

**Relationships of sea ice extent and bottom water temperature with abundance of snow crab (*Chionoecetes opilio*) on the Newfoundland - Labrador Shelf**

by

Earl G. Dawe, Donald G. Parsons and Eugene B. Colbourne  
Science Branch  
Fisheries and Oceans Canada  
Northwest Atlantic Fisheries Centre  
St. John's, NL A1C 5X1

**ABSTRACT**

It is widely believed that recent increases in crustacean resources, including snow crab, in Atlantic Canada are due to reduced predation (top-down effects). We advance an alternative hypothesis that snow crab production and early survival are regulated primarily by effects of ocean climate variation (bottom up effects) during early life history. We address this hypothesis by using time series analysis to establish relationships between recruitment indices and ocean climate indices at various time lags. We selected two indices of ocean climate variation, one to represent effects on epipelagic larval stages (ice coverage) and another to represent effects on early benthic stages (bottom temperature). Using catch per unit effort (CPUE) from the commercial snow crab fishery as our index of snow crab abundance we applied an autoregressive, integrated moving average (ARIMA) procedure with environmental input (transfer function) to explore relationships between biological production or early survival and changes in ocean climate. The procedure facilitated cross-correlation analysis between CPUE and each environmental index (corrected for autocorrelation) for each of four fishery areas. The approach was extended for our longest time series using ice coverage to illustrate how ocean climate variables can be incorporated into predictive models. We also compared our CPUE index with an index of predation - survey biomass of Atlantic cod (*Gadus morhua*). Our results showed consistent correlations for each of the ocean climate indices and across all areas. CPUE was positively correlated with ice cover for all three areas that are affected by ice, at lags of 8-10 years, approximating age at recruitment. These correlations were significant for the two longest time series, while there was no relationship for a fourth, most-southern area, that is unaffected by ice cover. Consistent negative relationships were found between CPUE and bottom temperature for all four areas, at lags generally one year shorter than the corresponding CPUE-ice relationships, although none were significant. Crab-cod relationships were not significant, the cod index being unidirectional. We conclude that abundance is regulated primarily by effects of ocean climate variation on early life history stages. Cold conditions in early life favor production or survival at either or both pelagic and early benthic stages but functional relationships remain unknown.

## INTRODUCTION

Snow crab (*Chionoecetes opilio*, Majiidae) support male-only fisheries in the north Atlantic and north Pacific oceans. Fisheries in the northwest Atlantic are prosecuted along the Newfoundland and Labrador continental shelf, in the Gulf of St. Lawrence, and on the eastern Nova Scotian Shelf (Fig. 1).

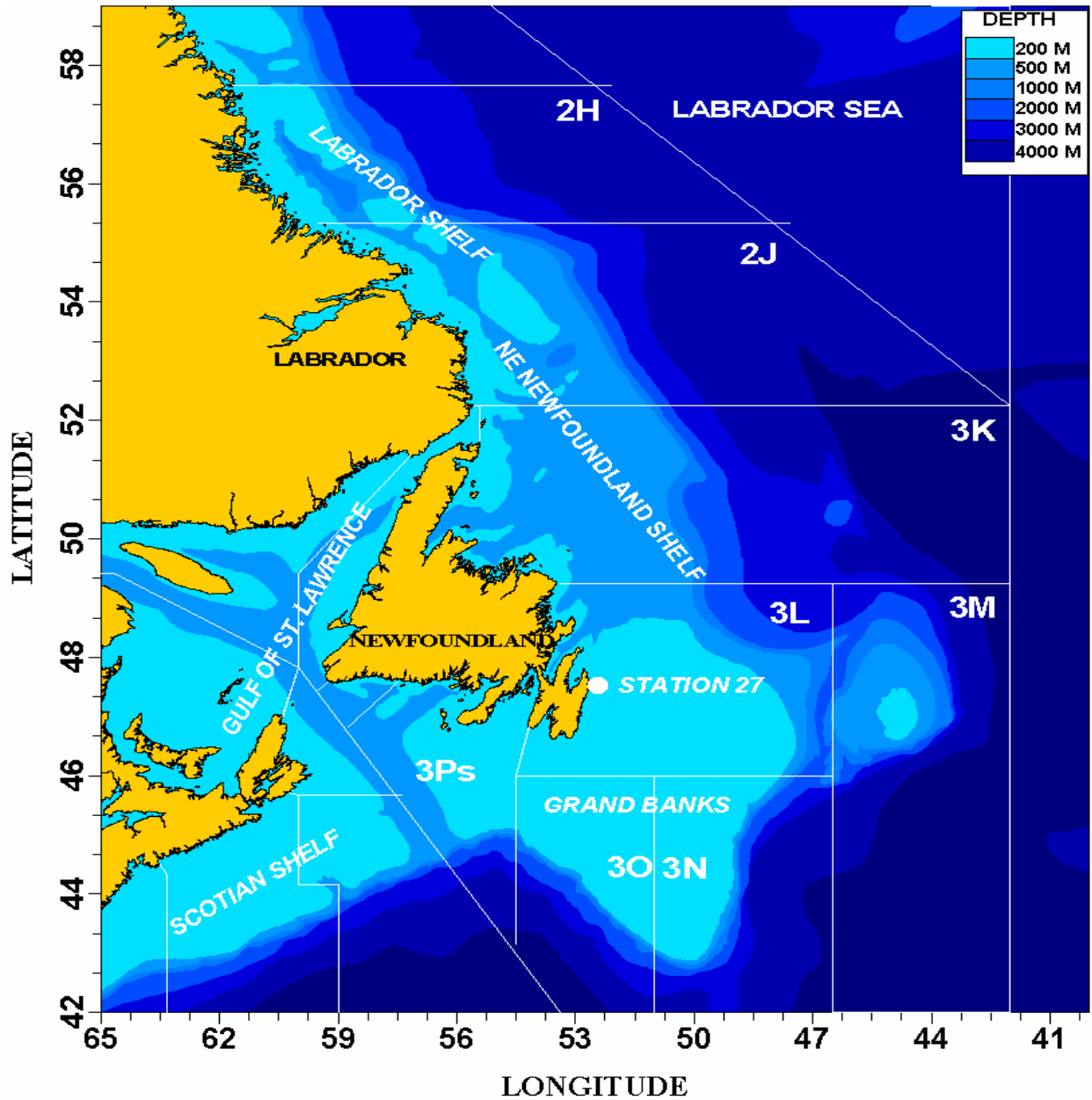


Fig. 1. Map of study area showing Northwest Atlantic Fisheries Organization (NAFO) Divisions and oceanographic monitoring Station 27.

