Relationship Between Wind and Year Class Strength of Tanner crabs in the Southeastern Bering Sea

Gregg E. Rosenkranz, Albert V. Tyler, Gordon H. Kruse, and H. Joe Niebauer

Relationship Between Wind and Year Class Strength of Tanner crabs in the Southeastern Bering Sea

Gregg E. Rosenkranz, Albert V. Tyler, Gordon H. Kruse, and H. Joe Niebauer

ABSTRACT: Knowledge of Bering Sea oceanography and the life history of Tanner crabs *Chionoecetes bairdi* led us to 2 hypotheses about the effects of wind on the formation of year class strength, defined as the number of crabs hatched in a given year that survive to maturity. First, year class strength is limited by food availability during the pelagic zoeal phase and is enhanced when wind-driven turbulent mixing or upwelling transports nutrients into the euphotic zone, increasing primary and secondary productivity. Second, wind-driven advection during the pelagic phase carries zoeae to either favorable or unfavorable habitat for settlement. We investigated these hypotheses by testing for statistically significant correlations between recruitment estimates, derived from a length-based model, and wind data from St. Paul Island in the eastern Bering Sea. We found a significant positive correlation between the intensity of average May–June wind vectors resolved along NE–SW axes and recruitment of male Tanner crabs 7 years later and female Tanner crabs 6 years later; there were no significant relationships when winds were resolved along NW–SE axes. Despite uncertainty about age of recruitment due to our poor understanding of Tanner crab growth rates, we interpret these statistical results as lending support for both the above hypotheses.

INTRODUCTION

Commercial fishing for Tanner crabs *Chionoecetes bairdi* in the southeastern Bering Sea began in the 1960s and has grown into a major industry producing yearly catches valued as high as $58.8 million (1993). The fishery is limited to taking only males with carapace widths (CW) ≥5.5 inches (140 mm). Population dynamics of the species is poorly understood, but annual National Marine Fisheries Service (NMFS) trawl surveys conducted since 1975 have shown a pattern of extreme variability in abundance (Stevens et al. 1996). Commercial catches have fluctuated widely as well; large harvests have been followed by declines in abundance and closed or restricted fishing seasons (Figure 1).

Zheng et al. (1998) applied a length-based model to the population of Tanner crabs that inhabits Bristol Bay (Bering Sea waters south of 58° 39'N and east of 168°W). Their primary goal was to reduce survey measurement error in abundance estimates; the work also produced a time series of estimated recruitments to

the modeled population (Figure 2). That population consisted of male Tanner crabs ≥93 mm CW and females ≥70 mm CW that were mature or close to maturity and fully recruited to NMFS survey gear. These estimates provided us with a response variable to investigate the possibility that interannual variation in the Bering Sea environment is related to variation in recruitment to the mature Tanner crab population.

A series of hypotheses on the determinants of Tanner crab year class strength, defined as the number of crabs hatched in a given year that survive and recruit to the mature population, were generated by a modeling workshop (Tyler and Kruse 1997) and served as the starting point for our research. In this brief preliminary paper, we explored 2 hypotheses concerning the effects of wind on larval survival of Tanner crabs in Bristol Bay:

1. Larval survival depends on food availability. Winds increase primary productivity by transporting nutrients into the euphotic zone through Ekman upwelling or vertical mixing, which in turn increases

the abundance of copepod nauplii as food for newly hatched Tanner crabs.

2. Wind-driven advection during the Tanner crab pelagic phase transports larvae to suitable or unsuitable habitats for settlement. Preferred benthic habitat for young-of-the-year Tanner crabs consists of mud, silt, and sand bottom, which occurs offshore from the shallow, rocky zone of inner Bristol Bay preferred by early juvenile red king crabs *Paralithodes camtschaticus*.

Bristol Bay Tanner crabs typically hatch in late April or early May and then metamorphose through 2 planktonic zoeal stages of about 30 d duration each to reach a megalops stage, which is transitional between the pelagic and benthic phases (Incze 1983). After settlement, juveniles molt through a series of up to 18 instars before reaching maturity (Donaldson et al. 1981).

