Abstract.—Female and sublegal-size male Tanner crabs, *Chionoecetes bairdi*, are often caught incidentally in the males-only fishery for this species. Effects of low air temperature during the winter fishery on juvenile and female adult crabs and on the developing eggs brooded by the females were simulated in the laboratory by exposing crabs to cold air (–20 to +5°C) up to 32 minutes; controls were not exposed. Exposure was expressed as degree·hours (°h), the product of temperature (°C) and time (hours). Severe exposure caused death: median lethal exposure stabilized at –3.3 ± 0.8°h for juveniles and –4.3 ± 0.5°h for adults after 16 days. Exposure also reduced vigor (measured by righting ability), caused pereiopod autotomy, and depressed adult feeding rates and juvenile growth. Exposures causing one-half the crabs to cease righting were –1.2 ± 0.3°h for juveniles and –2.1 ± 0.3°h for adults (measured immediately after exposure). Mean pereiopod autotomy ranged up to 44% for juveniles exposed to –2°h, and up to 10% for adults exposed to –10.6°h. Ecdysis of juveniles was not affected, but exposed juveniles frequently shed additional pereiopods with the molt. Prompt return of incidentally caught Tanner crabs to the sea when temperatures are below freezing should reduce adverse effects of cold aerial exposure.

Responses of Tanner crabs, *Chionoecetes bairdi*, exposed to cold air

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Tanner crabs, *Chionoecetes bairdi* Rathbun, 1893, are the target of a large commercial pot fishery and are an important commercial species in Alaskan waters (Otto, 1989). Landings of *C. bairdi* rose to a peak of 57,923 metric tons (t) in 1978, then declined to 5,390 t in 1987; landings increased to 23,507 t in 1990.[1]

Current Alaska fishing regulations require release of small (<139-mm carapace width) male and all female *C. bairdi*. Commercial fishery openings in recent years have generally ranged from November through April,[2] when minimum daily air temperatures can drop to –21°C.[3] The amount of time incidentally captured crabs remain on deck varies, ranging from a few minutes during pot fishing to hours in some trawling operations (Stevens, 1990). Exposure to cold air during fishing operations may be detrimental to individual crabs (Carls and O'Clair, 1990), exposed egg clutches, and possibly—with sufficient fishing pressure—to the population. Regulations also require that Tanner crabs caught incidentally by multispecies trawling operations in the eastern Bering Sea be returned to the sea, but these regulations may be ineffective because of poor survival (22 ± 3.6% for *C. bairdi*) of the culled crabs (Stevens, 1990).

Here we report the responses of juvenile and adult female Tanner crabs and their offspring exposed to cold air. Our objectives were to determine the effects (immediate

[1] Kruse, G. Alaska Dep. Fish and Game, Div. Commer. Fish., Juneau, AK 99802. Pers. commun., July 1992.

[2] ADF&G (Alaska Department of Fish and Game).

1989a. Report to the Alaska Board of Fisheries. Southeast Alaska and Yakutat (Region 1) 1988/89 shellfish fisheries. Regional Information Rep. No. 1J89-01. ADF&G, Div. Commercial Fisheries, Juneau, AK.

1989b. Westward region shellfish report to the Alaska Board of Fisheries. ADF&G Regional Information Rep. No. 4K89-3. ADF&G, Div. Commercial Fisheries, Westward Regional Office, 211 Mission Rd., Kodiak, AK 99615, 325 p.

1989c. Prince William Sound management area shellfish report to the Alaska Board of Fisheries. ADF&G Regional Information Rep. No. 2C89-03. ADF&G, Div. Commercial Fisheries, Central Region, 333 Raspberry Rd., Anchorage, AK 99581, 55 p.

1989d. Cook Inlet area shellfish management report to the Alaska Board of Fisheries, 1988–89. Regional Information Rep. No. 2H89-03. ADF&G, Div. Commercial Fisheries, 333 Raspberry Rd., Anchorage, AK 99581, 75 p.