Recruitment in Canadian Atlantic snow crab fisheries is periodic but sources of variation remain unknown. One hypothesis is that cyclic recruitment is maintained through cannibalism of settling year-classes by several previously settled year classes (Sainte-Marie et al. 1996, Lovrich and Sainte-Marie 1997). Alternatively, Frank et al (2005) feel that ecosystem structure is regulated at high trophic levels by predation pressure ('top-down' effects) and recent increases in snow crab abundance are due to declines in abundance of groundfish predators.

However recent increases in northern shrimp (*Pandalus borealis*) and snow crab abundance off Newfoundland and Labrador also coincided with a pronounced change in the mid-1990's from a cold oceanographic regime to a warm regime (Fig. 2). We believe that snow crab abundance and recruitment to fisheries are strongly affected by ocean climate variation, and that such 'bottom-up' effects on production or early survival are more important than predation pressure. This hypothesis is based on the observation that the snow crab is a highly stenothermal species. Foyle et al (1986) showed that snow crab are energetically confined to cold water and that slight temperature changes greatly affect their energy balance. Also, variation in temperature is closely related to the size at which snow crabs terminally molt (Dawe et al. in prep).

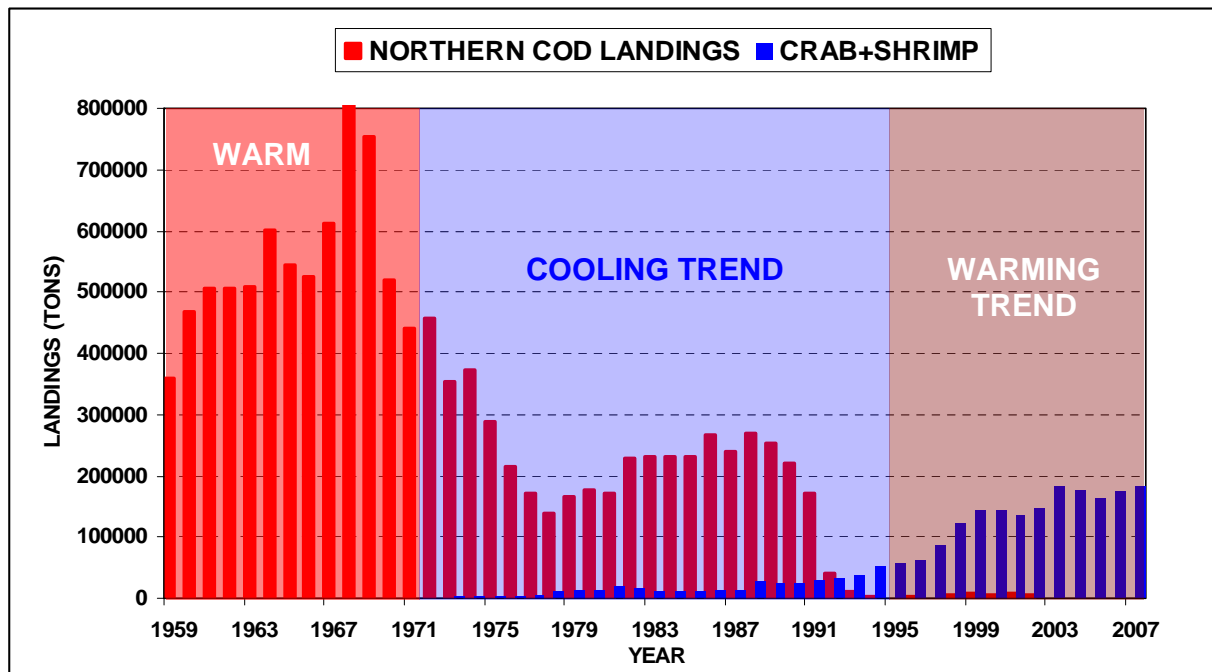


Fig. 2. Historical landings of the northern (Div. 2J3KL) cod stock and the combined landings of northern shrimp and snow crab in Newfoundland and Labrador waters. The general ocean climate regimes throughout the period are also indicated.

In this paper we advance the hypothesis that snow crab production and early survival are regulated primarily by effects of ocean climate variation during early life history. We address this hypothesis by using time series analysis to establish relationships between recruitment indices and ocean climate indices at various time lags. We also consider the relative effects of

ocean climate variation versus groundfish abundance on recruitment. Time series analysis was also used to develop transfer function models, illustrating how ocean climate variation can be incorporated into models to improve their predictive capability.

## DATA AND METHODS

### *Development of indices*

We used CPUE from the commercial snow crab fishery as our index of snow crab abundance. Trap fisheries for snow crab in Newfoundland and Labrador waters began in 1968. A 35-year time series (1973-2007) of CPUE data, expressed as kg of commercial-sized ( $\geq 95$  mm carapace width) crabs per trap haul, was available for the eastern Newfoundland Shelf that included the northern Grand Bank NAFO Division 3L (Figure 1). Shorter time series of CPUE were available from three other fishery areas (Fig. 1), in NAFO Divisions 2J (1985-2007), and 3K (1981-2007) and Subdivision 3Ps (1985-2007). Although the annual CPUE series is unstandardized (i.e. does not account for variation in fishing practices due to season, soak time, bait type, etc.), it is believed to generally reflect long-term trends in the abundance of the resource.

We selected two indices of ocean climate variation, one to represent likely effects on epipelagic larval stages and another on early benthic stages. The area of annual ice cover between  $45^{\circ}$  and  $55^{\circ}$  N off Newfoundland and Labrador ( $\text{km}^2$ ) was selected as the input epipelagic environmental variable. The selection was based on the assumption that abundance is determined at the pelagic larval stage and recognition that sea ice is one of the most important variables affecting energy flow in some sub-arctic ecosystems (Wyllie-Echeverria and Wooster 1998, Hunt and Stabeno 2002) Furthermore ice extent was thought to be an important factor in regulating snow crab production in the eastern Bering Sea (Somerton 1982).

We selected mean bottom temperature as our index of benthic ocean climate variation, based on known strong effects of temperature variation on snow crab physiology and size at terminal molt (Foyle et al. 1989, Dawe et al. in prep). Bottom temperatures used for NAFO Div. 3K and 3L were annual mean bottom temperatures from Station 27, located 10 nm off St. John's (Fig. 1). Bottom temperatures used for Div. 2J and Subdiv. 3Ps were mean temperatures from bottom trawl survey sets, collected using a trawl-mounted CTD system. Only data from shallow-water sets ( $<200$  m) were used because settlement and early benthic stages occur on shallow banks (Dawe and Colbourne 2002). Mean bottom temperatures for Div. 2J were derived using data from fall surveys, whereas those from Subdiv. 3Ps were derived using data from spring surveys.

