery during the 1981/82 to 1983/84 seasons (Koeneman, 1985b). Catch and effort increased ten-fold during the 1980s, while *CPUE* decreased (Fig. 10(a–c)): the SE Alaska/Yakutat Dungeness crab fisheries became recruitment fisheries. Before 1981, *CPUE* may have been a reasonable index of abundance, but after 1983 catch itself became the best available index of both annual recruitment and abundance of legal males (Koeneman, 1985a). Notice that during the first phase (pre-1981) both annual *CPUE* and its variance were high, while they were low during the second phase (post-1983, Fig. 10(d–e)). This disparity reflects the fact that during the second phase, boats continued fishing after *CPUE* reached very low levels and virtually the entire legal stock (basically the annual recruitment) was harvested, while during the pre-1981 years fishing stopped when a certain *CPUE* threshold (presumably controlled by market conditions) was reached during the season.

After 1978, other fisheries rebounded, peaked and declined serially.

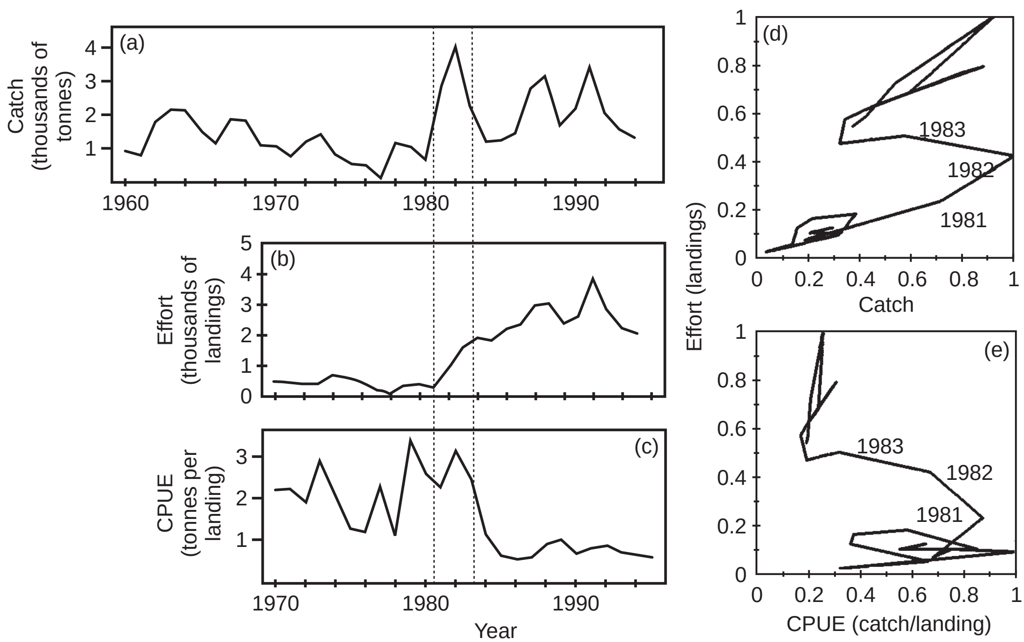


Fig. 10. Dungeness crab, South-east area. Left: catch (1960–1994), effort and *CPUE* (1970–1994); vertical dotted lines indicate the transitional 1981–1983 period. Right: relation between catch, *CPUE*, and fishing effort; notice transition between two states of the fishery during 1981–1983.

- In Prince William Sound, effort 'spiked' in 1978 and declined afterwards. Declining effort, as well as changes in the fleet associated with a major switch of fishing grounds, are reflected by an upward trend in *CPUE* that peaked in 1989. The Orca Inlet District, fished by small local boats under a 100 pot/vessel limit, had originally been the primary producing region. Reintroduction of sea otters into this area has contributed substantially to decline of crab abundance (Kimker, 1985b); annual ADF&G surveys since 1977 indicate little recovery, as a result of continued predation (Trowbridge, 1994a,b). The district was finally closed in 1980. The composition of the fleet changed as larger vessels with a 250 pot/vessel limit came into the area to fish the Copper River area. Greater holding capacity and pot limits probably contributed to increased *CPUE* during the 1980s. The fishery collapsed after 1989; the Copper River district was closed in 1992 owing to low abundance (Fig. 3). There have been no signs of substantial recruitment since 1986/87 (Welch, 1993).
- In Cook Inlet, fishing effort grew rapidly between 1977 and 1981, as Tanner and king crab declined and Dungeness crab was targeted more aggressively. Annual catch peaked in 1979 and has declined steadily ever since, while effort remained high through the late 1980s, which resulted in very low *CPUE* since the early 1980s.
- In Kodiak, effort rebounded after 1977, peaked in 1985, and has generally declined since. *CPUE* shows a slight declining trend since 1970. During the 1980s the Kodiak fishery became dependent on new recruits, as indicated by a drop in mean individual weight (Spalinger and Jackson, 1994). As in SE Alaska, catch is likely to be a reasonable index of recruitment and legal abundance after 1981.

SHRIMP TRAWL FISHERIES

Pink shrimp

The domestic shrimp fishery began in SE Alaska in 1915. Annual harvests reached 225 tonnes by 1924 (Hynes, 1929) and up to 1360 tonnes from 1945 to the mid 1950s (Gaffney, 1981). Invention of the mechanical peeler (1957) greatly increased the industry's processing capacity which, combined with high consumer demand and decreased production of penaeid shrimp in the Gulf of Mexico, led to rapid development of the Alaskan industry. Through the 1970s, Alaska was the dominant commercial producer of shrimp along the north-eastern Pacific coast (46–87% of total annual landings; PSMFC, 1995), but stocks and catches declined precipitously after 1978 (Fig. 2). For the last decade (1985–1995), Alaskan shrimp has accounted for less than 6% of annual West Coast pandalid production.

Kodiak Island and the adjacent Alaskan Peninsula, including numerous bays and inlets, were historically considered the richest shrimp production areas. Stocks around Kodiak were exploited beginning in 1958. After a Japanese pink shrimp fishery boomed and collapsed in the Bering Sea during the 1960s, Japanese trawlers moved south of the Peninsula and fished in the Gulf of Alaska along with a Soviet fishery that developed and declined between 1964 and 1973. The domestic catch from Kodiak peaked in 1971; harvest by both single and double otter trawlers declined steadily after 1975 (Fig. 11). The only available *CPUE*, catch weight/landing, did not show a trend while the fishery was heading towards its terminal demise, probably because (i) the area occupied by highly aggregated shrimp stocks shrunk while abundance dwindled (Kaiser and Nippes, 1979), (ii) vessels became effective at locating shrimp aggregations (Loverich, 1981), and (iii) vessels stayed at sea until completing their load. While landings declined in

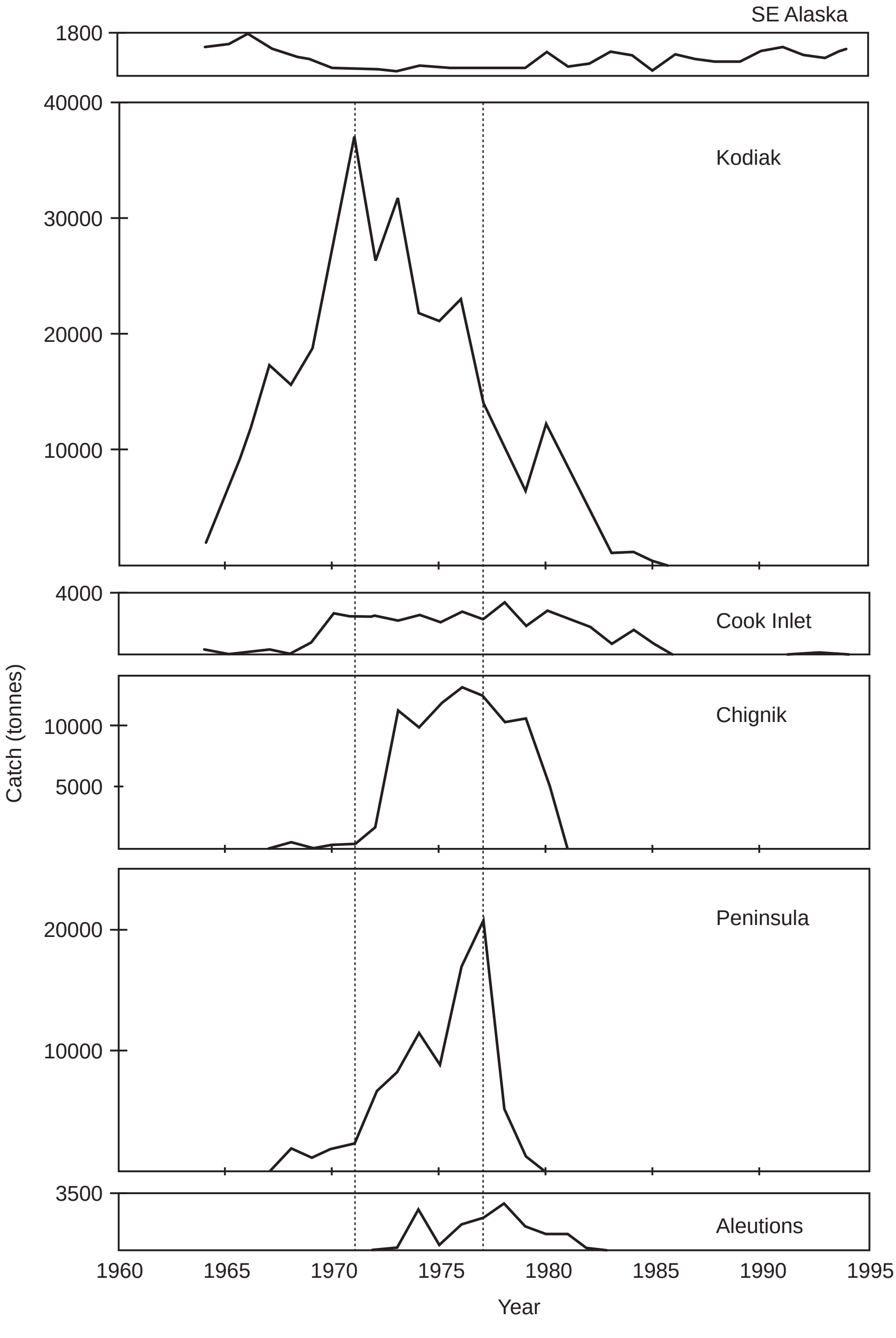


Fig. 11. Trends in catch of the pink shrimp trawl fishery, by management area. Dotted lines indicate peak years for Kodiak (1971), and other westward areas combined (1977). Notice 6 year lag between the two.