1989e. Synopsis of the Montague Strait experimental harvest area 1985–1988. ADF&G Regional Information Rep. No. 2C89-04. ADF&G, Div. Commercial Fisheries, Central Region, 333 Raspberry Rd., Anchorage, AK 99581, 21 p.

1989f. Report to the Board of Fisheries Norton Sound red king crab fishery (summer fishery only). ADF&G Regional Information Rep. No. 3N89-05. ADF&G, Div. Commercial Fisheries, Central Region, Juneau, AK, 14 p.

[3] NOAA. 1987. Local climatological data, monthly and annual summaries with comparative data. U.S. Dep. Commer., National Climatic Data Center, Asheville, NC 28801.

and long-term) of exposure to cold air on 1) survival; 2) sublethal responses, including righting response, limb autotomy, feeding rate, ecdysis (juveniles), and growth; and 3) reproductive responses including egg survival, zoeal production, zoeal viability, and subsequent egg extrusion and viability of the extruded clutch.

Methods

Experimental crabs were collected with crab pots. Juvenile crabs (both sexes) were collected in Auke Bay, Alaska (lat. 58°21'N, long. 134°41'W) on 14 and 19 January 1988. Ovigerous females were captured near Eagle River (lat. 58°31'N, long. 134°48'W) and Lena Point (lat. 58°24'N, long. 134°47'W) in Favorite Channel, Alaska, on 11 February 1988.

In the laboratory, carapace length (distance from the posterior margin of the right ocular orbit to the midpoint of the posterior margin of the carapace) was measured to the nearest millimeter. Carapace width was subsequently estimated by regressing carapace widths and lengths of Tanner crabs measured at a later date.[4] Live weight was measured to the nearest 0.1 g. Juvenile crab weights ranged from 26 to 229 g ($\bar{x}$=109 ±14 g), and carapace lengths ranged from 35 to 64 mm ($\bar{x}$=49 ±2.3 mm) (Fig. 1). Estimated juvenile carapace widths (for both sexes) ranged from 46 to 74 mm (width=-0.237 + 1.318 × length, r^2=0.994, n=145). The immature condition of males was determined solely by body size. Adult female crab weights ranged from 182 to 553 g ($\bar{x}$ = 329 ± 8 g), and carapace lengths ranged from 65 to 96 mm ($\bar{x}$=80 ±1.0 mm) (Fig. 1). Estimated female carapace widths ranged from 85 to 124 mm (width=1.746 × 1.274 × length, r^2=0.995, n=70).

Crabs were maintained in 500-L tanks at ambient seawater temperatures (6.0–6.9°C for juveniles, 5.3–6.0°C for adults) until exposure to test air temperatures; after exposure they were returned to the same tanks for 32–35 days of observation (4.7–6.7°C for juveniles, 4.7–5.2°C for adults). A subset of 40 female crabs was retained for an additional three months of observation.

Crabs were exposed in a modified chest freezer divided by a vertical baffle into two compartments of unequal size (Carls and O'Clair, 1990). Infrared heat lamps were

placed in the smaller compartment for temperature control. To ensure uniform temperatures, a small fan (in the center bottom of the baffle) drew air from the exposure chamber into the small chamber at 45 ± 5 cm/sec. Return air circulated over the baffle into the exposure chamber. Temperatures were measured with a thermistor located in the exposure area near the fan and were regulated manually by switching the heat lamps on or off. Temperatures were controlled to ±0.1°C after the chamber had cooled to the desired temperature. Crabs were exposed to cold air on the plywood bottom of the exposure chamber.