Trend in Atlantic cod biomass was used as an indicator of trend in predatory groundfish. Parsons (2005) showed that the trend for northern cod was reflective of the general trends for several commercial groundfish species. The cod index is survey biomass of northern cod (Div. 2J3KL) which we compare, unlagged, with crab CPUE by division.

### *Analysis and modeling*

Using the snow crab CPUE time series as a proxy for abundance we applied an autoregressive, integrated moving average (ARIMA) procedure (Box and Jenkins 1976) with environmental input (transfer function) to explore relationships between biological production or early survival and changes in ocean climate. The ARIMA procedure facilitated cross correlation analysis between CPUE and each environmental index for each of the four fishery areas. We extended our model to develop a predictive transfer function model of abundance using our most lengthy CPUE time series (Div. 3L), and the ice cover index.

The cross-correlation analysis for all areas and both indices was initially conducted using data up to 2004 inclusive. Also, the Div. 3L transfer function model was initially developed using data up to 2004 so that more recent data for 2005-2007 could be used to test the model by comparing abundance indices forecast by the model with recent empirical CPUE values. The cross-correlation analysis for all areas and both indices was also repeated with the most recent 3 years included, to test the effect of additional data on the relationships established.

## RESULTS

### *Effects of ocean climate variability*

The matrix resulting from the cross-correlation analyses showed an interesting general pattern (Table 1). Correlations were consistently positive for ice cover except for Subdiv. 3Ps, an area which remains ice free throughout the year. Correlations with bottom temperature were consistently negative, for all four areas, although none were significant.

Table 1. Results of cross correlation analysis of CPUE with each of two ocean climate indices, area of ice cover (Ice) and bottom temperature (BT) by NAFO Division, using data up to 2004. Correlations in bold are significant at approximately the 0.05 probability level.

Index	Division				
		<b>2J</b>	<b>3K</b>	<b>3L</b>	<b>3Ps</b>
<b>Ice</b>	Lag	8	8	10	NA
	Correlation	0.376	<b>0.425</b>	<b>0.341</b>	
<b>BT</b>	Lag	6	7 and 8	9	7
	Correlation	-0.303	-0.251	-0.309	-0.337

Lags were consistently longer for ice than for bottom temperature (Table 1, Fig. 3). Also, lags for correlations with both ice cover and bottom temperature were shorter in the warm northern areas (Div. 2J and 3K) than in colder Div. 3L, where the cold intermediate layer sits on the northern Grand Bank at depths of less than 100m.

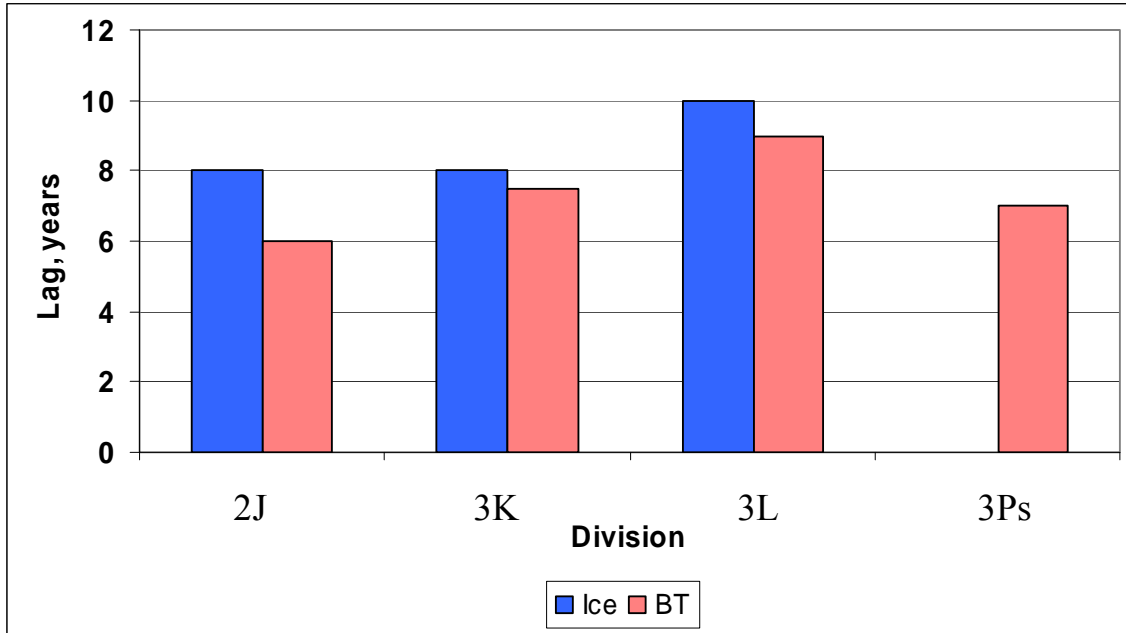


Fig. 3. Comparison of time lags with strongest cross-correlation between CPUE and ice extent or bottom temperature by NAFO Division, from north (left) to south (right). The 7.5 year lag presented for Div. 3K bottom temperature represents an average of two equally correlated lags.

### *Effects of ocean climate variation versus predation*

Comparison of trends indicated that the lagged relationships of the ocean climate indices with CPUE were stronger than the unlagged relationship of CPUE with cod biomass (Fig. 4-7). Relationships between cod and crab were unconvincing because the trend in cod was unidirectional. By contrast, the relationships of both ice extent and bottom temperature with CPUE were maintained within a higher degree of variability (Figs 4-7). Especially convincing is that in the three areas occupied by the northern cod stock (Div. 2J, 3K and 3L) both ice cover and bottom temperature maintained their relationships with CPUE after the cod stock collapsed (Fig. 4-6). This was most clear on the southern Labrador shelf (Div. 2J, Fig. 4). Also, on the St. Pierre Bank (Subdiv. 3Ps), where the cod stock has not collapsed, bottom temperature maintained its relationships with CPUE while cod biomass fluctuated without trend (Fig. 7).