Our research is complicated by uncertainty regarding the age of Tanner crabs when they recruit to the modeled population. Crabs lose hard body parts, the typical age-determination structures in fish, during molting, and it is impossible to accurately infer age from the measurements of shell widths collected during NMFS trawl surveys because of substantial size overlap of adjacent age groups. Donaldson et al. (1981) developed linear models of the relationship between Tanner crab age and carapace width from experiments conducted near Kodiak; these predict the mean age of recruitment to the length-based model at 6 years after

hatching for males and at 5 years for females. Growth rates of Bristol Bay Tanner crabs, however, may be considerably different because of colder average water temperatures and differences in food availability.

The NMFS survey gear does not census juvenile crabs accurately because of gear size selectivity (Zheng et al. 1998), and male or female crabs hatched in the same year may recruit to the modeled population over several years because of size differences caused by variation in individual growth rates (B.G. Stevens, NMFS, Kodiak, personal communication). For example, the pulse of recruitment to the modeled population of male Tanner crabs from 1988 to 1991 (Figure 2) may be due to the influx of 1–4 year classes. Nonetheless, the length-based model provides the best index of year class strength currently available. Our analysis assumed that most male or female crabs of the same age recruited to the modeled population in
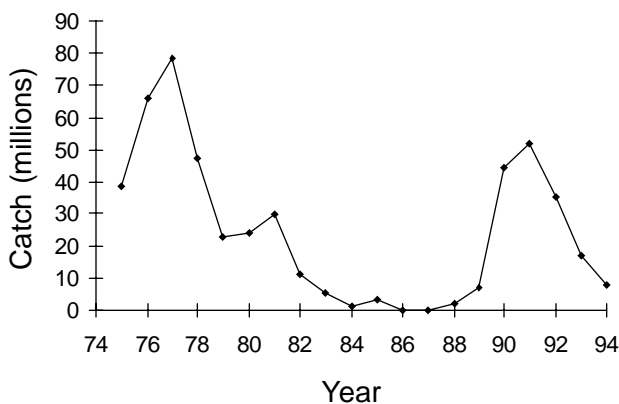

Figure 1. Catch of Tanner crabs in numbers of crabs in the southeastern Bering Sea over the past 20 years shows high variability. In those years when fishing seasons began in fall and continued to spring, fishing seasons are indexed by the later of the 2 years. Commercial fishing was closed due to low abundance in 1986 and 1987. Data are from ADF&G (1997).
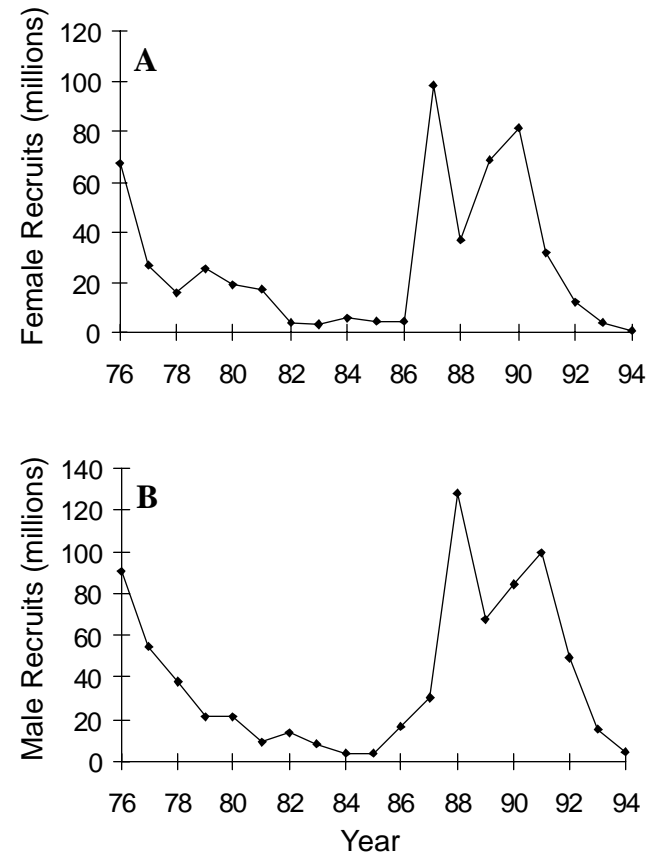
Figure 2. Estimates of recruitment in number of crabs to the length-based model for (A) female and (B) male Tanner crabs (from Zheng et al. 1998). Year corresponds to year of recruitment to the modeled population of males ≥93 mm CW and females ≥70 mm CW.

the same year and that estimated recruitment to the model is a good index of true recruitment. To acknowledge our uncertainty about the mean age of Tanner crabs entering the model, we explored the possibility of recruitment at ages 4–9 years for both males and females.