Kodiak they increased in adjacent Chignik and Peninsula, where the harvest peaked 6 years later, in 1977 (Fig. 11). After 1978, landings dropped rapidly in the three regions. The fisheries have been inactive since the early 1980s, and remain closed since 1986.

After the large stocks of the Westward Region declined, the Kodiak fleet redirected effort to a few remaining marginal stocks. Single otter trawlers moved to Prince William Sound from the early 1970s to early 1980s (Kimker, 1985c). A peak harvest of 593 tonnes was taken in 1984 (Fig. 3); afterwards the fishery collapsed within 3 years. By 1992, biologists recognized that *CPUE* (catch per hour towed) in the north-west of the area had declined to half of the 1990 level (Trowbridge, 1993). In Cook Inlet, harvests by single otter trawlers peaked at 3420 tonnes in 1978 (Fig. 11), then declined steadily after 1980, until the fishery was closed in 1986; it was resumed at a very low level in 1995.

Sidestripe shrimp

Before 1988 this species was caught in small quantities with otter trawls, but these were gradually replaced by beam trawls after that year. The Statewide catch grew rapidly, peaking at 160 tonnes in 1992, but has declined precipitously in recent seasons. In the Port Wells fishery of Prince William Sound, *CPUE* (catch/hour trawled) dropped by 50% from 1991 to 1992 (Trowbridge, 1994a, p. 21). Targeting this small resource was a result of severe depletion of primary shrimp stocks in all management areas. In Prince William Sound, for example, sidestripes accounted for over 99% of the shrimp caught in 1988 (Fig. 3; Donaldson, 1989).

SHRIMP POT FISHERIES

Two pandalid shrimp species have been targeted by the Alaska pot fisheries: spot prawn and coonstripe shrimp. Although the volume of annual landings has been insignificant compared with trawl fishery harvests, great demand for prawn-size shrimp keeps the ex-vessel value very high, particularly in the case of spot prawn. Main shrimp-pot fisheries arose in Prince William Sound and Cook Inlet in 1960, and in SE Alaska in 1969 (Imamura and Botelho, 1990), initially as an off-season activity to supplement income wherein the product was marketed locally. Vessels are classified by ADF&G according to keel length; almost the entire catch and effort data recorded in ADF&G's ticket database correspond to short-keel vessels of less than 50 feet (15 m).

Primarily spot prawn

Harvests in SE Alaska were sporadic before 1978 (Koeneman and Botelho, 1990). There has been no directed research to assess the abundance or distribution of spot shrimp stocks. Effort (potlifts) and catches increased steadily since 1980, while *CPUE* fluctuated around 2 kg/potlift during the 1985–1994 decade (Fig. 12, left); *CPUE* data for the pre-1985 years (when effort was still incipient) are erratic and presumably unreliable. The apparent reason for *CPUE* stability is shifting allocation of effort between the many bays and fjords inhabited by spot prawn (Fig. 12, right).

The Prince William Sound fishery expanded rapidly after 1975, as number of vessels increased more than ninefold between 1978 and 1987 (Kimker, 1985c). Catch peaked in 1986, then declined precipitously in 1989 owing to area closures after the *Exxon Valdez* oil spill (Fig. 3). The fishery was closed by emergency order in 1990 because of low stock abundance. Fishing was allowed during the autumn of 1991 to validate earlier

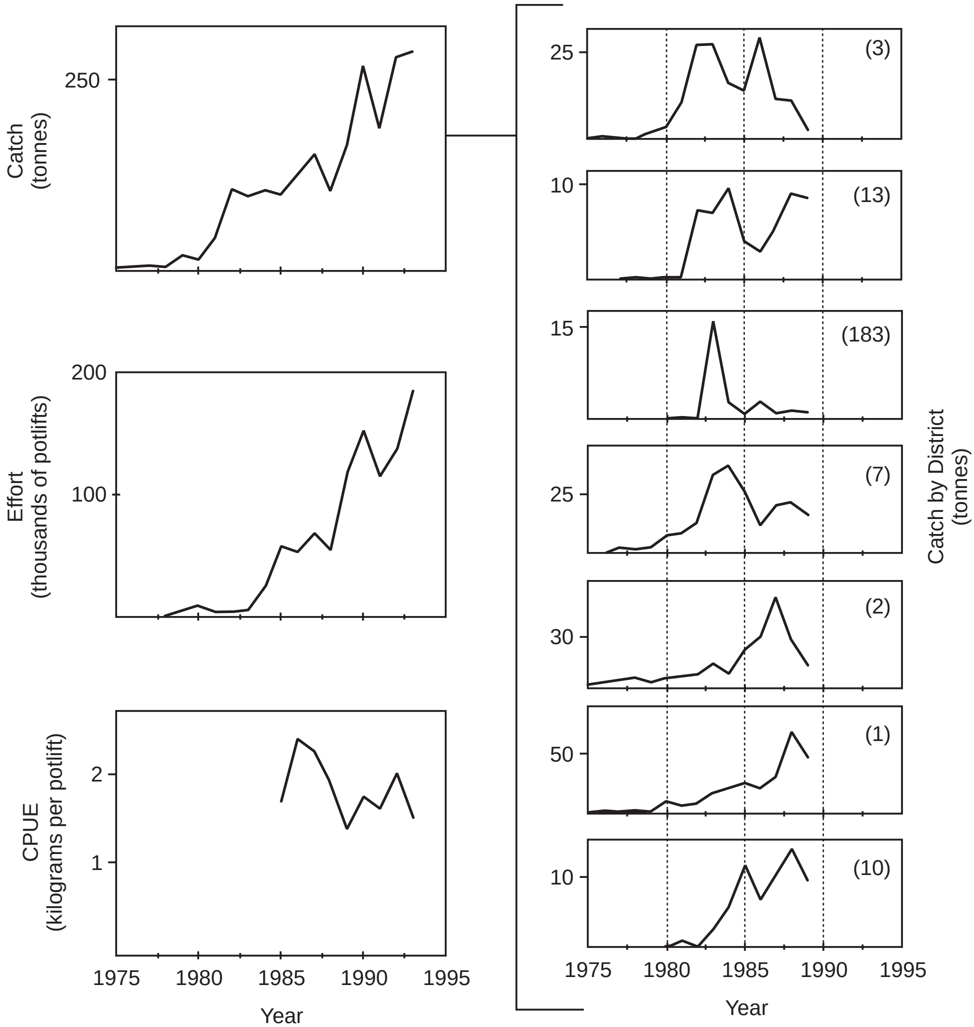


Fig. 12. Spot prawn, pot fishery from South-east Alaska, 1975–1994. Left: trends in catch, effort and *CPUE* for the entire management area. Right: trends in catch from major producing districts during the period 1975–1988 (data from Imamura and Botelho, 1990). Vertical dotted lines separate five-year blocks of time; numbers between parentheses are district numbers.

survey results indicative of severely depressed stocks; the season closed early when a reduced guideline harvest level was reached. After two successive years of depressed harvests, the fishery was closed in 1992 and remains closed.

Primarily coonstripe shrimp

Coonstripe shrimp have been captured with short- and long-keel vessels (70% and 22% of the cumulative catch respectively), as well as single otter trawls (8%). The most important producing area has been Cook Inlet (58% of the cumulative catch), followed by SE Alaska (20%), Prince William Sound (17%) and Kodiak (4%). Harvests from

Cook Inlet increased rapidly during the 1970s, peaking in 1974 at 362 tonnes (Kimker, 1994). After 1980 (when ADF&G ticket data started to be recorded), catch and *CPUE* declined continuously. The fishery has been closed since the 1989–90 season (some districts were closed earlier). Stocks remained depressed through 1994–95 in spite of the protracted closure (Kimker, 1994). The smaller Prince William Sound fishery showed a similar pattern of demise. While the Cook Inlet/Prince William Sound fisheries were collapsing, catches started to rise in SE Alaska. A marked decline in *CPUE* in recent years suggests rapid depletion, very similar to that preceding the collapse of fisheries in the Central Region.

An assortment of stock declines and fishery collapses, and of possible causes

The pervasive portrayal of resource-by-resource demise chronicled in the preceding section, summarized in Table 4, is worrisome. It deals largely with a *fait accompli*: how one of the richest shellfisheries in the world, based on multiple resources spread over a vast and diverse geographic domain, vanished over the 30 year period 1960–1990. In 1994 the most valuable crab fisheries of the state (exclusive of the eastern Bering Sea), from the West Aleutians to the panhandle, continued to be closed, as they were in 1990/1991 when reviewed by Kruse (1993). Since then the Dungeness crab fishery from the Copper River District (Prince William Sound) and the Tanner crab fisheries of Kodiak, Cook Inlet and the East Aleutians also have been closed. All the major pink shrimp fisheries were inactive owing to low stock levels. Most of the fisheries that remained open registered catch levels below 6% of their historical maxima, including the red king crab fisheries from the West Aleutians and SE Alaska and the brown king crab fisheries of SE Alaska and Prince William Sound (all of marginal historical significance). The only fisheries showing average to high catch levels were the brown king crab fisheries from the Aleutians (52% of maximum in 1987), the Tanner crab fishery of SE Alaska (51% of maximum in 1982), and the spot prawn fishery of SE Alaska, which in 1994 was relatively new and still expanding.

How is this multifaceted collapse perceived in hindsight? What was the reason for the demise of so many stocks over such a brief period? Only in the case of a few small, local fisheries is there some certainty about causes, e.g. the depletion of the Dungeness crab stock from Orca Inlet by reintroduced sea otters in 1979 (Kimker, 1985b), or the overfishing of spot prawn in Prince William Sound (Trowbridge, 1994c). In most cases, however, some evidence exists supporting different hypotheses; these are not exclusive, as every stock decline could conceivably have more than one cause, or might be the result of synergistic causes. Most of the hypotheses advanced fall into two broad categories: (1) *climatic change*, including climate-mediated increments in rates of *predation* or *disease*, and (2) *overfishing*, including the effects of *incidental fishing mortality* (e.g. handling of females and sublegal males in the case of pots, non-selective harvests in the case of shrimp trawls, and protracted ‘ghost’ fishing by lost pots). Both are discussed below.