Juvenile crabs were randomly placed in six groups with 10 crabs per group and were exposed to cold air on 21 and 25 January (about one week after capture). Exposure temperatures ranged from -5.0 to -20.0°C; exposure durations were 0, 12, 16, or 24 minutes to yield 0, -1.0, -1.5, -2.1, -4.0, and -8.0°h exposures (Table 1). The lengths ($F_{5,54}$=0.06, P>0.99) and
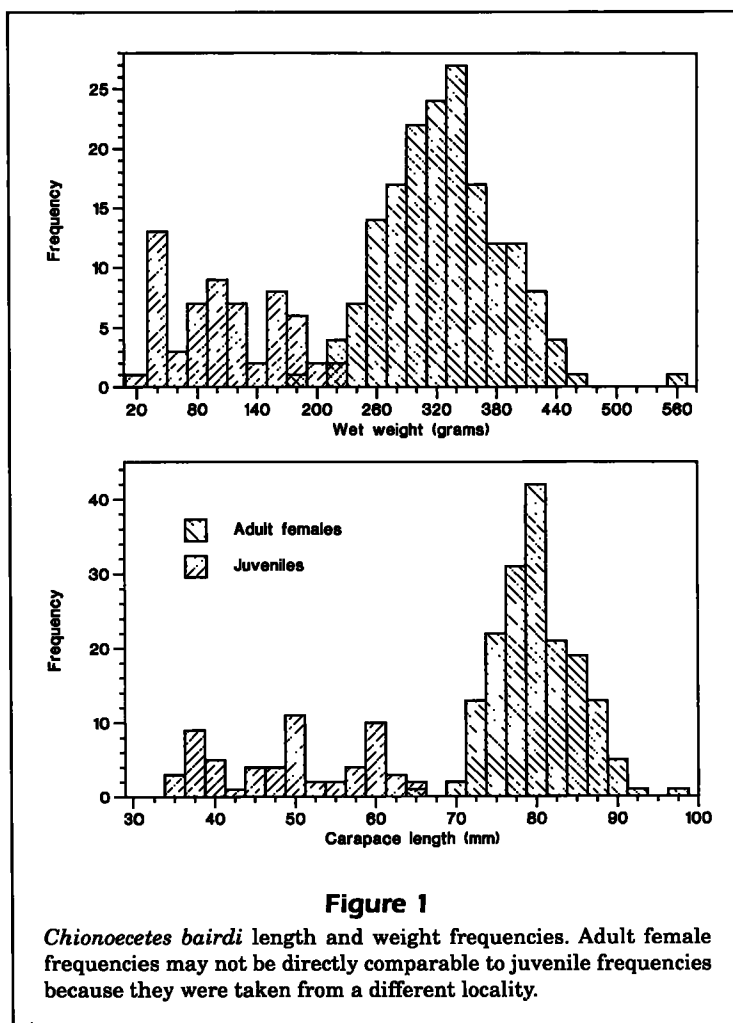

Figure 1

Chionoecetes bairdi length and weight frequencies. Adult female frequencies may not be directly comparable to juvenile frequencies because they were taken from a different locality.

[4] r^2>0.99. Stone, R. NMFS Auke Bay Lab., Juneau, AK 99801-8626. Unpubl. data, May 1992.

Table 1

Temperature and duration of exposure of *Chionoecetes bairdi* to cold air. The number of crabs exposed (*n*) is also indicated. Controls were not exposed to air. SE = standard error.

Air temperature (Celcius) mean	SE	Exposure time (minutes)	Degree-hours	*n*
Juveniles				
—	—	0	0.00	10
-5.0	0.02	12	-0.99	10
-7.5	0.05	12	-1.50	10
-10.2	0.24	12	-2.05	10
-15.0	0.03	16	-4.00	10
-20.0	0.07	24	-8.02	10
Adults				
5.1	0.12	8	0.683	7
5.0	0.01	32	2.672	7
—	—	0	0.000	31
-3.2	0.21	4	-0.211	8
-3.1	0.04	8	-0.411	8
-3.1	0.06	16	-0.813	8
-3.0	0.03	32	-1.621	8
-8.2	0.19	4	-0.544	8
-8.1	0.11	8	-1.075	8
-8.1	0.06	16	-2.149	8
-8.1	0.03	32	-4.299	7
-13.1	0.18	4	-0.875	8
-12.9	0.08	8	-1.720	8
-13.0	0.03	16	-3.472	7
-13.0	0.02	32	-6.933	8
-20.3	0.34	4	-1.353	8
-20.1	0.15	8	-2.676	8
-18.4	0.08	16	-4.899	8
-19.9	0.04	32	-10.597	8

weights ($F_{5,54}$=0.02, P>0.99) of the crabs did not differ significantly between treatments. Change in juvenile crab body weight was estimated from initial and final measurements (32 d).