METHODS

We investigated our 2 hypotheses by calculating correlation coefficients between recruitment estimates obtained from Zheng et al. (1998) and monthly means of wind data collected at St. Paul Airport in the Pribilof Islands (archived at the Institute of Marine Science, University of Alaska Fairbanks). Correlation coefficients significantly different from 0 were identified using the *t*-distribution (Zar 1974); then, linear regression models were fit by least squares to aid in assessing the strength of relationships between recruitment and winds.
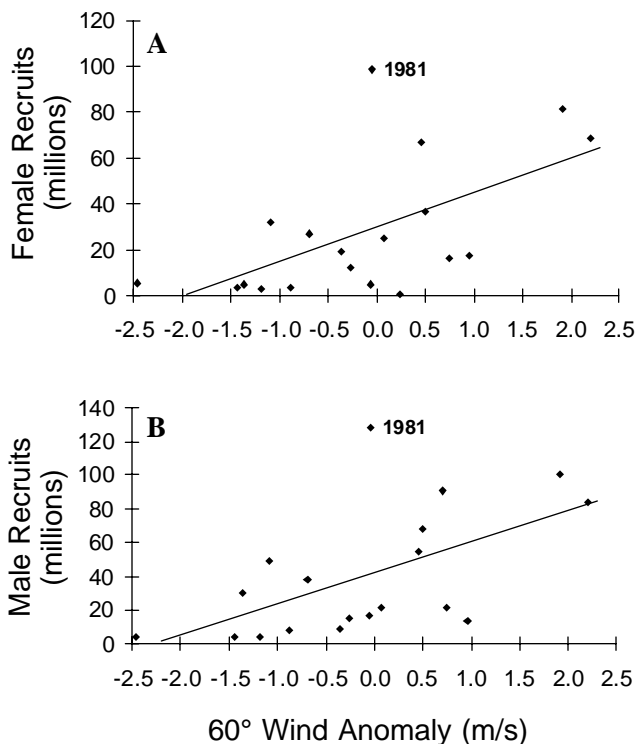
Figure 3. Fit of linear models to (A) female and (B) male year class strength in number of crabs assuming recruitment ages of 7 years from hatching for males and 6 years for females, with the 60° wind anomaly as the independent variable. The regression equations are $y = 29.86 + 15.01\ x$, $r^2 = 0.344$ for females, and $y = 42.32 + 18.60\ x$, $r^2 = 0.337$ for males. Outliers correspond to the large year class we assume hatched in 1981.

We chose winds measured at the Pribilof Islands because of availability over the period of interest, proximity to Bristol Bay, and lack of local orographic effects (i.e., wind deflection caused by nearby mountains). We resolved the monthly average wind vectors along a series of axes from 0° to 165° in increments of 15°, which effectively covered all points of the compass; we then converted each of these to anomalies from their 1965–1996 means. For reference, a positive 0° anomaly corresponds to wind blowing from north to south; the north shore of the Alaska Peninsula, which borders Bristol Bay, lies approximately along a 50° axis. We averaged the time series of May and June wind anomalies to correspond to the pelagic zoeal phase of Bristol Bay Tanner crabs (Incze 1983). Because of uncertainty in mean age of recruitment, we calculated correlation coefficients between each wind time series and estimates of male and female recruitment 4–9 years later.

RESULTS

For wind intensities resolved along the 30°, 45°, 60°, and 75° axes, correlation coefficients were positive and significantly different from 0 at the 95% confidence level for males recruited to the mature population at age 7 and for females at age 6 (Table 1). The correlation analysis indicated that no other wind directions or ages were significant.

Based on these results, we assumed recruitment at age 7 for male Tanner crabs and age 6 for females and fit linear regression models, with wind as the independent variable, to estimated year class strength. Although the strongest relationships were between 30° winds and female recruitment and between 75° winds and male recruitment, for parsimony we chose 60° wind anomalies as the independent variable in both models. This seemed reasonable because Tanner crab zoeae are not sexually dimorphic and because the 60° wind time series produced correlation coefficients close to the maximum attained for both males and females when treated separately (Table 1). The models fit reasonably well, although the largest year class (assumed to be hatched in 1981) was an outlier in both cases (Figure 3).