CLIMATIC FORCING

Possible effects of climate on recruitment have been discussed in the context of recent interest in decadal change in the North Pacific and the Bering Sea (Wooster, 1992; Beamish, 1995). After 1976 the Aleutian Low atmospheric pressure system intensified and there was a transition from high to low barometric pressure anomalies (Trenberth and Hurrell, 1994). Crab stocks of the eastern Bering Sea are the best documented in the region. Year-class ('brood') strength of red king crab was consistently low after 1976 compared with the 1966–1975 decade (Tyler and Kruse, 1996), while brood strength of Tanner crab was at very low levels during the 1970s and high during the early 1980s (Tyler and Kruse, 1997). After 1976, temperature increased through the NE Pacific (Royer, 1993). Mütter *et al*. (1995) explored cross-correlation between king crab catch and SST (sea surface temperature) in the Gulf of Alaska and the eastern Bering Sea. They found that catch increased significantly 10–12 years after a high SST anomaly and decreased after a low anomaly, suggestive of an effect of positive anomalies on year-class strength. However, the positive SST anomalies of the 1980s have not been conducive to improved recruitment during the 1990s.

Shifts in the oceanic climate are likely to influence the reproductive calendar of crustacean populations, as well as advection and survival of pelagic larvae (Tyler and Kruse, 1996, 1997). They may also have indirect cascading effects that propagate through biotic interactions such as predation or disease. Results from a series of annual trawl surveys conducted in Pavlov Bay since 1972 indicate that pink shrimp virtually disappeared between 1978 and 1979, while cod (among other fishes) increased greatly and persisted throughout the 1980s (Piatt and Anderson, 1996). As cod is a major predator of pink shrimp, consumption by this fish alone could have been the cause of the failure of the pink shrimp stock to rebuild in Pavlov Bay following closure of the commercial fishery in 1979 (Albers and Anderson, 1985), and perhaps in other areas of the Gulf of Alaska as well (Spalinger and Jackson, 1994). Yet, it remains unexplained why catches started to decline in Kodiak (the traditional fishing grounds) 6 years earlier than in adjacent Peninsula and Chignik (Fig. 11).

The hypothetical causal connections between recruitment and climatic regimes remain the subject of speculation. Sinclair and Frank (1995) summarized the issue concisely: "even though the large-scale description of shifts in atmospheric conditions and in SST are robust, the more detailed descriptions of circulation and mixing on time and space scales of relevance to specific fish populations are lacking. The lack of detail makes it difficult to consider the underlying processes by which the physical environment influences population responses."

Evidence of climatic forcing, whatever the processes involved, may be found in the geographical correlation ('coherence') of year-class strength across stocks: the larger the geographical scale at which the correlation is preserved, the more suspect climate is of forcing the pattern. Various stocks for which an index of abundance is available fluctuated (and eventually declined) in distinctive ways. Major patterns were consistent within species, but very different among species, as best appreciated when the rise and fall of the Tanner and red king crab fisheries are compared. In the case of Tanner crab, virtually the same pattern was observed across a wide geographical region encompassing the Gulf of Alaska and the eastern Bering Sea. Abundance, as indicated by *CPUE* and (when it could be estimated) recruitment, increased everywhere during the early 1970s, peaked around the mid 1970s, and declined afterwards (Fig. 9). In the Gulf of Alaska, effort and harvest rate increased through the early 1980s and have dropped ever since. The result is a cycle in which abundance and harvest rate apparently grew, then declined to the neighbourhood of the initial condition between the late 1960s and the early 1990s (Fig. 9, right). In the case of red king crab, two of the three episodes of precipitous decline described above appear to be very large-scale phenomena, involving stocks from both the Gulf of Alaska and the Bering Sea during the late 1960s and the early 1980s (Fig. 7). Trends in recruitment and abundance of legal-size males were remarkably similar across management areas of the Gulf of Alaska (Kodiak, Peninsula, East Aleutians) between 1970 and 1982 (when the fisheries were closed). When the Tanner and king crab cases are pondered jointly and across large geographic domains, two general conclusions can be drawn: (1) there is a high level of intraspecific coherence in the fluctuation of segments of the metapopulations (segments or 'stocks' defined by management areas), including the simultaneous decline of several harvested stocks that, in the end, led to the collapse of these fisheries; and (2) while intraspecifically consistent, large-scale patterns differ among species. The implications of these comparisons are simple: whichever the factor(s) underlying trends in recruitment, its (their) effects are species specific, and its (their) geographical operational scale must be fairly large. Among the factors possibly governing year-class strength, climate may have those signatures. However, fishing-down synchronously across stocks (Myers *et al*., 1995b), or a recruitment pulse originating from a subpopulation but dispersed over the entire metapopulation may have a similar effect. Whichever the case, suggestion of climatic forcing of recruitment is strong even without resorting to evidence of correlation between recruitment and environmental variables.

Investigation of the hypothetical processes involved in the climatic forcing of recruitment and the measurement of their effects are subjects of unquestionable scientific merit. Yet, the significance of climatic forcing for improved management is limited (Walters and Collie, 1988; Walters and Parma, 1996). Fluctuations in abundance driven by climate, whether explicable or not, are just part of the background variability that managers and the industry have to live with; a posteriori speculation or explanation is of little help to cope with unpredictable and uncontrollable fluctuations into the future.

OVERFISHING

While it seems likely that forcing by climate had a significant effect on the recruitment of major Alaskan crustacean stocks during the post-1960 years, evidence leading to suspicion of collective overfishing is compelling. The pattern of collapse was not haphazard: rise and fall of these fisheries proceeded serially, starting with the most valuable resources both at the large regional scale (Fig. 2) and within particular management areas (Fig. 3); stocks of each resource were depleted in a sequence that, when documented, matches distance from fishing ports. However, when the possible role of overfishing is scrutinized stock-by-stock from a reductionist perspective the evidence is inconclusive or contradictory in most particular cases. Year-class strength of red king crab from the eastern Bering Sea, for example, fell after the mid 1970s, well before the heaviest catches of the late 1970s, and prior to decline of the reproductive stock (Tyler and Kruse, 1996). The pink shrimp fishery of Pavlov Bay was closed in 1979 following a crash of the stock, but many adjacent areas that were lightly or seldom harvested underwent comparable declines (Anderson and Gaffney, 1977; Anderson, 1991).

Recruitment overfishing and depensatory dynamics are usually investigated in fin-fisheries through stock–recruitment analysis (Myers *et al*., 1995a). Desired levels of recruitment are associated with reference spawning stock levels via some form of stock–recruitment relation. An example is the minimum biomass at which recruitment is expected to be seriously reduced, e.g. the stock size that produces one-half of the expected maximum recruitment (Mace, 1994; Myers *et al*., 1994). Kruse *et al*. (1996) calculated two biological reference points, F_{30} and F_{40}, to examine possible recruitment overfishing in Alaskan red king crab stocks. Those reference points correspond to the levels of fishing mortality that reduce spawning stock biomass per recruit to 30% (Clark, 1991) and 40% of the virgin condition (Clark, 1993; Mace, 1994). Kruse *et al*. concluded that the Kodiak stock was overfished. Population declines during the periods 1966–1968 and 1980–1982 coincided with annual harvest rates exceeding 41%, which for that stock corresponds to F_{30}. Interpretation of these results, though, is problematic for two reasons. First, the rationale for F_{30} was based on an empirical examination of life history parameters of groundfish stocks (Clark, 1991). Second, Kruse *et al*. (1996) based their analysis on the *male* stock. In the case of sex-selective harvests, calculation of reference points and other criteria to assess recruited overfishing should consider (i) the size of the female stock, and (ii) the sex ratio. Any specified level of female spawning could result from different combinations of those two factors.

A more pervasive and fundamental problem with the assessment of recruitment overfishing originates from the general difficulties encountered by stock–recruitment analysis when applied to spatially complex metapopulations. Beyond the total abundance of spawners and recruits, the spatial distribution of a stock also matters in the case of benthic stocks. First, source–sink configurations of metapopulations of benthic adults with pelagic larvae are complex: settlement at one site reflects conditions of the breeding stock at other sites. Second, within each population, a thousand crabs dispersed over an extended shelf where the densest spots have been thinned-out by fishing are not equivalent to a thousand crabs inhabiting a small bay, where individuals are within searching distance of each other, and consequently able to aggregate and mate. Spatial location (the first-order properties of the spatial pattern), and particularly spatial location of individuals relative to each other (the second-order properties of the pattern), does matter (Orensanz *et al*., 1998), and matters at multiple scales.

Crabs offer a unique opportunity to detect *directly* the spatial and temporal variability of reproductive potential, because the rate of egg-carrying by females and the size of the egg clutch are direct indices of a female's reproductive output. If egg-carrying rate and clutch size do not show signs of decline as a stock is fished down by a male-only fishery, then simply there is no indication of recruitment overfishing. If female per-capita contribution (as measured in the same way) does not decline at low population levels, then there is no indication of a depensatory dynamic response. This type of direct evidence of recruitment overfishing has been examined directly for two of Alaska's commercially significant species, red king crab and Dungeness crab, the dynamics of which are most contrasting: while the per-capita reproductive contribution of females declined in Kodiak's red king crab as the fishery slipped towards collapse (Fig. 6), some Dungeness crab stocks have sustained extremely high harvest rates. Hankin *et al*. (1997) examined egg production in the female Dungeness crab population from northern California, where the annual harvest rate of legal males exceeds 90%, and found no direct evidence of recruitment overfishing. There are important differences in the reproductive dynamics of the two species: skip-moulting Dungeness crab females are capable of storing viable sperm across reproductive seasons, while red king crab are not. Dungeness crab are among the most mobile crab species; males presumably have great capabilities to search for mates. Adult red king crab are relatively slow moving, and appear to have complex reproductive podding behaviour unsuspected until very recently (Dew and Cumminskey, 1995). Areas of reproductive aggregation are likely to be selectively targeted by the fleet. Even if geographically small, those regions contribute most of the population's reproductive output. These contrasting cases highlight the importance of understanding the mating systems and spatial dynamics of exploited crustacean stocks.