Female crabs were randomly placed in 20 groups (including controls) in a complete 4 (temperature) by 5 (length of exposure) design, with 7 to 8 crabs per group. Treatment temperatures ranged from −3.1 to −20.3°C and exposure duration ranged from 0 (controls) to 32 minutes (Table 1). Two additional groups were tested at 5°C for 8 and 32 minutes (Table 1). The crabs did not differ significantly in length ($F_{21,149}$=1.13, P=0.324) or weight ($F_{21,149}$=1.36, P=0.149) between treatments. Exposure took place 16 and 17 February (about six days after capture). Observation continued through 22 June.

Mortality and limb autotomy were monitored daily. Crabs were judged dead when scaphognathite move-

ment stopped. Generally, dead crabs were rechecked the following day before they were removed from test tanks. The number of legs missing on each crab was counted and autotomized legs were removed from the tanks.

Righting response (the time it took a crab to right itself when placed on its back underwater), which we considered to be a measure of vigor, was timed to the nearest 0.01 second immediately after aerial exposure and 1, 2, 4, 8, 16, 24, and 32 days thereafter. Crabs that could not right themselves after 2 minutes were recorded as "not righting" and were placed upright in the tank.

A subset of 40 female crabs randomly selected from the entire exposure range was used for reproductive observations. The crabs were isolated 32 days after exposure in covered 70-L tanks that overflowed into 19-L buckets containing conical 363-μ mesh nets designed to trap zoeae. Flow rates were approximately 1.5 L/minute; 95% turnover time was 2.3 hours and water temperatures ranged from 5.2 to 5.9°C during this period (23 March–11 May).

Feeding rates were measured before and after the zoeal hatch while the 40 ovigerous females were individually isolated. Mussels, *Mytilus trossulus*, were fed ad libitum to crabs during each feeding period. Live mussels were cut in half and drained tissue-side down on paper towels for five minutes, weighed, then placed in the tanks. Twenty-four hours later the remaining food was removed, drained, and weighed as before. At each feeding, four food portions were placed as controls in tanks without crabs. Consumption was corrected for the mean weight changes in the control portions. Feeding observations were repeated every 1 to 3 days, from 41 to 60 and from 85 to 98 days after exposure.

Zoeae were collected daily, rinsed from the nets, concentrated in a known volume, and subsampled with a 5- or 10-mL Hensen-Stemple pipette (Carls and O'Clair, 1990). Subsamples, which contained a minimum of 200 zoeae, were preserved in 5% formalin and counted later; the occasional large subsample was divided with a Folsom plankton splitter before being counted. After zoeal hatching, all debris from each tank bottom was preserved to determine the number of dead eggs and zoeae.

Responses of the crabs were related to aerial exposure, expressed as the product of air temperature (°C) and length of time in air (hours), i.e. degree-hours (°h). In a similar experiment, Carls and O'Clair (1990) demonstrated the usefulness of this technique for interpreting responses to aerial exposure in adult king crabs, *Paralithodes camtschaticus*. Because the responses of the Tanner crabs to exposure (in °h) were similar in form to those of the king crabs over identi-

cal treatment ranges (0–32 minutes, –20 to +5°C; see Results section) and could be described by the same types of simple linear or nonlinear models, we used the same technique here.