DISCUSSION

Significant correlations between time series of average May–June wind vectors resolved along NE–SW axes and estimated Tanner crab year class strength sup-

Table 1. Correlation coefficients and *P* values for vector winds along the given axes and Tanner crab recruitment at ages 4–9 years. Shading indicates significance at the 95% confidence level; outlines denote recurrent significant correlations for age-6 females and age-7 males.

		Males		Females				Males		Females	
Wind	Age	r	P	r	P	Wind	Age	r	P	r	P
0	4	0.351	0.141	0.385	0.103	90	4	0.189	0.439	0.329	0.168
	5	0.408	0.083	-0.033	0.895		5	0.278	0.249	0.409	0.082
	6	0.037	0.880	0.533	0.019		6	0.485	0.035	0.415	0.077
	7	0.302	0.209	-0.059	0.809		7	0.547	0.015	0.497	0.031
	8	0.082	0.738	0.008	0.973		8	0.356	0.135	0.262	0.278
	9	-0.221	0.364	-0.296	0.219		9	0.285	0.237	-0.295	0.219
15	4	0.367	0.123	0.431	0.065	105	4	0.094	0.701	0.229	0.345
	5	0.449	0.054	0.072	0.770		5	0.170	0.488	0.420	0.073
	6	0.153	0.532	0.597	0.007		6	0.479	0.038	0.271	0.261
	7	0.415	0.078	0.068	0.782		7	0.473	0.041	0.520	0.023
	8	0.152	0.535	0.063	0.797		8	0.338	0.157	0.266	0.272
	9	-0.143	0.559	-0.339	0.155		9	0.360	0.131	-0.209	0.390
30	4	0.363	0.126	0.453	0.051	120	4	-0.020	0.935	0.096	0.696
	5	0.463	0.046	0.166	0.497		5	0.040	0.872	0.398	0.092
	6	0.254	0.295	0.625	0.004		6	0.432	0.065	0.094	0.702
	7	0.497	0.030	0.183	0.454		7	0.353	0.139	0.502	0.029
	8	0.212	0.383	0.113	0.645		8	0.280	0.246	0.239	0.324
	9	-0.063	0.797	-0.366	0.123		9	0.402	0.088	-0.094	0.702
45	4	0.345	0.148	0.455	0.050	135	4	-0.139	0.572	-0.055	0.823
	5	0.452	0.052	0.248	0.305		5	-0.100	0.685	0.339	0.156
	6	0.339	0.156	0.621	0.005		6	0.343	0.151	-0.099	0.687
	7	0.552	0.014	0.284	0.239		7	0.192	0.431	0.436	0.062
	8	0.265	0.274	0.159	0.516		8	0.191	0.434	0.186	0.446
	9	0.020	0.936	-0.378	0.110		9	0.399	0.090	0.031	0.899
60	4	0.311	0.195	0.437	0.061	150	4	-0.240	0.322	-0.197	0.419
	5	0.418	0.075	0.318	0.185		5	-0.230	0.344	0.250	0.302
	6	0.408	0.083	0.587	0.008		6	0.223	0.359	-0.280	0.245
	7	0.580	0.009	0.372	0.117		7	0.013	0.958	0.327	0.171
	8	0.309	0.198	0.201	0.409		8	0.092	0.709	0.119	0.626
	9	0.106	0.665	-0.374	0.115		9	0.359	0.132	0.144	0.558
75	4	0.260	0.282	0.397	0.093	165	4	-0.311	0.195	-0.309	0.198
	5	0.361	0.129	0.373	0.116		5	-0.335	0.161	0.143	0.560
	6	0.459	0.048	0.519	0.023		6	0.091	0.711	-0.428	0.068
	7	0.581	0.009	0.444	0.057		7	-0.158	0.519	0.195	0.423
	8	0.342	0.151	0.237	0.328		8	-0.001	0.996	0.053	0.830
	9	0.196	0.421	-0.348	0.144		9	0.295	0.221	0.232	0.340

port both hypotheses. For the hypothesis that primary and secondary production are increased by the transport of nutrients into the euphotic zone, 2 explanations are possible: (1) NE winds blowing alongshore relative to the Alaska Peninsula lead to Ekman drift of surface water and upwelling of subsurface water, and (2) sufficiently strong winds from any direction cause vertical mixing of the water column. The fact that significant correlations occur only for winds resolved along NE–SW axes favors upwelling rather than vertical mixing as the relevant mechanism, although our use of mean winds tends to obscure the total amount of mixing energy when the average wind differs substantially between May and June. For example, an average May wind of 10 m/s from 0°, combined with an average June wind of 10 m/s from 180°, would result in a net 0 m/s average May–June wind from all directions, yet a great deal of mixing energy would have been input.