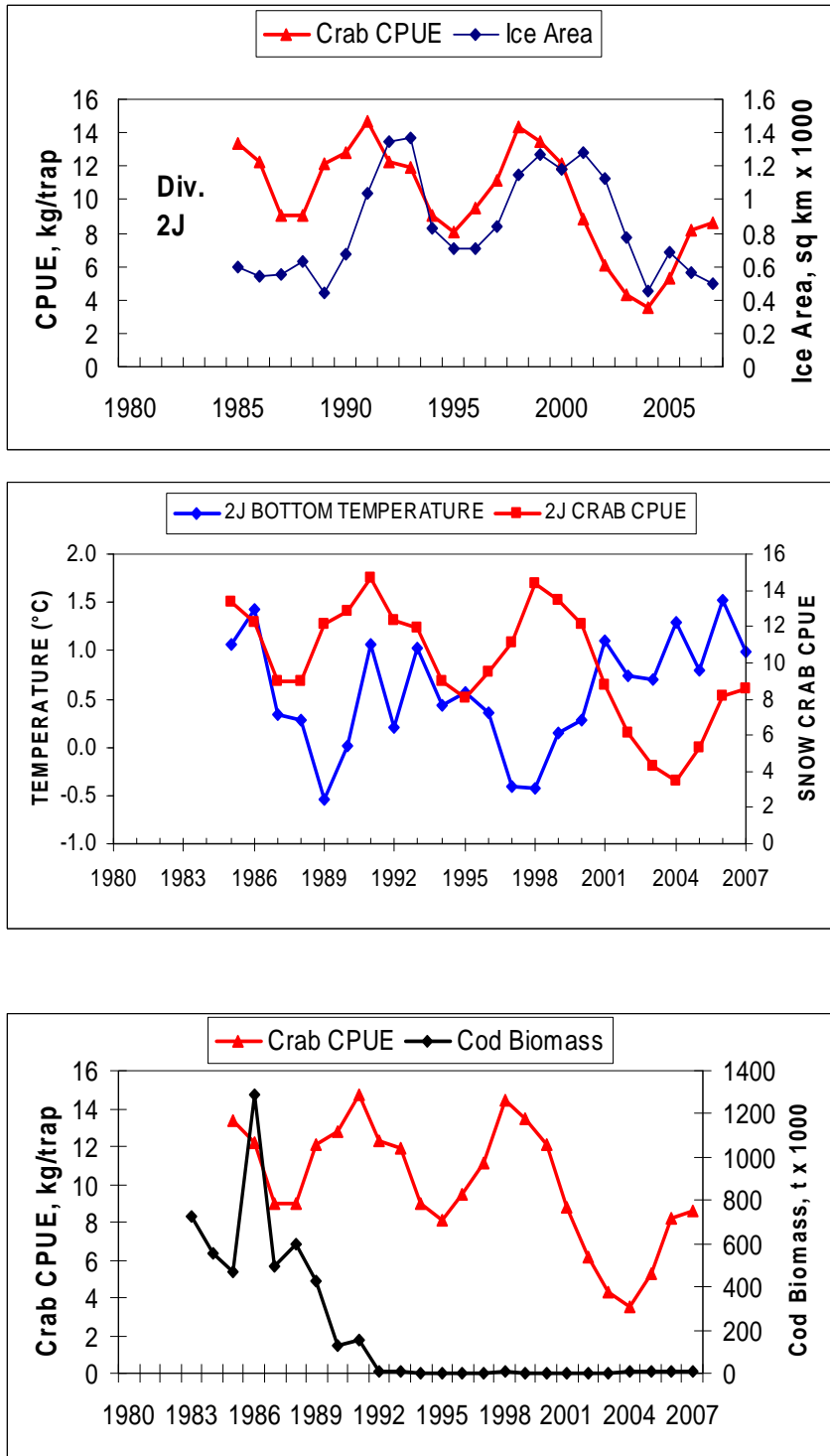


Fig. 4. Trends in Div. 2J snow crab CPUE compared with trends in ice extent, lagged 8 years (top), bottom temperature lagged 6 years (middle) and cod biomass, unlagged (bottom).

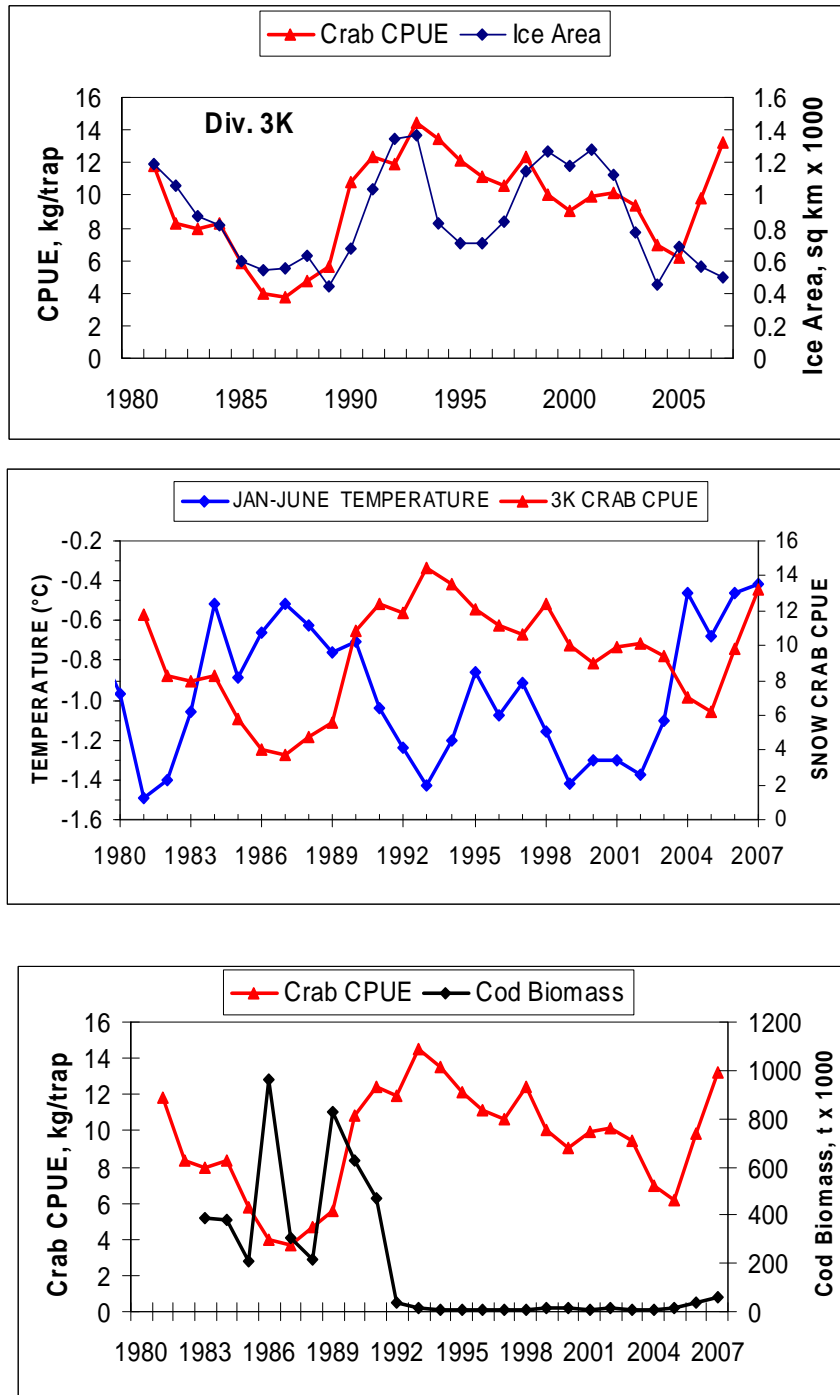


Fig. 5. Trends in Div. 3K snow crab CPUE compared with trends in ice extent, lagged 8 years (top), bottom temperature, lagged 8 years (middle) and cod biomass, unlagged (bottom)