Regression techniques and logit analysis were used to relate response variables to exposure (Berkson, 1957; BMDP, 1983). We compared median lethal responses with log-likelihood ratio tests (Fujioka, 1986). Multiple regression was used to test for differences in the slopes of regression lines and to adjust for covariates (Kleinbaum and Kupper, 1983). The relation of selected response variables to one another was tested with parametric correlation. After one-way analysis of variance, comparisons of treatment means were made with Tukey's or Dunnett's a posteriori multiple comparison tests and judged significantly different if $P \leq 0.05$. Proportional data were arcsine transformed. Reported error ranges are ±95% confidence limits.
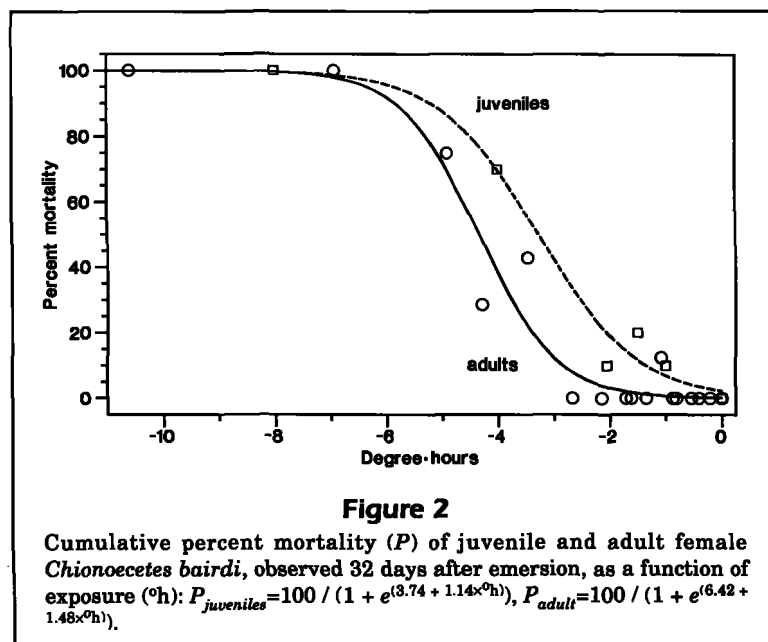
Results

Mortality

Below –1 to –3 degree hours, exposure to cold air killed crabs. Almost all mortality occurred 1–2 days after exposure; in groups where more than half the crabs died, mortality always reached 50% within 2 days. Mortality was inversely related to exposure and increased rapidly below –1°h for juveniles and below –3°h for adults (logistic regressions [large P-values indicate good fits], $P_{juvenile}=0.959$, $P_{adult}=0.882$;

Fig. 2). Nearly all deaths occurred within 8 days after exposure; no crabs died after day 16. For juveniles, calculated median lethal exposures rose from –7.7 ± 3.4°h 1 day after exposure to –3.3 ± 0.8°h 16 days after exposure, and for adults from –7.2 ± 1.6°h to –4.3 ± 0.5°h over the same time period (Table 2).

Righting response

The speed with which crabs righted themselves when placed on their backs was inversely related to exposure (Fig. 3A). The response was most clearly described by the percentage of crabs not righting within two minutes (logistic regressions, $P=0.799$ [$n=6$] for juveniles; $P=0.978$ [$n=22$] for adults; Fig. 3B). Percentages of crabs not righting increased sharply below –1.0°h for juveniles and below –2.2°h for adults, and crabs ceased righting entirely after exposure to $\leq$–4.0°h for juveniles and $\leq$–6.9°h for adults (Fig. 3B). Median exposures causing one-half the crabs to cease righting (EC50) were –1.2 ± 0.3°h for juveniles and –2.1 ± 0.3°h for adults, measured immediately after exposure; values declined to –1.6 ± 0.3°h for juveniles and –3.8 ± 0.5°h for adults measured 32 days after exposure (Table 3). The percentage of crabs unable to right themselves immediately after exposure was significantly correlated with cumulative mortality ($P_{juvenile}=0.003$, $r^2_{juvenile}=0.91$, $n=6$; $P_{adult}<0.001$, $r^2_{adult}=0.67$, $n=22$) and, therefore, could serve as a predictor of death.