Management in the aftermath

THE MANAGEMENT SYSTEM: FRAMEWORK AND RESPONSE

Alaska's fishery management policies are delineated by the Alaska Board of Fisheries (ABOF), a body appointed by the governor and confirmed by the state's legislature (ADF&G, 1994: Sec. 16.05.221), which implements by regulation Fisheries Management Plans (FMPs); these provide the Alaska Department of Fish and Game (ADF&G) with guidelines to be followed in making fishery management decisions. The primary goal of FMPs "is *to protect the sustainable yield* of the state's fishery resources while at the same time providing an equitable distribution of the available harvest between various users" (ADF&G, 1994, Sect. 5AAC39.200). The stated mandate of ADF&G is to "*protect, maintain, improve, and extend resources* for the greatest overall benefit to Alaska and the nation". Major current management tactics for crustacean stocks are summarized in Table 4.

In the face of stock decline, each fishery was managed through a series of reactive ad hoc measures. Consider as an example the well-documented case of Kodiak's red king crab fishery (WRSMS, 1996). Management evolved through a series of stages, each defined by the addition of a new tier of measures on top of the pre-existing ones: 2-S (size and sex) during the exploratory years, 3-S (size, sex and season) in 1965, guideline harvest levels (GHLs) in 1974, threshold levels in 1983 (males) and 1986 (females), and finally a fixed harvest rate policy in 1990 (the last two measures were adopted after the fishery was closed, and so were never implemented). The fate of the stock was sealed under the provisions of the 1981 FMP: two seasons, reduced size for the second season, increased number of pots/vessel, global harvest tactics. For the first time, data on stock distribution from the pre-season survey were made available to the fleet. Scientists raised the expectations after a recruitment pulse (1979–1981, Fig. 5(a)) was detected: "*substantial* recruitment coming into the fishery in all district will provide for [...] a doubling of the harvest over current season levels" (Kaiser and Nippes, 1979, p. 131). Management reflected these expectations, and the limitations of a system which, under pressure from an oversized industry, exposed the entire stock to terminal depletion. The recruitment pulse of 1979–1981 turns out to be a modest event when seen in historical perspective (Fig. 5(a)). In 1982 the largest harvest in 14 years was taken from a stock that had reached an unprecedented low level of abundance. Whether or not low recruitment after the collapse is related to climate, there is little ground to question that the steady increase in harvest rate from 20% in 1971 to 70% in 1982 led in the end to the virtual removal of the entire legal male stock, and to a reduction in the per-capita reproductive contribution of females.

In retrospect, the management system did not accomplish the political mandate bestowed upon the ABOF, with its strong emphasis on resource conservation. 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 challenge now faced by Alaskan managers and scientists is to develop effective strategies to rebuild the depleted stocks, and to provide for sustainable use afterwards. To that end, two subjects introduced earlier need careful consideration: harvests are sex-selective (male-selective in crabs, female-selective in protandric pandalid shrimp), and stocks have strong spatial structure at several scales. Their implications are further considered in the sections that follow.

SEX-SELECTIVE HARVESTS AND RECRUITMENT OVERFISHING

The first element of stated management policy for king and Tanner crab resources is to maintain stock's *long-term reproductive viability* (ABOF, 1990). Policy goals also emphasize the monitoring of crab resources to detect changes and *prevent damage to the reproductive potential of each stock*, and maintaining an adequate brood stock to rebuild populations when they are depressed. "*Maintenance of an adequate broodstock takes precedence over short term economic considerations*."

Male-selective harvesting may be the most effective amongst measures currently implemented to maintain an adequate broodstock and prevent recruitment overfishing; besides, it is easily enforceable and well accepted by the industry. Yet, there are suggestions in favour of its eventual relaxation. A policy statement of the ABOF (ADF&G, 1994: p. 46) indicates that "[the male-only] restriction may be eliminated if it is demonstrated that [during periods of average to high stock abundance] the abundance of females results in no increase in recruitment to the fishery". Coincidentally, Schmidt and Pengilly (1990, p. 7) stated that "there is little justification for not exploiting female red king crabs when female numbers are in excess of reproduction requirements" and "harvesting females provides the only management tool available with the potential to stabilise recruitment of crab to the sexually mature population". However, estimating the *female numbers in excess of reproduction requirements* is a hopeless proposition in a world in which even the TAC calculated for a fixed harvest rate is marred by uncertainty. The assessment of stock–recruitment relations and the identification of compensatory regulation in the aggregated dynamics of a metapopulation present formidable conceptual, formal and statistical difficulties. The suggestion that the male-only tactic could be relaxed after insights derived from inadequate models is dangerous at least.

In the difficult case of female-selective shrimp fisheries, rotational strategies may be an alternative to explore. Consider for example the spot prawn fishery from SE Alaska (Fig. 12). Spot prawns are rather long lived, changing sex at a comparatively advanced age (Armstrong *et al*., 1995; Table 3). Adults appear to be rather sedentary; populations are confined to some fjords and bays (loosely associated with 'districts'). One of the management measures implemented in SE Alaska consists of closures to protect females during the spawning season. However, the loss of reproductive contribution by a given female is the same whether she is harvested before or during the spawning season. While frequently implemented in fisheries worldwide (and often well accepted by fishermen), spawning season closures do not have the intended effect (Shepherd, 1993) and are unlikely to circumvent the risk of recruitment overfishing. A management alternative would be to open districts on a rotational basis, allowing in each district a pulse-fishery of large females at intervals of a few years. The resting period should allow males to grow, change sex and reproduce as females before the next pulse of the fishery. Catch data, in fact, are suggestive of spontaneous rotation with quasi-pulses spread 3–4 years apart (Fig. 12). Such a system naturally lends itself to an experimental programme of rotational harvests.

CONSIDERATION OF SPATIAL STRUCTURE

Even though the extent to which fishing contributed to the collapse of most crustacean fisheries in the Gulf of Alaska is unknown, it is unquestionable that the harvest levels of the late 1970s and early 1980s were not sustainable. How and why did these fisheries grow to such high levels? Three basic paths may have led to an overestimation of productivity and, ultimately, to extensive overfishing.

- Because many of these species are long lived (Tables 2 and 3), fisheries may have expanded during their initial years by cashing on an *accrued biomass of old/large individuals* (e.g. as discussed in general by Francis, 1986). This is well exemplified by early changes in the size structure of Kodiak red king crab as a result of fishing (Nickerson *et al*., 1966). During the initial expansion of the Kodiak and Cook Inlet Dungeness crab fisheries (late 1960s to early 1970s), mean weight in the landings declined from about 2 kg to an average 1 kg, while *CPUE* was also dropping sharply (data from ADF&G ticket files).
- Some fisheries may have developed by *tracking exceptional year classes*. The pink shrimp fishery of Pavlov Bay (and perhaps other grounds as well), for example, boomed briefly during the 1970s, cashing on the strong 1971 and 1975 year classes (Anderson, 1991). The Dungeness crab fishery of SE Alaska changed dramatically in response to recruitment of the strong 1978 year class (Koeneman, 1985b).
- The third path is *expansion of the area fished and serial depletion* as fisheries develop. The *apparent* recruitment pulse of Kodiak's red king crab stock in 1964–65 is perhaps the most prominent feature in the aggregated dynamics of the stocks considered in this review. Yet, as discussed above, even this most conspicuous event is explicable as the result of changes in the spatial dynamics of the fleet, coupled with the spatial structure of the stock (Rothschild *et al*., 1970).

The third path was the most pervasive. All Alaskan crustacean fisheries started as small-scale inshore operations, initially targeting fishable concentrations close to towns or canneries. Later they gradually expanded into deeper or more distant waters as market conditions changed, technology improved and/or fishers gained experience. Examples of serial depletion of fishing grounds within management areas abound. The Kodiak crab fisheries provide good examples. The red king crab fleet targeted inshore regions during the early 1960s, but expanded over offshore areas between 1967 and 1970 (WRSMS, 1996); as vessel size increased, fleets were able to follow the offshore migration of crabs into the deeper waters where they remain during the late summer and the fall (Johnson, 1991). Large vessels, able to operate offshore, entered the Kodiak Dungeness crab fishery in 1962, effectively expanding the area fished. Harvest levels of Dungeness crab in SE Alaska were sustained during the 1980s only because the fleet moved constantly to new areas after local depletion occurred (Koeneman, 1985a). The trawl fishery targeting pink shrimp in the Westward Region underwent serial declines during the 1970s: Kodiak after 1971, Chignik and Peninsula fisheries after 1977, the Aleutians after 1978.

While it is well acknowledged (albeit often ignored) that spatial stock structure and the spatial dynamics of the fishing process may result in a distorted picture of stock size and productivity, the most dangerous effect of the expansion of the area fished and serial depletion is that, in the end, stocks are effectively deprived of geographic harvest refugia. Koeneman *et al*. (1995) describe exactly that situation for the Dungeness crab metapopulation of SE Alaska: peripheral fishing grounds which previously served as unfished sanctuary areas were lost owing to saturation and increased fishing effort throughout the district; once natural reproductive refugia are accessed by the fishery, the stage is set for recruitment overfishing. Trowbridge (1994c) stated the problem very clearly:

> the department's [ADF&G's] experience in managing crustacean fisheries has shown that once a drop in *CPUE* occurs on a fishery-wide basis, overharvest has already occurred.

Carl Walters (quoted by Orensanz and Jamieson, 1998) made a forceful statement at the *North Pacific Symposium on Invertebrate Stock Assessment and Management* (Nanaimo, Canada, 1995):

> If we look at fisheries that have been successful over the long term, the reason for their success is not to be found in assessment, learning and management models, but in the existence of a *spatial accident*, something about the spatial structure of population dynamics interacting with regulatory systems, or about the behavior of the species and fishers, that creates a *large scale refuge* for a substantial segment of the spawning population.