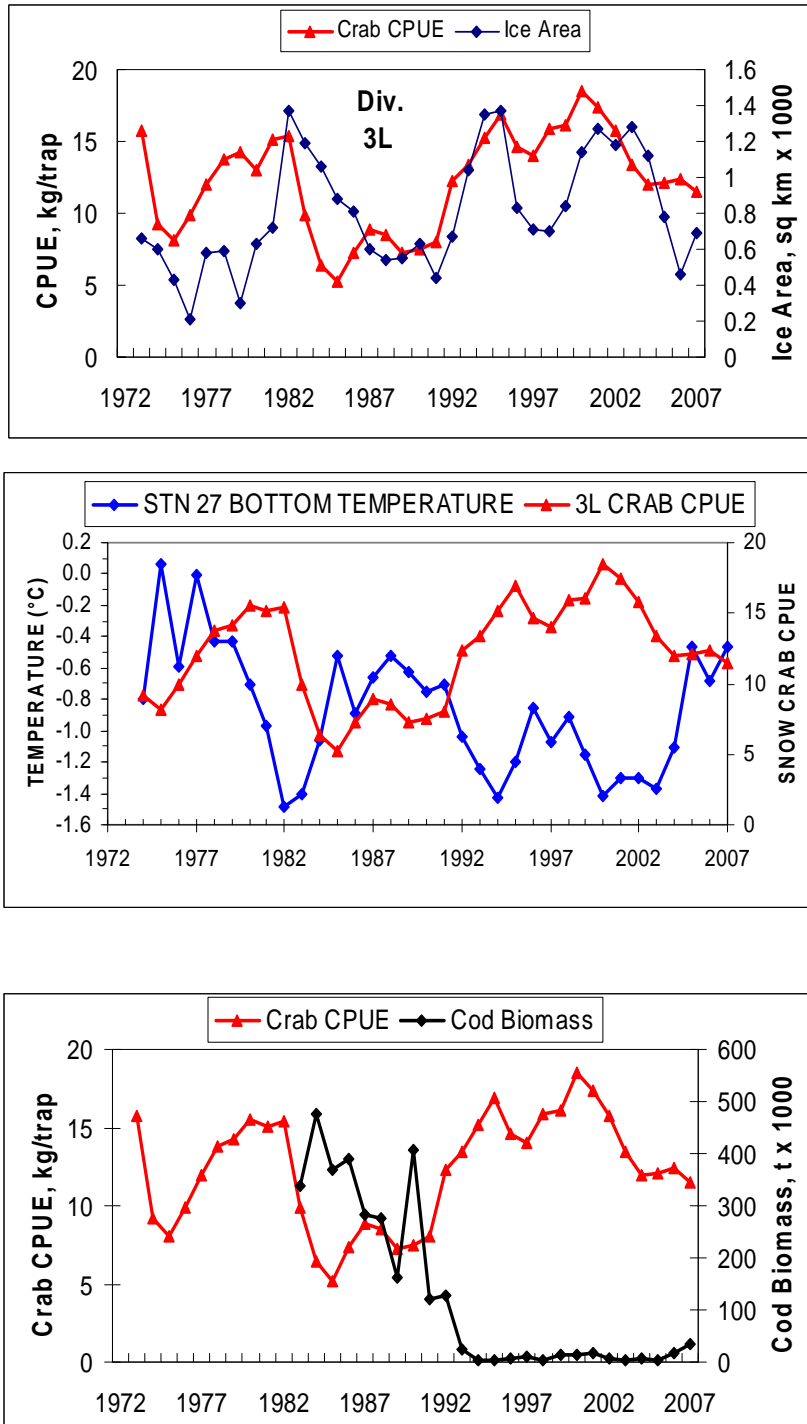


Fig. 6. Trends in Div. 3L snow crab CPUE compared with trends in ice extent, lagged 10 years (top), bottom temperature, lagged 9 years (Middle) and cod biomass, unlagged (bottom).

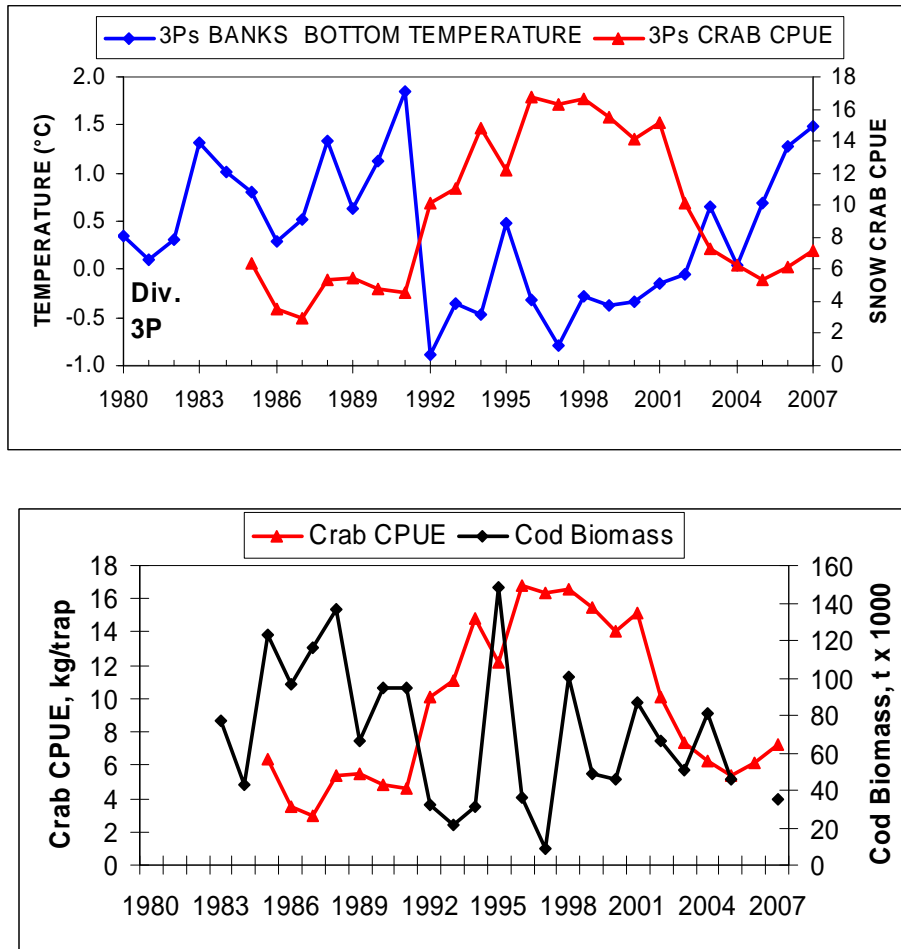


Fig. 7. Trends in Subdivision 3Ps snow crab CPUE compared with trends in bottom temperature, lagged 7 years (above) and cod biomass, unlagged (below)