Righting times tended to improve (decrease) during the first eight days after exposure, but this recovery was generally not statistically significant.

Figure 2

Cumulative percent mortality (*P*) of juvenile and adult female *Chionoecetes bairdi*, observed 32 days after emersion, as a function of exposure (°h): $P_{juveniles}=100 / (1 + e^{(3.74 + 1.14 \times °h)})$, $P_{adult}=100 / (1 + e^{(6.42 + 1.48 \times °h)})$.

Righting times of juvenile crabs from all exposures tended to decrease over time (Fig. 4). The righting times of adult crabs exposed to ≤–2.2°h generally showed little evidence of recovery. Median exposures causing one-half the crabs to cease righting also generally declined, but 95% confidence bars overlapped.

Pereiopod autotomy

Exposure to cold air caused pereiopod autotomy. Juvenile pereiopod losses increased from 0 to –2°h but declined towards the most severe exposure (–8°h), possibly because early mortality precluded autotomy (Fig. 5A). Juvenile crabs often dropped legs or chela during aerial exposure, but losses also continued after exposure (Fig. 5B), often during ecdysis (Fig. 6).

Adult crabs autotomized fewer pereiopods than juveniles; as with juveniles, loss was most frequent immediately after exposure. Loss of pereiopods in adults was directly related to severity of exposure ($P<0.001$, $r^2=0.85$, $n=19$; Fig. 5A). Autotomy was correlated with mortality in adult crabs ($P<0.001$, $r^2=0.81$, $n=19$) but not in juveniles ($P=0.621$, $r^2=0.07$, $n=6$). Autotomy was also correlated with the percentage of adult crabs not righting as measured immediately after exposure ($P<0.001$, $r^2=0.81$, $n=22$).

Ecdysis

Juvenile crabs began molting 22 January and continued through 21 February. Molt timing was not correlated with exposure ($r^2=0.09$). Juveniles exposed

Figure 3

Righting times of juvenile and adult female *Chionoecetes bairdi* capable of righting (A), and percentage not righting (B) observed 32 days after emersion as functions of exposure (°h). Percentages not righting were $100/(1 + e^{(6.235 + 1.651 \times °h)})$ for adults and $100 / (1 + e^{(4.701 + 2.858 \times °h)})$ for juveniles. Error bars are ±1 standard error. The ability of the single surviving –4.9°h adult crab improved over time; its righting time 32 days after exposure was similar to that of controls.
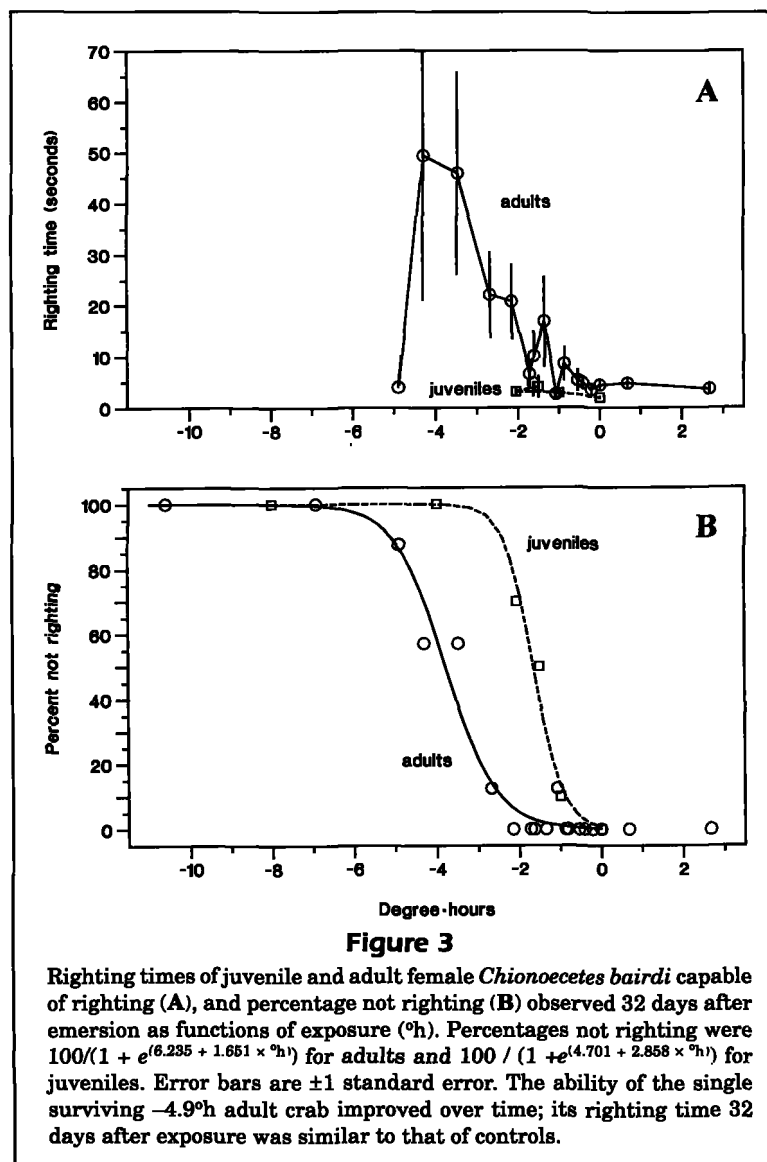
Table 2