When such 'natural accidents' do not exist, the first priority of any sensible management plan should be to create their equivalents: *reproductive refugia* that, through regulation and enforcement, are off limits to fishery operations. Reproductive refugia have received renewed attention in recent years in situations that combine resources with complex spatial structure, little available information, and difficulties of enforcement (Roberts and Polunin, 1991, 1993; Bohnsack, 1996). Lauck (1996) provided the appropriate economic rationale based on an application of portfolio theory. Criteria prescribed for the design of systems of reproductive refugia must contemplate (1) the position of refuge areas relative to current systems and potential mechanisms for larval advection, and (2) the spatial pattern of the spawners within refugia (Caddy, 1989).

Data and knowledge potentially useful in the design of spatially explicit management options have accumulated in Alaska over the years, mostly through the efforts of ADF&G fishery biologists. Information pertains to four subjects.

- Spatial distribution of abundance. Pot surveys, and more recently trawl surveys, conducted over the years by ADF&G contain a phenomenal volume of information on the large-scale spatial distribution of several stocks (Denby and Tukey, 1990; Tukey, 1990).
- Spatial patterns of effort allocation. The observer programme conducted by ADF&G since 1988 (Beers, 1991) is a largely untapped source of extremely fine data on the spatial allocation of effort and the spatial distribution of *CPUE*. The overlay of data from survey and observer data holds much potential for investigation of the spatial dynamics of the fishing process.
- Reproductive migrations and gregarious behaviour. Several tagging studies conducted in the past provided insights into patterns of movement and seasonal or ontogenetic migrations. Recent discoveries on the gregarious reproductive behaviour of king crab (Dew and Cumminskey, 1995) and Tanner crab (Stevens *et al*., 1994, 1996) point to

the subtleties and spatial recurrence of those phenomena, with substantial implications for the design of reproductive refugia.
- Oceanographic scenarios for larval dispersal/retention.

Every crisis entails an opportunity. With a substantial body of knowledge at hand and an appropriate mandate in place, the declines and collapses of Alaskan crustacean fisheries should provide the stimulus for a renewed approach to their future assessment and management. The design of a system of reproductive refugia that effectively sequesters a sizeable part of spawning stocks from both the fishery and traditional assessment/management practices should be given serious consideration. Some decisions may have to be made in the face of limited information, but imperfect plans that address the right issues may be preferable to elaborate plans rooted in an unsuitable paradigm.

Epilogue

Biologists and managers familiar with Alaskan commercial crustacean fisheries have recurrently singled serial depletion of stocks as a cause of overfishing, something that is readily suggested by inspection of catch and *CPUE* data. Yet, stock assessments and management plans have paid little attention to spatial stock structure and the processes that influence and are influenced by it. In the past, a ‘stock’-by-‘stock’ focus created a sort of myopic perception: the geographic scale and multiresource nature of serial declines in Alaskan crustacean fisheries were not highlighted in the management context; connectedness among stocks did not receive serious consideration in stock assessment. Conversely, a presbyopic perception prevailed at the individual ‘stock’ level: implicit assumptions of homogeneity ignored the distribution and behaviour of organisms and fishers. In spite of their persistent multiscale structure, ‘stocks’ were assessed and managed under the umbrella of traditional fin-fishery science, epitomized by the unit stock concept and the dynamic pool assumption (Caddy, 1989). Within this framework, guideline harvest levels, harvest rates, threshold levels of abundance and TACs were calculated and implemented for each aggregated ‘stock’. This repertoire is inadequate for several reasons.

- Faulty rationales of the dynamic model. In cases like the ones considered here, there is simply no rationale available to determine ‘stock’-by-‘stock’ harvest rates, biological reference points or threshold levels of abundance that are consistent with the desire to prevent recruitment overfishing.
- Insufficiency of quota systems. *How much* is allowed to be taken (the TAC question) is only one of the considerations to be made with regards to recruitment overfishing: *where* the catch is taken is likely to be at least as important. The *where* aspect is central because different segments of a metapopulation contribute in variable degrees to its renewal.
- Uncertainty about abundance. While this is a universal problem in stock assessment (Walters and Pearse, 1996), spatially structured benthic stocks are the worst possible scenario for the use of *CPUE* as an index of abundance.

The seas around Alaska harbour (or have harboured) the largest and most diversified high-latitude crustacean resources in the world. Their demise bears a significant message to be pondered in the assessment and management of crustacean fisheries elsewhere. Crab stocks offer a unique opportunity to monitor and timely detect signs of recruitment overfishing and depensation *directly*, based on expedient and objective analysis of female clutch size variation in time and space. Formal investigation of this approach should receive priority over 'reference points' and other criteria of questionable applicability. Generally, and most important, spatially explicit management options should be seriously considered, including reproductive refugia, rotation, and experimental management with spatial experimental units.

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Appendix. The assessment of Alaskan king and Tanner crab stocks

In this Appendix we briefly discuss the assessment of king and Tanner crabs in the Greater Gulf of Alaska, including mention of existing pertinent data and of assessments conducted in previous studies. We introduce simple, pure observation-error (no process error) models that we used to investigate trends in ratios which are presumably informative about population size and recruitment: *CPUE* (catch per potlift) and aggregated descriptors of the composition of the catch (average weight, percentage of 'new-shells', percentage of recruits). The models incorporate growth parameters provided by previous studies (Table 5). Our own results are compared with those of previous authors. Dungeness crab stocks were not modelled because in recent years the harvest rate of the main stocks has been so high that catch itself is a good index of recruitment and legal male abundance. In the case of shrimp stocks the information available was insufficient for modelling purposes.

These analyses share the same problems of all the analyses that model aggregated abundance without consideration of the spatial dynamics of the populations and the fleets. Serial depletion has a pervasive and inextricable effect on all the estimations of abundance based on *CPUE*, including ours and those by previous authors (e.g. Zheng *et al.*, 1996). Because catchability is generally expected to increase as the stock is depleted, a constant catchability coefficient will tend to bias upwards (inflate) stock size at low abundance levels. This implies that the decline of some stocks was more dramatic than shown in results presented here and by others before us. The data

Table 5. Growth parameters for king and Tanner crabs

Species	Model for	Equation	Parameter estimate	Management area	Source
Red king crab	Length:weight relation	$w = aCL^b$	$\hat{a} = 7.12E - 07$	Kodiak	Data from Wallace *et al.* (1949)
			$\hat{b} = 3.19$		
	Hiatt diagram	$\Delta CL = c + dCL_{pre\text{-}moult}$	$\hat{c} = 41.05$	Kodiak	Powell (1967)
			$\hat{d} = -0.159$		
	Probability of moulting conditioned on size	$P\ (moulting \mid CL) = \dfrac{1}{1 + \exp(-(25 - 0.17(CL - A)))}$	$\hat{A} = 12.403$	Kodiak	McCaughran and Powell (1977)
Brown king crab	Length:width relation	$CW = a + bCL$	$\hat{a} = -0.68$	Japan	Hiramoto (1985)
			$\hat{b} = 1.09$		
	Width:weight relation	$w = aCW^b$	$\hat{a} = 5.62E10 - 4$	Japan	Hiramoto (1985)
			$\hat{b} = 2.98$		
	Hiatt diagram	$CL_{post\text{-}moult} = c + dCL_{pre\text{-}moult}$	$\hat{c} = 25.12$	SE Alaska	Koeneman and Buchanan (1985)
			$\hat{d} = 0.941$		
Tanner crab	Width:weight relation	$w = aCW^b$	$\hat{a} = 4.33E - 04$	Prince William Sound	Donaldson *et al.* (1981)
			$\hat{b} = 2.936$		
	Hiatt diagram	$CW_{post\text{-}moult} = c + dCW_{pre\text{-}moult}$	$\hat{c} = 14.75$	Prince William Sound	Donaldson *et al.* (1981)
			$\hat{d} = 1.07$		
	Probability of skip-moulting, conditioned on size	$P\ (skip\text{-}moulting \mid CW) = [1 + (n - 1)\exp(-m(CW - CW_0)n^{\frac{n}{n-1}})]^{\frac{1}{1-n}}$	$\hat{m} = 0.0405$	Kodiak	Somerton (1981, 1982)
			$\hat{n} = 23.02$		
			$\widehat{CW_0} = 158.6$		

available to us have no spatial resolution below the scale of management areas. Even when the data exist, availability is constrained by confidentiality restrictions.

RED KING CRAB

Kodiak

We first analyse the Kodiak stock because substantial biological information on growth as well as some survey estimates of abundance are available, and it is the only stock to have had its dynamics formally analysed (Collie and Kruse, 1995; Zheng *et al*., 1996). ADF&G has collected different types of data that can be used in the assessment of abundance and recruitment, including the following.

- Pot surveys conducted from 1972 to 1986 (Blau, 1985; Peterson *et al*., 1986), later replaced by trawl surveys. Johnson (1990) analysed the spatial distribution of the survey *CPUE* ($CPUE_s$), and calculated mean bootstrap estimates.
- Trawl surveys starting in 1987.
- A mark–recapture programme conducted concurrently with pot surveys (Peterson *et al*., 1986, their table 3).
- Catch and effort data. The logbook programme, started in Kodiak in 1964 (Rothschild *et al*., 1970), was the source of potlift data for the period 1964–1982. In addition, data are available on permits (vessels) for 1960–1982, and on landings for 1967–1982.
- Size and shell condition ('old', 'new') were sampled from the commercial catch (1964–1982) and during the surveys (Blau, 1985).

These data have been utilized for stock assessment in three ways.

- Mark–recapture estimates of pre-season abundance of legal-size males have been presented by Blau (1985, his table 6) and Spalinger and Jackson (1994, their table 3). The same data were used by Zheng *et al*. (1996, p. 577) to estimate the catchability of the pot surveys. The supporting analyses, however, have never been formally presented.
- Catch-survey analysis (CSA). Survey *CPUE*, composition of the male population by shell condition, and commercial catch data were used by Collie and Kruse (1995) to estimate annual recruitment, and then calculate pre-season abundance of legal males and harvest rate.
- Catch-length analysis. Commercial catch and effort, and composition of the commercial catch by size and shell condition were used by Zheng *et al*. (1996) to estimate parameters describing growth and selectivity, as well as annual recruitment.