### *Modeling snow crab abundance*

To illustrate how effects of ocean climate variation can be incorporated into predictive models we focused on Div. 3L, using ice cover as the input environmental variable (Table 1).

The cross-correlation analysis (Fig. 8) showed that ice-cover dimensions, with delays (shifts) of 0 and 10 years, were significantly correlated with catch rates after accounting for autocorrelation by prewhitening.

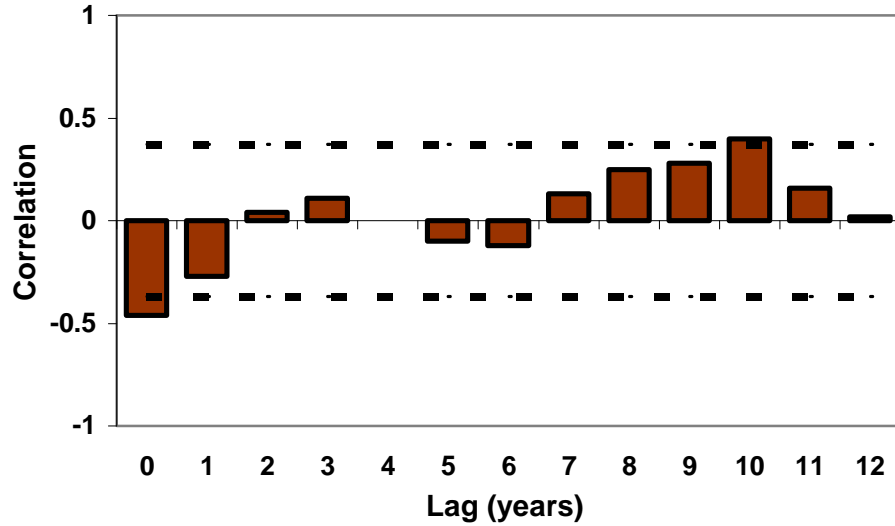


Fig. 8. Crosscorrelation of snow crab CPUE and ice cover after correction for autocorrelation (pre-whitening). Broken lines represent  $\pm 2$  standard errors.

In addition to the mean term, first and second-order autoregressive parameters were significant determinants of CPUE, reflecting strong autocorrelation within the CPUE series. The ice cover inputs (at shifts of 0 and 10) also were estimated as significant parameters within the model (Table 2). Autocorrelation check of residuals indicated that, other than the mean and the autoregressive parameters, there was no additional information in the residual series for CPUE that required more complex modeling (i.e. autocorrelations at lags 1 through 12 were not significant indicating “white noise” residuals). Similarly, crosscorrelation check of residuals with the ice cover inputs confirmed that the specified transfer functions also achieved white noise residuals with non-significant crosscorrelations from lags 0 through 11.

Table 2. Estimation of transfer function parameters for Division 3L snow crab CPUE model and tests for uncorrelated (white noise) residuals. CPUE = catch rate response series, ICE = ice cover input series, DF = degrees of freedom.

Parameter	Estimate	Std. Error	t Value	Pr> t	Lag	Variable	Shift
Mean	10.4491	1.68300	6.21	<0.0001	0	CPUE	0
Autoregressive 1	1.28962	0.18196	7.09	<0.0001	1	CPUE	0
Autoregressive 2	-0.50246	0.17961	-2.84	0.0086	2	CPUE	0
Input series 1	-2.69952	1.30814	-2.06	0.0492	0	ICE	0
Input series 2	4.11498	1.19653	3.44	0.0020	0	ICE	10

Autocorrelation Check of Residuals

To Lag	$X^2$	DF	Prob > $X^2$	-----Autocorrelations-----					
6	3.55	4	0.4698	-0.124	0.179	0.016	-0.216	0.054	0.002
12	10.14	10	0.4285	-0.164	0.102	-0.274	-0.027	-0.081	-0.143

## Crosscorrelation Check of Residuals with Input ICE (shift = 0)

To Lag	$X^2$	DF	Prob $>X^2$	-----Crosscorrelations-----					
5	1.98	6	0.9214	-0.090	-0.142	0.124	0.056	-0.131	0.014
11	9.96	12	0.6194	-0.044	0.400	0.266	0.127	0.050	-0.077

## Crosscorrelation Check of Residuals with Input ICE (shift = 10)

To Lag	$X^2$	DF	Prob $>X^2$	-----Crosscorrelations-----					
5	2.25	6	0.8954	0.079	-0.121	-0.010	-0.020	-0.089	0.279
11	5.33	12	0.9462	0.061	0.054	0.008	-0.269	-0.147	-0.214

In general, the modeled estimates fit the observed CPUE well (Figure 9). The 10-year forecast, facilitated by the lagged autoregressive and delayed input parameters, indicated that CPUE would continue to decline until 2006, in response to less ice (warmer conditions) since 1996, and stabilize thereafter. Typically, however, uncertainty in the forecast, as reflected in the 95% confidence intervals, is greater than within the observed period and increases with time.