On the other hand, our results also support the advection hypothesis. The velocity of surface currents is highly correlated with the alongshore component of wind in the southeastern Bering Sea (Brower et al. 1988); the St. Paul wind anomalies may be an indicator of surface water flow, which advects Tanner crab larvae to favorable or unfavorable habitat for settle-

ment. Little is known about the habitat preference of early juveniles, but Tanner crabs <20 mm CW have been caught as bycatch by the Bering Sea scallop dredge fishery in depths of 95–115 m (J. Barnhart, Alaska Department of Fish and Game, Kodiak, personal communication). In addition, Paul (1982) found juveniles of this same size range in depths of 35–175 m near the mouth of Cook Inlet in the Gulf of Alaska, the highest densities occurring at 150–166 m. Sharma (1974) noted that gravel and coarse sand occur nearshore in the Bering Sea, whereas sediments become progressively finer farther offshore. We speculate that juveniles rely on burial for protection from predators and that advection to inner Bristol Bay before settlement adversely affects their survival.

Incze et al. (1987) hypothesized that *Pseudocalanus* copepod nauplii are important prey for newly hatched Tanner crabs in Bristol Bay due to the size of the nauplii and the reproductive rate and spatial distribution of the adults. The morphology and behavior of Tanner crab larvae allows them to capture microzooplankton such as copepod nauplii (Paul et al. 1979). Although stomach content analyses have shown that zoeae also consume diatoms, feeding experiments suggest that energy derived from grazing on phytoplankton present at densities typical of Bristol
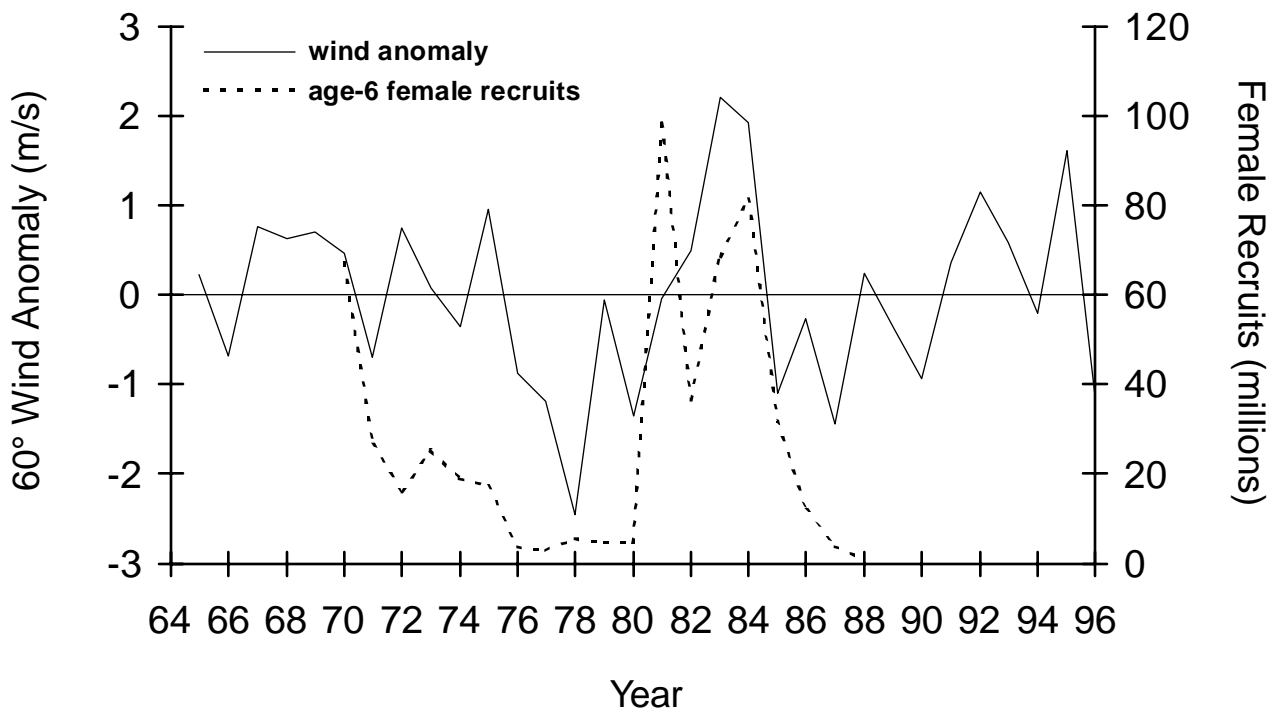

Figure 4. Time plots of 60° wind anomalies and female Tanner crab recruitment estimates back-shifted 6 years to the assumed year of hatching. The horizontal line is the mean wind during 1965–1996.