Here we consider the population of legal males as a mixture of three size stages or 'instars': one corresponding to the recruits (individuals that just moulted into the legal population), and those that moulted once and twice after being recruited (Fig. 13). Given the size frequency distributions shown in the literature, variation in size for a given adult instar, and growth parameters estimated by other authors (Table 5), this seems a reasonable simplification of the composition by instars of the legal male population, at least for the post-1960 years; while a few crabs may moult three times after recruitment, their contribution to the total population is negligible. Size increment per moult, conditioned on pre-moult length, is well approximated for males larger than 80 mm (CL) by the linear relationship

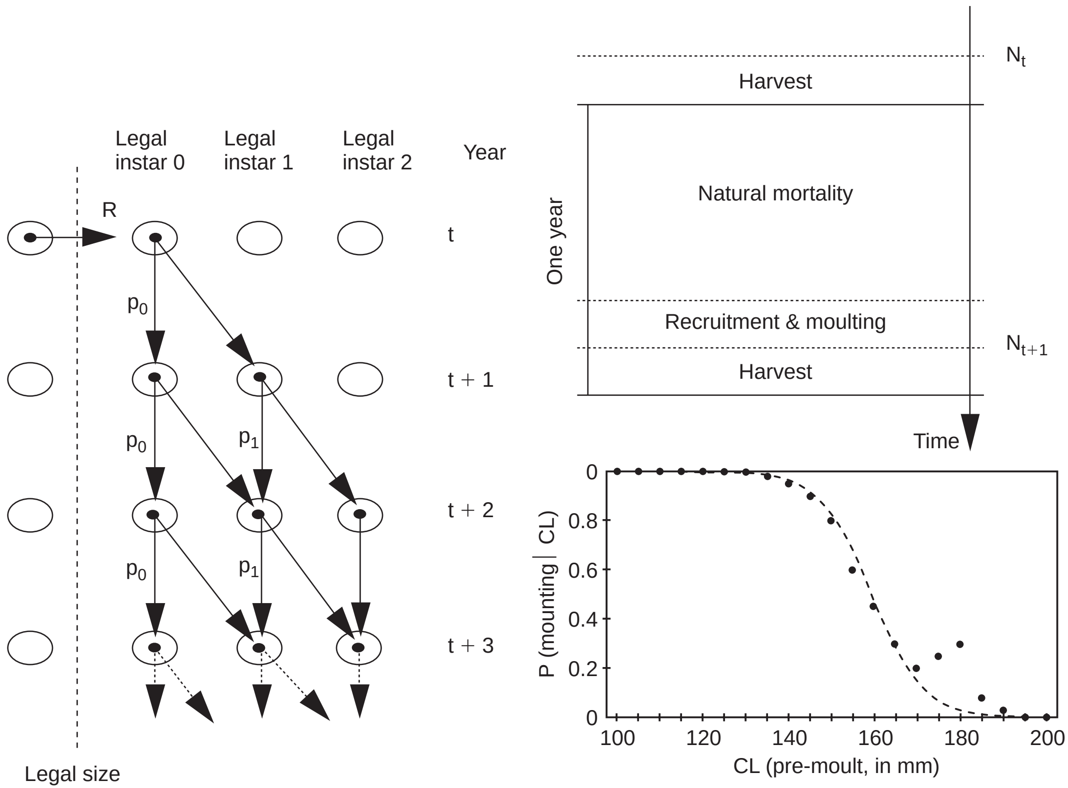

Fig. 13. Red king crab: components of the population model. Left: recruitment and growth of a cohort; ellipses indicate size stages (instars); p_0 and p_1 are the fractions of crab in legal-size instars 0 and 1, respectively, that skip-moult during a given year (one moulting opportunity per year). Top right: temporal sequence of events during one year in the life cycle of the legal-size male stock. Bottom right: probability of moulting, conditioned on pre-moult carapace length (data digitized from fig. 4 in McCaughran and Powell, 1977).

$$\Delta CL = c + dCL_{pre\text{-}moult}. \tag{A1}$$

Parameters in this relation were estimated by Powell (1967) for the Kodiak population (Table 5). The probability of moulting during a given year (adults only, one moulting opportunity per year) was investigated for the Kodiak population by McCaughran and Powell (1977), who proposed the model

$$\mathrm{P}(\text{moulting}|CL) = \frac{1}{1 + \exp\left(-(25 - 0.17(CL - A))\right)} \tag{A2}$$

and estimated parameter A for various moulting-history combinations. We used values digitized from their figure 4 (mean fractions unconditioned on moulting history) and estimated parameter A using the same model (Fig. 13).

The stock of legal-size males at time $t+1$ is the sum of legal-size crabs that survived from the previous year, plus the new recruits (Fig. 13):

$$N_{t+1} = (N_t - C_t)e^{-M} + R_{t+1} \tag{A3}$$

where N_t denotes the pre-harvest abundance of legal-sized males at time t, C_t is the observed catch, and R_{t+1} is the number of new recruits entering (i.e. moulting into) the legal population. Moulting is assumed to occur during an arbitrarily short period, just before the onset of the fishing season (Fig. 13); moulters include sub-legal-size crab that become the new recruits, and recruits from the previous year moulting to a larger instar. The harvest is assumed to be taken over a relatively short interval, during which natural mortality is negligible. Although a second season was allowed during some years (with a larger legal size), its relative contribution to total annual catch was small. The number of crab in each of the three legal instars at time $t+1$ is

$$N_{(t+1,0)} = R_{(t+1)} + (N_{(t,0)} - C_{(t,0)})e^{-M}p_0 \tag{A4}$$

$$N_{(t+1,1)} = (N_{(t,0)} - C_{(t,0)}e^{-M}(1 - p_0) + (N_{(t,1)} - C_{(t,1)})e^{-M}p_1 \tag{A5}$$

$$N_{(t+1,2)} = (N_{(t,1)} - C_{(t,1)}e^{-M}(1 - p_1) + (N_{(t,2)} - C_{(t,2)})e^{-M} \tag{A6}$$

where $N_{i,j}$ and $C_{i,j}$ are, respectively, pre-season abundance and catch of individuals in instar j during year i; M is the instantaneous coefficient of natural mortality (on an annual basis), and p_0 and p_1 are the fractions of individuals in instars 0 and 1, respectively, that *do not* moult (skip-moult); individuals that reach instar 2 stop moulting.

The average weight of the three groups is denoted as $\overline{w}_0$, $\overline{w}_1$, $\overline{w}_2$. Because much of the information available in the literature is reported in terms of carapace length (CL), parameters in the power function $w = aCL^b$ were estimated using data for Kodiak from Wallace *et al*. (1949) (Table 5). Because size-selectivity in the fishery was ignored, mean weight in the pre-season legal population and in the catch are identical,

$$\overline{w}_t = \frac{N_{(t,0)}\overline{w}_0 + N_{(t,1)}\overline{w}_1 + N_{(t,2)}\overline{w}_2}{N_t} \tag{A7}$$

$$= \frac{C_{(t,0)}\overline{w}_0 + C_{(t,1)}\overline{w}_1 + C_{(t,2)}\overline{w}_2}{C_t} \tag{A8}$$

CPUE is assumed to be proportional to average abundance during the fishing season (we indicated earlier the circumstances under which this assumption can be consequentially wrong). Average abundance during the fishing season was approximated by

$$\overline{N}_{c_t} \approx N_t - \frac{C_t}{2}.$$

The observation equations for the two ratios of interest are:

$$\ln(CPUE_t) = \ln(q_c \overline{N}_{c_t}) + \varepsilon_{1t} \quad \text{(A9)}$$

where q_c is the catchability coefficient for commercial pots, and

$$\ln(\overline{w}_{obs,t}) = \ln(\overline{w}_{pred,t}) + \varepsilon_{2t}. \quad \text{(A10)}$$

Parameters were estimated with the least-squares method, minimizing:

$$SS = \sum^{t}[\lambda_{cpue}(\ln CPUE_{pred,t} - \ln CPUE_{obs,t})^2 + \lambda_{\overline{w}}(\ln \overline{w}_{pred,t} - \ln \overline{w}_{obs,t})^2] \quad \text{(A11)}$$

where the λs are weighting factors. A spreadsheet (EXCEL) was used to inspect the data, estimate the parameters (Newton search method), and explore the behaviour of the model. Natural mortality (M) was fixed, but the behaviour of the model was explored for a range of values (0.2 to 0.5, the same explored by Zheng *et al*., 1996). The catchability coefficient (q_c) was not included in the vector of parameters estimated numerically; it was calculated at the end of each iteration as

$$q_c = \exp\left[\frac{1}{n}\left[\sum_t \ln\left(\frac{CPUE_t}{\overline{N}_{c_t}}\right)\right]\right] \quad \text{(A12)}$$

where n is the number of data points (years). The parameters estimated are $\overline{w}_0$, $N_{(1,2)}$ (the pre-season number of crab in instar 2 at the first year of the period of interest), and R_i (one parameter per year). Explorations with the Kodiak and other data sets indicated that including extra parameters for $N_{(1,0)}$ and $N_{(1,1)}$ had a negligible effect on the results of interest (trends in total legal population and recruitment). In all cases $N_{(1,0)}$ and $N_{(1,1)}$ were set equal to, respectively, 0 and R_1. Thus, the number of parameters estimated was equal to the number of years plus two. Exploration of several data sets indicated that, generally, estimated $\overline{w}_0 \approx \overline{w}_{LS}$ (where $\overline{w}_{LS}$ is average weight at legal size). Thus, the number of parameters was in some cases reduced further by setting $\overline{w}_0 = \overline{w}_{LS}$. Short-term changes in legal size (e.g. the higher legal size enforced during some years for Kodiak's second season) were disregarded.

Results for the period 1964–1982, for which potlift data are available, are considered first. This is also the period investigated by Zheng *et al*. (1996).