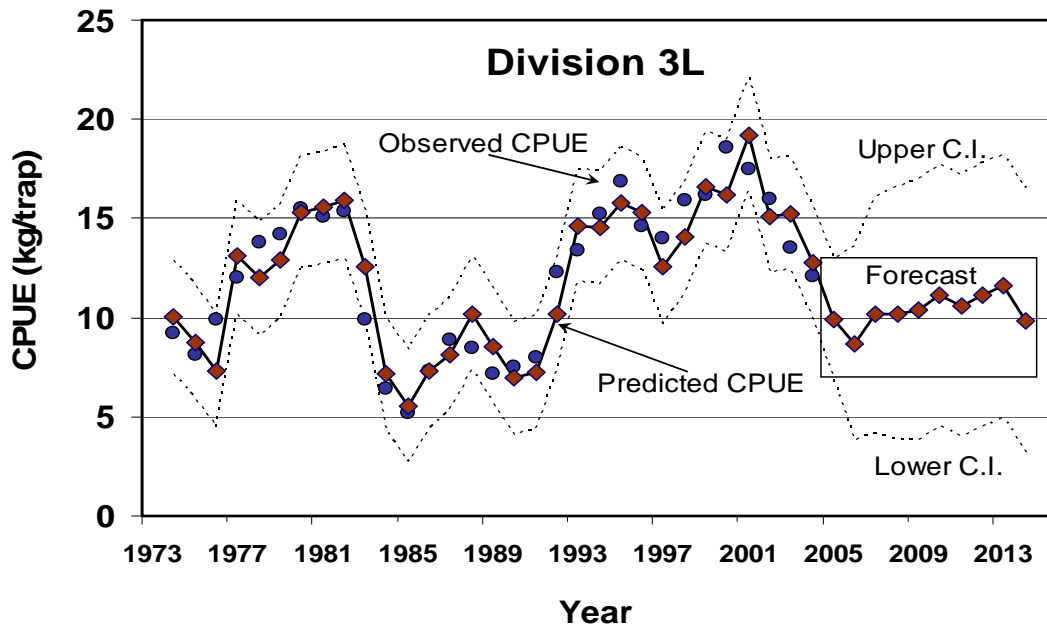


Fig. 9. Div. 3L snow crab transfer function model, based on data up to 2004.

### Updated analyses and modeling

Comparison of observed Div. 3L CPUE values for 2005-2007 with those predicted by the model (Fig. 10) indicated that CPUE did not decline in 2005 and 2006 as the model predicted but remained considerably higher. When the model was re-run including all data up to 2007 the cross-correlation of ice extent and CPUE remained strongest at lag 10 years (coefficient = 0.312), but it was no longer statistically significant. Similarly, the updated cross-correlation analyses indicated that the Div. 3L relationship of bottom temperature with CPUE remained strongest at a lag of 9 years, but it too had weakened (coefficient = -0.296).

The updated cross-correlations for the more northern areas (Div. 2J and 3K) also deteriorated and the previously identified lags could no longer be supported with the revised analysis. The sole exception to this general pattern of erosion was for Subdiv. 3Ps, where the relationship of bottom temperature with CPUE improved and became statistically significant (coefficient = -0.548,  $p < 0.05$ ).

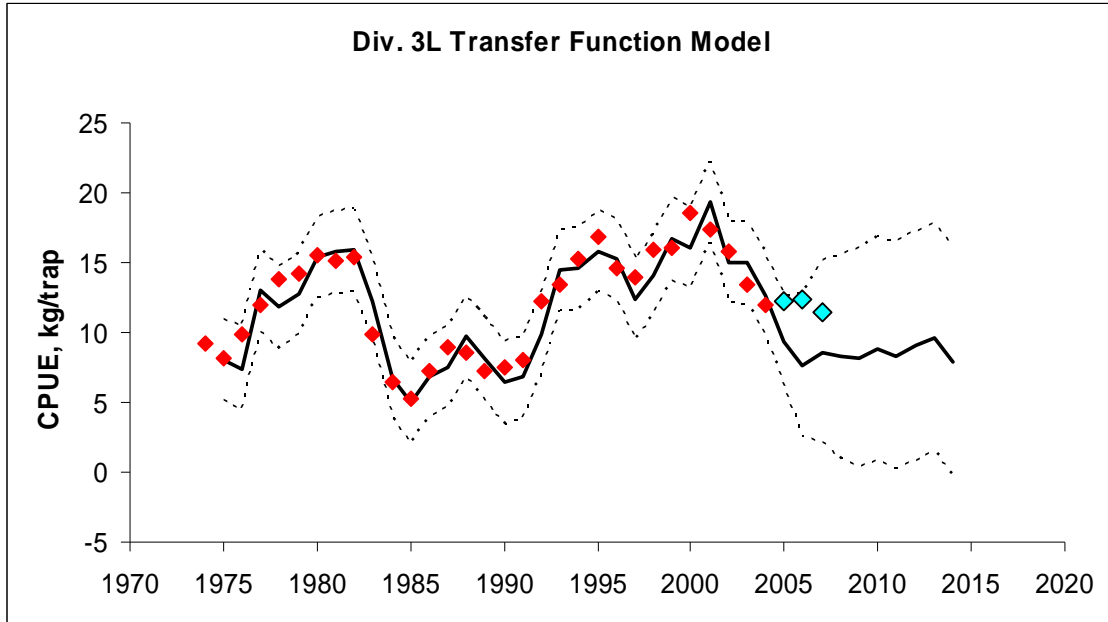


Fig. 10. Div. 3L snow crab transfer model (solid line), with confidence intervals (dotted line) based on updated data to 2004 (red data points), with observed CPUE values for 2005-2007 overlain (blue data points).

## DISCUSSION

### *Effects of ocean climate variation versus predation*

Our results indicate that snow crab recruitment is more strongly related to effects of ocean climate variability on production or survival at early life history stages ('bottom-up' processes) than to effects of predation ('top-down' processes). Both ocean climate indices, appropriately lagged, maintained convincing relationships with CPUE over several cycles in all areas. These relationships were maintained in 3 areas after the northern cod stock collapsed as well as in one area where cod biomass fluctuated without trend. Furthermore these relationships showed a consistent pattern with lags of strongest correlations with sea ice at 8-10 years, consistent with an effect of ice on pelagic larval stages. Lags of strongest correlation with bottom temperature were shorter, at 6-9 years, consistent with an effect of bottom temperature on early benthic stages. Also lags were shorter for northern areas (Div. 2J and 3K) than for the colder northern Grand Bank (Div. 3L), consistent with the widely-held concept that crustaceans molt more frequently and grow more quickly in warm than in cold waters.

By contrast, no consistent relationships between crab CPUE and cod biomass were evident. We recognize that relationships of CPUE with cod biomass should be lagged as well because snow crab preyed upon by cod are predominately small and several years from recruitment to the fishery. However it was not possible to identify lags through crosscorrelation, and indiscriminate lagging would not have improved those relationships. For example, lagging by about 5 years would have resulted in apparent positive relationships in some cases. The apparent unimportance of predation in regulating snow crab abundance is consistent with studies that have shown that snow crab represents a minor component of the diet of cod on the Newfoundland-Labrador shelf (Lilly 1984, 1991).

We conclude that snow crab abundance is primarily regulated by ocean climate variation during early life history. This disagrees with Frank et al. (2005) who hypothesized that ecosystem structure is regulated primarily by predation. They cited increased snow crab landings on the Nova Scotian Shelf following the collapse of groundfish stocks as evidence of such ‘top-down’ control. However, as we noted, such relationships are unconvincing.