Bay in May and June would be insufficient to sustain Tanner crab larvae (Incze 1983; Incze and Paul 1983). Synchronous timing of the Tanner crab hatch with sufficient prey abundance may also be important. Kon (1979) found that zoeae of the congener snow crab *C. opilio,* starved more than 3 d, displayed reduced molting and survival. Starr et al. (1994) showed that detrital rain from a spring phytoplankton bloom can act as a chemical cue to initiate hatching of snow crabs. This mechanism provides a built-in time lag between the onset of the bloom and hatching of crab larvae that mirrors the lagged development of the microzooplankton community responding to primary production.

The pulse of recruitment to the length-based model from 1987 to 1991 is a dominant feature in the time series of our response variables (Figure 2). Given our assumption about mean age of recruitment of 7 years for males and 6 years for females, this pulse began with the entrance of a large 1981 year class to the mature population, following a succession of poor recruitment dating back to the 1972 year class. Sampling of zooplankton over the middle Bering Sea shelf indicated that *Pseudocalanus* copepods were an order of magnitude more abundant in May 1981 than in May 1980 (Smith and Vidal 1986). Given the abundance and distribution of mature female Tanner crabs, Incze et al. (1987) found lower than expected numbers of Tanner crab larvae in the water column in May 1980, coinciding with low zooplankton abundance. Sambrotto et al. (1986) noted that nitrate uptake and chlorophyll levels were higher in the euphotic zone of the middle shelf in early June of 1981 than in 1979 or 1980, attributing this to the development and persistence of a subsurface chlorophyll-*a* maximum layer. This nursery-type layer is important for the survival of larval walleye pollock *Theragra chalcograma* (Nishiyama et al. 1982), and its presence was attributed to relatively calm post-bloom conditions in 1981 (Sambrotto et al. 1986).

Spurious correlations are a serious problem in empirical studies such as ours, and the difficulty is increased here due to uncertainty about crab ages at recruitment. The time series of average May–June 60° wind anomalies resembles noise about a mean for much of its span (1965–1996; Figure 4) but features a distinct shift from strong SW winds in 1978 to strong NE winds in 1983. When we checked for correlation between the 60° wind time series and recruitment estimates 4–9 years later, we essentially slid the recruitment time series along the *x*-axis of Figure 4, while holding the wind series fixed, and looked for the best match within those bounds. The pulse of recruitment to the mature population from 1987 to 1991 (Figure 2) followed the change from negative to positive 60° wind anomalies by about 6 years (Figure 4) and was primarily responsible for the significant correlation we found. Therefore, while it is possible that the pulse of recruitment was due, at least in part, to the change in average May–June winds, it is important to note that a shift of this magnitude occurred only once over the 31 years of wind data.

Positive autocorrelation in time series of recruitment estimates and environmental variables also increases the probability of finding spurious correlations (e.g., Bakun 1996). Autocorrelation was significant for male Tanner crab recruitment estimates at a lag of 1 year ($r_1 = 0.533$) but was not significant for female recruitment estimates nor for the 60° wind time series at any lag, so we eliminated autocorrelation as a serious problem with the analysis.

In conclusion, we believe that statistically significant positive correlations between recruitment estimates and average May–June wind vectors resolved along NE–SW axes support the hypotheses that food availability and advection during the pelagic larval stage significantly affect Tanner crab year class strength in Bristol Bay. Although the exact nature of this relationship is unclear, we have presented plausible causal mechanisms that link these variables. We wish to stress the preliminary nature of this analysis—the significant statistical relationship reported here does not guarantee a biologically meaningful connection. Our intent with this brief paper was to stimulate discussion and research about the recruitment process. As work on this project continues, we will explore the relationship between wind and year class strength further and examine additional hypotheses generated by the Tanner crab modeling workshop (Tyler and Kruse 1997).