Degree-hours causing death (LC) in *Chionoecetes bairdi* exposed to cold air, estimated with logit analysis. The LC number indicates the percentage of crabs affected; e.g. LC50 is the median lethal degree-hours. The error term (CI) is the estimated 95% confidence interval.

Day	LC10	LC30	LC50	LC70	LC90	CI
Juveniles						
1	−0.9	−5.1	−7.7	−10.4	−14.6	3.4
2	−1.0	−4.6	−6.8	−9.0	−12.6	2.6
4	−1.3	−3.9	−5.5	−7.1	−9.7	1.7
8	−1.3	−2.9	−3.9	−4.8	−6.4	1.1
16	−1.3	−2.5	−3.3	−4.0	−5.2	0.8
32	−1.3	−2.5	−3.3	−4.0	−5.2	0.8
Adults						
1	−3.1	−5.6	−7.2	−8.8	−11.3	1.6
2	−2.8	−5.2	−6.7	−8.2	−10.6	1.5
4	−2.6	−4.8	−6.2	−7.5	−9.7	1.3
8	−3.0	−4.0	−4.6	−5.1	−6.1	0.6
16	−3.2	−3.9	−4.3	−4.8	−5.5	0.5
32	−2.8	−3.8	−4.3	−4.9	−5.8	0.6

Table 3

Effective degree-hours causing cessation of righting (EC) in *Chionoecetes bairdi* exposed to cold air, estimated with logit analysis. The EC number indicates the percentage of crabs affected; EC50 is the median effective degree-hours. The error term (CI) is the estimated 95% confidence interval.

Day	EC10	EC30	EC50	EC70	EC90	CI
Juveniles						
0	−0.2	−0.8	−1.2	−1.6	−2.2	0.3
1	−0.7	−1.2	−1.5	−1.7	−2.2	0.3
2	−0.6	−1.1	−1.5	−1.8	−2.3	0.3
4	−0.5	−1.1	−1.4	−1.7	−2.2	0.3
8	−1.1	−1.4	−1.7	−1.9	−2.3	0.3
16	−0.9	−1.3	−1.6	−1.9	−2.4	0.3
24	−0.8	−1.4	−1.7	−2.1	−2.6	0.3
32	−0.9	−1.3	−1.6	−1.9	−2.4	0.3
Adults						
0	−1.3	−1.8	−2.1	−2.5	−3.0	0.3
1	−2.0	−2.7	−3.1	−3.5	−4.1	0.4
2	−1.8	−2.4	−2.8	−3.2	−3.8	0.4
4	−2.3	−2.8	−3.1	−3.4	−3.9	0.4
8	−2.1	−2.7	−3.0	−3.4	−4.0	0.4
16	−2.2	−2.7	−3.1	−3.5	−4.0	0.4
24	−2.2	−2.9	−3.4	−3.8	−4.6	0.5
32	−2.4	−3.3	−3.8	−4.3	−5.1	0.5