Estimated annual abundance of recruits and legal males were very similar whether *CPUE* data were used or not ($\lambda_{CPUE} = 0$), as shown in Fig. 14(a) (N_t scaled to $CPUE_t$ with the calculated constant catchability coefficient). This implies that the *CPUE* and mean weight data are consistent with each other, given the model. Exploration with several values of λ_{CPUE} led us to choose a value of 0.1; for larger values the model tends to fit the *CPUE* trajectory alone. This is to be expected, because the growth component of the model has only one free parameter ($\overline{w}_0$). Predicted and observed

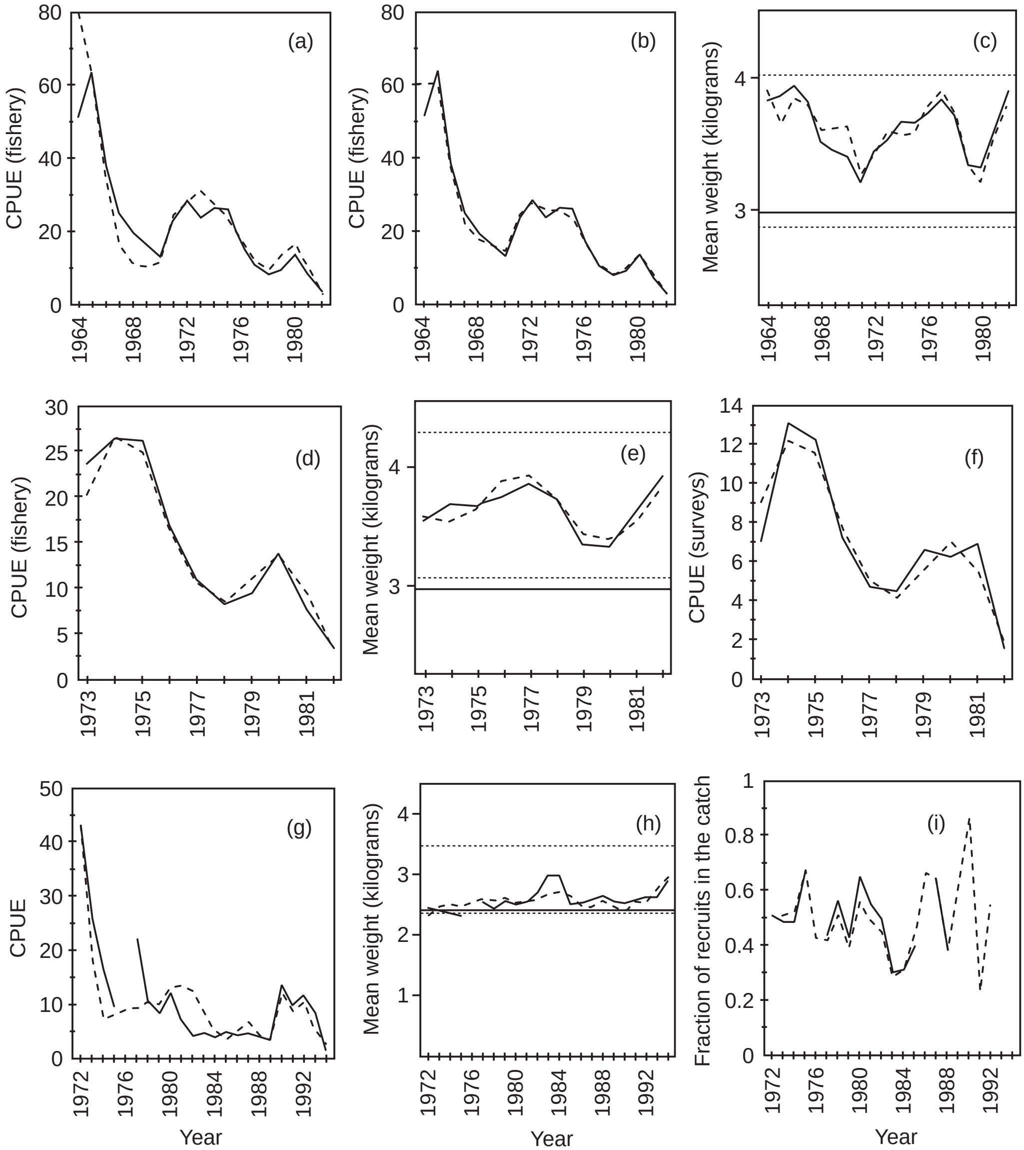

Fig. 14. Red king crab, model fits of data from Kodiak and West Aleutian management areas; solid lines, observations, dashed lines, model predictions. Kodiak management area. (a) Period 1964–1982, fit of *CPUE* by model using only data on total catch and mean weight in the commercial catch (i.e. $\lambda_{CPUE} = 0$), with $M = 0.4$ year^{-1}. (b) and (c) Period 1964–1982, observations and model prediction of commercial *CPUE* and mean weight in the commercial catch ($M = 0.4$ year^{-1}; $\lambda_{CPUE} = 0.1$). (d), (e) and (f) Period 1973–1982, observations and model prediction of commercial *CPUE*, average weight in the commercial catch, and survey *CPUE*($M = 0.4$ year^{-1}; $\lambda_{CPUE} = 0.1$; $\lambda_{survey} = 0.1$). West Aleutians management area. (g), (h) and (i) Period 1972–1994; observed and predicted commercial *CPUE*, mean weight in the commercial catch, and percentage of recruits. Solid horizontal lines in (c), (e) and (h) indicate weight at legal size; dotted horizontal lines correspond to estimated $\overline{w}_0$ and $\overline{w}_1$ (mean weight of legal instars 0 and 1).

CPUE and mean weight for the period 1964–1982 ($\lambda_{CPUE} = 0.1$; $M = 0.4\ \text{year}^{-1}$) are shown in Fig. 14(b,c). Our series of recruitment estimates and those from Zheng *et al.* (1996; all weighting factors set equal to 1, which was their choice) are compared in Fig. 5(a) for $M = 0.4\ \text{year}^{-1}$, their favoured choice. Trajectories estimated by us and Zheng *et al.* (1996) are very similar towards the lower values of *M*; Zheng *et al.*'s estimates tend to increase faster with *M*. The period 1960–1963 was not considered by Zheng *et al.* (1996) because no potlift or size data are available. This period is, however, of most interest: in 1964 estimated abundance and recruitment were at a historical high (at least for the period 1964–1983), but it remains uncertain what the situation had been in preceding years. Data on $\overline{w}$ and permits (another measure of effort) are available for the likely crucial 4 year period 1960–1963. Examination of the relation between permits and potlifts for the period 1964–1982 (for which both are available) shows a rather good linear relationship. A linear relation was fitted, and number of potlifts was extrapolated to the period 1960–1963 based on the data for 1964–1982. The model could then be fitted to the 23 year period 1960–1983. The fit, as before, was very satisfactory; the different pieces of information (including now the four extrapolated effort figures) were consistent with each other, as for the period 1964–1982. The trend for the 1960s is very similar to that estimated by Rothschild *et al.* (1970) using standardized catch/landing data.

Pot survey *CPUE* data are also available for the period 1973–1982 (Johnson, 1990). Mean survey *CPUE* estimates available for Kodiak for the period 1973–1982 (Johnson, 1990) can be combined with the fishery-based data discussed above, adding a third observation equation,

$$\ln(Surv.\ CPUE_t) = \ln(q_s N_t) + \varepsilon_{3t} \tag{A13}$$

where q_s is the catchability coefficient for the pot survey; notice that *survey CPUE* is proportional to pre-season abundance (N_t), while *commercial CPUE* is proportional to average abundance during the fishing season ($\overline{N}_{c_t}$). The corresponding version of the SS is then:

$$\text{SS} = \sum^{t}[\lambda_{cpue}(\ln CPUE_{pred,t} - \ln CPUE_{obs,t})^2 + \lambda_{\overline{w}}(\ln \overline{w}_{pred,t} - \ln \overline{w}_{obs,t})^2 + \lambda_{Surv.}(\ln Surv.\ CPUE_{pred,t} - \ln Surv.\ CPUE_{obs,t})^2]. \tag{A14}$$

Figure 14(d–f) shows the observed and predicted trajectories of $CPUE_c$, $\overline{w}$ and $CPUE_s$. The three pieces of information appear very consistent with each other. The analysis also yields an estimate of the catchability coefficient for the pot survey ($\hat{q}_s = 1.22\text{E} - 06$), about one-third the commercial catchability coefficient for the same period ($\hat{q}_c = 3.13\text{E} - 06$). The estimated q_s can be used to calculate pre-season abundance of legal males during the years 1983–1986, when the fishery was closed but pot surveys were still being conducted. Figure 5(b) compares the pre-season abundance of legal males estimated (i) with our simple model for the period 1973–1982, (ii) from mean $CPUE_s$ (calculated as mean $CPUE_s/\hat{q}_s$) for the period 1973–1986, (iii) from mark–recapture estimates from Blau (1985), and (iv) in survey-based estimates from Zheng *et al.* (1996), the two latter for the period 1973–1986. All the analyses show similar trends, but the survey-based estimates from Blau (1985) and Zheng *et al*. (1996) are extreme and disparate in some years (e.g. 1974, 1980).

Piecing together the results for the different periods gives a picture of the trend in pre-season legal male abundance longer than any presented before, covering the 27 year period 1960–1986 (Fig. 5(c)).

Peninsula and East Aleutians

Because growth is not well documented for the Peninsula and East Aleutians areas, more growth parameters were freed in the analysis. One candidate is parameter A, which controls the frequency of moulting and is likely to be temperature dependent; parameters in the length–weight relation and those that describe size-increment per moult are likely to be less variable. The model was fitted to commercial *CPUE* and mean weight data from Peninsula (1969–1982) and the East Aleutians (1971–1982), leaving parameter A free. The estimated value of A was smaller for Peninsula $\hat{A} = -0.72$) than for Kodiak (Table 5), meaning that the probability of moulting (conditioned only on pre-moult size) was somewhat smaller, as expected. An arbitrarily high value ($\sim$100) was estimated for the East Aleutians, implying that the probability of moulting is close to one for all legal-size males. This reflects lack of information on growth: legal size for that area was smaller (16.25 cm), and mean weight was small, meaning that much of the legal-size stock was composed of small males with a high probability of moulting. The same values of M (0.4 year^{-1}) and λ_{CPUE} (0.1) were used for the three areas.