REFERENCES

ADF&G (Alaska Department of Fish and Game). 1997. Annual management report for the shellfish fisheries of the Westward Region, 1995. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Regional Information Report 4K97-16, Kodiak.

Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. California Sea Grant College System, University of California, La Jolla, in cooperation with Centro de Investigaciones Biologicas del Noroeste, La Paz, Mexico, Publication T-037.

Brower, W. A. Jr., R. G. Baldwin, C. N. Williams, Jr., J. L. Wise, and L. D. Leslie. 1988. Climatic atlas of the outer continental shelf waters and coastal regions of Alaska. National Climate Data Center, Asheville, North Carolina.

Donaldson, W. E., R. T. Cooney, and J. R. Hilsinger. 1981. Growth, age, and size at maturity of Tanner crab, *Chionoecetes bairdi* M. J. Rathbun, in the northern Gulf of Alaska. Crustaceana 40:286–302.

Incze, L. S. 1983. Larval life history of Tanner crabs, *Chionoecetes bairdi* and *C. opilio,* in the southeastern Bering Sea and relationships to regional oceanography. Doctoral dissertation, University of Washington, Seattle.

Incze, L. S., D. A. Armstrong, and S. L. Smith. 1987. Abundance of larval Tanner crabs (*Chionoecetes* spp.) in relation to adult females and regional oceanography of the southeastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences 44:1143–1156.

Incze, L. S., and A. J. Paul. 1983. Grazing and predation as related to energy needs of stage I zoeae of the Tanner crab *Chionoecetes bairdi* (Brachyura, Majidae). Biological Bulletin 165:197–208.

Kon, T. 1979. Ecological studies on larvae of the crabs belonging to the genus *Chionoecetes* - I. The influence of starvation on the survival and growth of the zuwai crab. Bulletin of the Japanese Society of Scientific Fisheries 45(1):7–9.

Nishiyama, T., K. Hirano, and T. Haryu. 1982. Nursery layer of the walleye pollock (*Theragra chalcograma*) larvae. Transactions of the American Geophysical Union, EOS. 63:943.

Paul, J. M. 1982. Distribution of juvenile *Chionoecetes bairdi* in Cook Inlet. Pages 173–190 *in* Proceedings of the international symposium on the genus *Chionoecetes*. University of Alaska Fairbanks, Alaska Sea Grant Report 82-10.

Paul, A. J., J. M. Paul, P. A. Shoemaker, and H. M. Feder. 1979. Prey concentrations and feeding response in laboratory-reared stage-one zoeae of king crab, snow crab, and pink shrimp. Transactions of the American Fisheries Society 108:440–443.

Sambrotto, R. N., H. J. Niebauer, J. J. Goering, and R. L. Iverson. 1986. Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Continental Shelf Research 5:161–198.

Sharma, G. D. 1974. Contemporary depositional environment of the eastern Bering Sea, part 1: contemporary sedimentary regimes of the eastern Bering Sea. Pages 517–539 *in* D. W Hood and E. J. Kelley, editors. Oceanography of the Bering Sea with emphasis on renewable resources. Institute of Marine Science, University of Alaska Fairbanks.

Smith, S. L., and J. Vidal. 1986. Variations in the distribution, abundance, and development of copepods in the southeastern Bering Sea in 1980 and 1981. Continental Shelf Research 5:215–239.

Starr, M., J. C. Therriault, G. Y. Conan, M. Comeau, and G. Robichaud. 1994. Larval release in a sub-euphotic zone invertebrate triggered by sinking phytoplankton particles. Journal of Plankton Research 16:1137–1148.

Stevens, B. G., J. A. Haaga, and R. A. MacIntosh. 1996. Report to the industry on the 1995 eastern Bering Sea crab survey. National Marine Fisheries Service, Alaska Fisheries Science Center, Processed Report 96-01, Kodiak.

Tyler, A. V., and G. H. Kruse. 1997. Modeling workshop on year-class strength of Tanner crabs, *Chionoecetes bairdi*. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Regional Information Report 5J97-02, Juneau.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Toronto, Ontario, Canada.

Zheng, J., G. H. Kruse, and M. C. Murphy. 1998. A length-based approach to estimate population abundance of Tanner crab, *Chionoecetes bairdi*, in Bristol Bay, Alaska. Pages 97–105 *in* G. S. Jamieson and A. Campbell, editors. Proceedings of the North Pacific symposium on invertebrate stock assessment and management. Canadian Special Publication of Fisheries and Aquatic Sciences 125.