Our conclusion is consistent with numerous previous studies that have described relationships between ocean climate indices and abundance for snow crab as well as other crustaceans. Somerton (1982) found that Eastern Bering Sea snow crab abundance was directly related to ice cover at a lag that implied a pelagic larval process. Recruitment in many commercially important crab stocks in the Bering Sea and Gulf of Alaska appeared to be related to decadal shifts in ocean climate (Zheng and Kruse 2000). Strong year classes in king and tanner crab stocks in this area were significantly associated with strong cyclonic winter circulation, as indexed by the Aleutian Low and low sea-surface temperatures. Year-class strength of snow crab in the Eastern Bearing Sea was noted to be quite different from that of other crab stocks, but appeared to be negatively, although not significantly, associated with surface temperature. Parsons and Colbourne (2000) found that northern shrimp CPUE was positively correlated with ice cover, at a lag that implied an effect during the pelagic larval period.

### ***Relative effects of sea ice versus bottom temperature on snow crab abundance***

The results of our analyses showed that a cold oceanographic regime during early life history is associated with increased production or survival of snow crab. However critical stages are uncertain and functional processes remain unknown. Trends in ocean climate indices are closely correlated (Colbourne and Anderson 2003) and snow crab CPUE appears to be related to variation in several ocean climate indices at differing lags. It is possible, in a most highly adaptive scenario, that both sea ice and bottom temperature affect production and/or survival of consecutive early life history stages. Alternatively only one of these correlated variables may be important. It is also quite possible that neither is important but that one or both of these indices is correlated with some other variable that directly affects abundance.

We feel it is likely that bottom temperature has an important effect on survival of early benthic stages. This is based primarily on the negative correlation of CPUE with bottom temperature, that became significant in our updated analysis, for the St. Pierre Bank (Subdiv. 3Ps), our only area unaffected by ice. This belief is consistent with the known sensitivity of this species to

temperature variation. Dawe et al (in prep) have shown that slight changes in bottom temperature regulate the size at which snow crabs will commit to their terminal molt. Also, Foyle et al. (1989) showed that snow crabs are bioenergetically limited to cold water and have their maximum positive energy balance at 1 °C.

The direct relationship of CPUE with ice cover at lags of 8-10 years suggests that some process related to ice cover, during the pelagic larval period, regulates production or early survival. However, the inverse relationship of CPUE with bottom temperature at lags of 6-9 years suggests that a cold benthic regime soon after settlement somehow promotes survival and subsequent recruitment.

Any effect of ice coverage on production or early survival is currently unknown. It is possible that ice extent is simply correlated with a subsequent benthic process involving bottom temperature. However, it is known that ice coverage affects timing of the spring production cycle as well as snow crab larval release (Starr et al 1994). Ice coverage may also indirectly affect larval survival through effects on other variables such as surface temperature or stratification. Somerton (1982) found that snow crab abundance was related to area of ice coverage in the eastern Bering Sea and hypothesized that this was due to an effect of sea ice on primary production and larval survival. Zheng and Kruse (2000) found that strong year classes in king and tanner crab stocks were generally associated with low sea-surface temperatures, although the inverse relationship of snow crab abundance with sea-surface temperature was not significant.

### ***Snow crab abundance model***

The significant negative correlation between Div. 3L CPUE and ice cover with no delay could reflect a negative effect of cold conditions on the catchability of crabs by baited traps and/or the inaccessibility of portions of productive crab fishing grounds in the spring of heavy ice years. The positive correlation with a delay of 10 years is consistent with the hypothesis that cold conditions early in the life cycle (e.g. pelagic larval stage, settling megalopal stage or early juvenile stages) are favorable for production or early survival.

Our time series model demonstrates how a delayed response in fishery performance to variation in ocean climate can be used to obtain a forecast which might be useful in the management of valuable marine resources. Other studies have shown that environmental information can be useful in developing predictive models. For example, Dawe et al (2007), in modeling abundance trends of two annual squid species, determined that accuracy of time-series models can be improved by incorporating environmental variables.

However, our snow crab model is impractical in its current form as the signal-to-noise ratio is low and the forecasted decline in CPUE in 2005 and 2006 was not observed. Several year classes are represented in the CPUE index and the difficulty in teasing out cohorts prevents more detailed age-based analyses which might be more revealing. Furthermore, our model is incomplete in that multiple processes no doubt interact to regulate production and survival to recruitment.

Most of our cross-correlations deteriorated with inclusion of the most recent three years of data. CPUE remained high or increased in all but one area despite anticipated negative effects of warm conditions earlier in life. Correlations of such time series notoriously erode (e.g. Mann and Drinkwater, 1994), at times losing their statistical significance. Parsons and Colbourne (2000) found that northern shrimp CPUE was significantly directly related to ice cover, at a lag that implied an effect during the pelagic larval period, but this correlation also eroded with inclusion of more recent data. This may reflect lack of understanding of underlying true functional relationships and/or changes in the relative importance of interacting processes, including anthropomorphic effects. Zheng and Kruse (2006) showed that abundance trends differed among crab species and stocks in the eastern Bering Sea and they concluded that functional processes differed among stocks. They hypothesized that a northward shift in the distribution of mature females, associated with warm conditions following a 'regime shift' in the late 1970's, has resulted in failure of larval advection to much of the distributional area for snow crab as well as red king crab.

The deterioration of our correlations was likely due to changes in the fishery that affected our CPUE index of abundance. These changes included reductions in quotas and landings, as well as changes in fishing seasons that resulted in reduced mortality on pre-recruits. Effects of other changes in fishing practices are unknown. This illustrates the uncertainties inherent with using fishery performance as an index of abundance. It is advisable to use a research survey index of abundance but, unfortunately, our time series of survey data is insufficient.

## **CONCLUSIONS AND RECOMMENDATIONS**

We conclude that effects of ocean climate variation (bottom-up processes) are more important than effects of predation (top-down processes) in regulating snow crab abundance. A cold regime during early life promotes snow crab production or early survival. Bottom temperature appears to affect survival of early benthic stages. Sea ice could have a direct effect on snow crab production or larval survival through its effect on timing of the spring bloom and snow crab hatching. Sea ice could be associated with some other important pelagic process (eg. stratification, ice edge production, near surface temperature). It is also possible that sea ice may simply be associated with other variables such as bottom temperature that may have an important effect slightly later in life.

Such studies are useful in identifying effects of ocean climate variation on production during early life history that can be detected in later stages at higher trophic levels. Therefore broad scale studies of consistency of such effects across species groups (eg. crustaceans) should be conducted. Studies of direct ocean climate effects on primary and secondary production would also be very useful in explaining associations at higher trophic levels.

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