West Aleutians

For this area, the percentage of recruits in the commercial catch ($100R_t/N_t$) was reported for most fishing seasons over the period 1972–1989 (Griffin and Ward, 1994, their table 1). A 'recruit' is defined as a male crab with a new shell (i.e. recently moulted), and a size in the range between legal size and an estimated moult increment beyond legal size (Kruse and Collie, 1991; Collie and Kruse, 1995). A variation of our simple model was fitted by minimizing

$$\mathrm{SS} = \sum^{t} \Bigg[\lambda_{cpue} (\ln CPUE_{pred,t} - \ln CPUE_{obs,t})^2 + \lambda_{\overline{w}} (\ln \overline{w}_{pred,t} - \ln \overline{w}_{obs,t})^2 + \lambda_{Recr.} \left(\ln \left(\frac{R_t}{N_t} \right)_{pred,t} - \ln \left(\frac{R_t}{N_t} \right)_{obs,t} \right)^2 \Bigg]. \qquad \text{(A15)}$$

Exploration with varying weighting factors gave comparable results for the abundance of legal-size males, recruits, and harvest rate. A fit of *CPUE*, $\overline{w}$ and percentage of recruits in the catch during the period 1972–1984 is shown in Fig. 14(g–i) ($\lambda_{\overline{w}} = 1$; $\lambda_{CPUE} = 0.01$; $\lambda_{Recr.} = 0.1$; $M = 0.4$ year^{-1}; $\hat{A} = -12.9$).

South-east Alaska

The stock has been recently assessed by Woodby (1994), who applied a form of catch-survey analysis (Collie and Sissenwine, 1983; Collie and Kruse, 1995) to estimate the abundance of legal males, and historical harvest rates. The data consisted of commercial catch and survey catch rates (catch per pot per day). Pot surveys were conducted since 1979 in ten areas (bays, coves, canals), corresponding to four districts, and legal males were partitioned into recruits and post-recruits according to their size and shell condition.

BROWN KING CRAB

The simple population model introduced for red king crab was also used to explore the dynamics of brown king crab stocks from the Aleutians. Growth parameters have been estimated for stocks from Central Japan (Hiramoto, 1985) and SE Alaska (Koeneman and Buchanan, 1985) (Table 5). Frequency of moulting, however, has not been modelled. Size-frequency distributions from various geographic regions show that the fraction of the legal-size male population larger than 200 mm (*CL*) is negligible. Furthermore, size-frequency distributions and shell condition suggest that most crab below 120 mm moult every year, while moulting becomes a rare event for crab larger than 170 mm (a pre-moult size of 170 mm corresponds *on average* to a post-moult size of 185 mm). These figures suggest a guesstimate of $\hat{A} \approx 0$.

Given its relative significance, we first focus our analysis on the West Aleutians stock. Information on *CPUE* (catch per potlift) and mean weight was available for the period 1976–1994 (ADF&G ticket files; Griffin and Ward, 1994); additionally, Griffin and Ward (1994, their table 2) present information on the percentage of new-shell crab in the catch for the seasons 1980/81 to 1991/92. We first applied a variation of the model introduced above for red king crab from the West Aleutians, but using data on percentage of 'new-shells' in the commercial catch; the latter are a mixture of recruits and post-recruits that moulted to a larger instar. We first left parameter A free. Legal size, which was originally 16.25 cm, was reduced in the two Aleutian areas to 15 cm between 1984 and 1985; consequently, two values of $\overline{w}_0$ were estimated (pre- and post-change periods). As expected, values of $\hat{A}$ were very close to 0. The two parameters describing $\overline{w}_0$ were slightly below $\overline{w}_{LS}$. Because shell condition data are available only for some years, the simpler model version (using *CPUE* and mean weight data only) was also explored. Estimates of recruitment and legal-size male abundance obtained with the two models were very similar.

Comparison of trends in *CPUE* and $\overline{w}$ between the East and West Aleutian areas showed that they were very similar. Subsequently, catch and effort data from the two areas were pooled, and only Model I was applied; all parameters describing growth were fixed ($A = 0$; $\overline{w}_0 = \overline{w}_{LS}$) because results varied little when they were left free.

TANNER CRAB

Existing data usable in stock assessment include the following.

- Pot surveys, initiated by ADF&G in 1973 in Kodiak, in 1974 in the lower Cook Inlet, Prince William Sound and South Peninsula areas, and in 1975 (through 1977) in the Aleutians. The primary purpose was to survey red king crab, but information was collected also on Tanner crab. An index of abundance was estimated, initially with the hope of predicting recruitment to the fishery (legal size) 2–4 years in advance (Colgate, 1982). Use of this information was considered difficult owing to problems with design and continuity, and unexplained sources of variation in catchability.
- Trawl surveys. During the late 1980s, ADF&G replaced pot surveys by trawl surveys (Urban, 1993). Annual trawl surveys have been conducted in Kodiak since 1987, in

Peninsula since 1988, in Chignik since 1989 (Urban, 1993), in parts of Cook Inlet since 1990 (Kimker *et al.*, 1993), and in Prince William Sound since 1991 (Trowbridge, 1992, 1994a). Trawl surveys, as compared to pot surveys, were expected by ADF&G to provide a more direct measure of abundance (Kimker and Trowbridge, 1992; Trowbridge, 1992), and to yield information on juvenile crab (which are not caught in pots). Trawl surveys, however, have a number of problems of their own. First, trawl *CPUE* is just an index of abundance, as is pot *CPUE*. *CPUE* over the area swept by the trawl cannot be simply equated with abundance: the efficiency of the trawl is unknown (it has been shown to be low in other fisheries), and varies between locations, through a daily cycle, and seasonally. A depletion experiment conducted in the Bering Sea during the summer of 1993 (Somerton and Otto, unpubl.) suggested that efficiency may be well below the 100% that has been assumed over the years in the assessment and management of crab stocks. Besides, deep regions and rough bottoms in the Gulf of Alaska are beyond the reach of trawls.
- Mark–recapture. Experimental tagging programmes have not yielded reliable results on fishing mortality or abundance due to large tag loss and low recovery rates (Colgate, 1982). Tagging programmes conducted by ADF&G have been generally small, orientated to understand movements, and subordinate to other routines.
- Catch and effort data are available in ADF&G's ticket database for the period 1969–1994 for Kodiak and Cook Inlet, and 1969–1989 for Chignik and Peninsula (both closed since 1990). Data for Prince William Sound and South-east Alaska are fragmentary and inconsistent. A logbook programme was initiated by ADF&G in 1974 (Colgate, 1982). An observer programme, mandated by the ABOF, started in 1988 (Beers, 1991).

Assessment of Tanner crab has received far less attention than given red king crab stocks. Two approaches have been followed.

- Area swept estimates based on data from the trawl surveys (Urban, 1993).
- Catch-length analysis following a modelling approach previously developed for red king crab stocks (Zheng *et al.*, 1996) has been applied only to Bering Sea stocks (Zheng *et al.*, 1995).

A simple model, similar to the one introduced above for red king crab, was used by us to explore trends in abundance and recruitment. The legal male population was considered to be composed, on average, of two instars. Legal size (introduced in 1976) is 140 mm carapace width (*CW*) in most of Alaska, the only exception being Prince William Sound where it is 135 mm. The two instars correspond approximately to instars 16 and 17 (Donaldson *et al.*, 1981), with the first making up the bulk of the harvest. A power function was used to transform *CW* measurements into weights, required because (as in the case of red king crab) the size index available for modelling was mean weight ($\overline{w}$). Following Donaldson *et al.* (1981), Hiatt's model,

$$CW_{post\text{-}moult} = c + d\,CW_{pre\text{-}moult} \tag{A16}$$

where c and d are constants, was used to calculate size increments at moult. The growth of male *Chionoecetes* has been the subject of intense debate in recent years, particularly with regards to the existence of a so-called 'terminal moult'. Three models have been proposed in the literature. (1) The probability of 'skip-moulting' (not moulting in a given year) is a function of size only. (2) The probability of skip-moulting is conditioned both on size and moulting history (i.e. whether the crab has moulted or not during previous years). (3) According to the now widely accepted terminal moult hypothesis (Elner and Beninger, 1992), males stop growing after undergoing a morphometric change involving the relative size of their claws. Such large-claw ('morphologically mature') males differ in their mating behaviour from small-claw males. In Tanner crab, morphological maturity can be reached at instars 15–17. Somerton (1981, 1982) estimated probabilities of skip-moulting under growth models (1) and (2), based on shell condition data. He fitted the indeterminate form

$$\mathrm{P}(\text{skip} - \text{moulting}|CW) = \left[1 + (n-1)\exp\left(-m(CW - CW_0)n^{n/n-1}\right)\right]^{1/1-n}, \tag{A17}$$

where m, n and CW_0 are parameters to model probability of skip-moulting conditioned on size. We utilized growth model (1) for the analyses; use of growth model (2) did not change the results. Factors governing terminal moult are poorly understood. Trends in mean weight of the catch are virtually featureless, as $\overline{w} \approx \overline{w}_{(instar16)}$, consistent with results reported by Donaldson *et al*. (1981). This implies that only a small fraction of the legal male population moults to a larger size after recruitment, at least in exploited stocks. For that reason mean weight data are virtually non-informative for stock assessment in this case; assessment models must incorporate other pieces of ancillary information.

Trawl surveys overlapped in time with the fishery only in Kodiak. In this case we used a model form that includes in the objective function terms for both the proportion and number of recruits (or, equivalently, terms for the total number of recruits and post-recruits). Recruits observed in the trawl surveys are expected to enter the fishery in the subsequent season, during the winter of the next calendar year; recruitment predicted by the model was adjusted to account for natural mortality during that time interval. It was assumed that no further recruitment occurs between the time of the survey and the fishing season. In the case of Chignik and Peninsula, trawl surveys began shortly before the closure of the fishery, and so could not be used jointly with the data from the fishery. Spalinger and Jackson (1994) provide data on the proportion of recruits in the commercial catch during the period 1980–1989 for Chignik, and 1978–1989 for Peninsula; these data were incorporated in the analysis as described earlier for red king crab from the West Aleutians. No ancillary information was available for Cook Inlet. Exploration with various weighting schemes had little effect on the results of interest and so all the weighting factors were set equal to 1.

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