to cold air frequently lost pereiopods during ecdysis; losses increased from 0 to −4°h. The only crab exposed to −8°h that attempted to molt lost no limbs, but died during ecdysis (Fig. 6).

Feeding rates

Feeding rates of adult female Tanner crabs were significantly depressed by exposure to cold air $(P_{ANOVA} \le 0.001)$. In general, adult females exposed to $<-2.7°h$ (62% of the median lethal exposure) ate significantly less than did controls (Tukey test). Feeding rates measured shortly before zoeal hatching (41 to 60 days after exposure) were significantly less $(P \le 0.05)$ for all crabs than feeding rates after zoeal hatching (85–98 days after exposure), but the slopes (feeding rate/exposure) before and after hatching did not differ (multivariate regression, $P > 0.50$; Fig. 7). The frequency of feeding also increased significantly after zoeal hatching $(P < 0.001)$ and was significantly related to aerial exposure before and after larval hatching $(P_{linear} < 0.001)$. The most severely treated crabs $(-4.9°h)$ did not eat before zoeal release but ate 57% of the time after release.

Weight change

Change in weight of juvenile crabs was reduced by exposure to cold air. Wet weights of juvenile crabs that did not molt declined with increasing exposure severity $(P=0.002, r^2=0.42, n=20;$ Fig. 8). The weight

increment of juvenile crabs that molted also declined with decreasing exposure (Fig. 8). This trend was not significant until an outlier at −2.0°h was removed $(P=0.021, r^2=0.56, n=9)$. Pereiopod autotomy probably influenced these weight outcomes. The weight changes of juvenile crabs that did not molt were correlated with righting response measured immediately after exposure $(P=0.018, r^2=0.88, n=5, Y=a + bx^3)$. Changes in weight of adult crabs were not correlated with exposure $(P \ge 0.07, r^2=0.08, n=44)$.

Reproduction

Exposure of ovigerous female crabs to cold air generally did not affect the eggs or subsequently released zoeae unless the female died; all eggs died if the female died. Timing of initial zoeal release (20 April ± 1 day), duration of release (11 ± 1 day), and median release date (26 April ± 1 day) did not vary with exposure $(r^2=0.04, n=44;$ Fig. 9). Zoeae placed in separate containers for two days were not significantly affected by exposure prior to hatching $(P=0.425, r^2=0.02, n=43)$, and 87 ±3% continued swimming through the test period. Larval mortality, measured as the percentage of zoeae that sank to tank bottoms and died (0.4 ±0.2%), did not vary with exposure $(r^2=0.03, n=44)$. Zoeal mortality (2 ±2%) during swimming tests was not correlated with exposure $(r^2=0.09)$.

The percentage of eggs that hatched may have been slightly affected by exposure, but our results were inconclusive ($P_{regression:arcsin}$=0.036, but $P_{lack\ of\ fit}$<0.019, and r^2=0.10). The percentage of eggs hatching in the –5.3°h treatment differed significantly from the control (Dunnett's test), but the difference was minor (99.1% versus 99.8% hatching).

Egg extrusion may have been influenced by exposure, but the data were inconsistent. Elapsed time between larval hatching and subsequent egg extrusion tended to be prolonged by exposure, but the response was variable (P_{linear}=0.005, $P_{lack\ of\ fit}$=0.719, r^2=0.19, n=41). Egg extrusion generally occurred two days (median) after zoeal release but ranged from 0 to 18 days; only crabs in the two most severe treatments (≤–4.3°h) exceeded nine days. The date of ex-
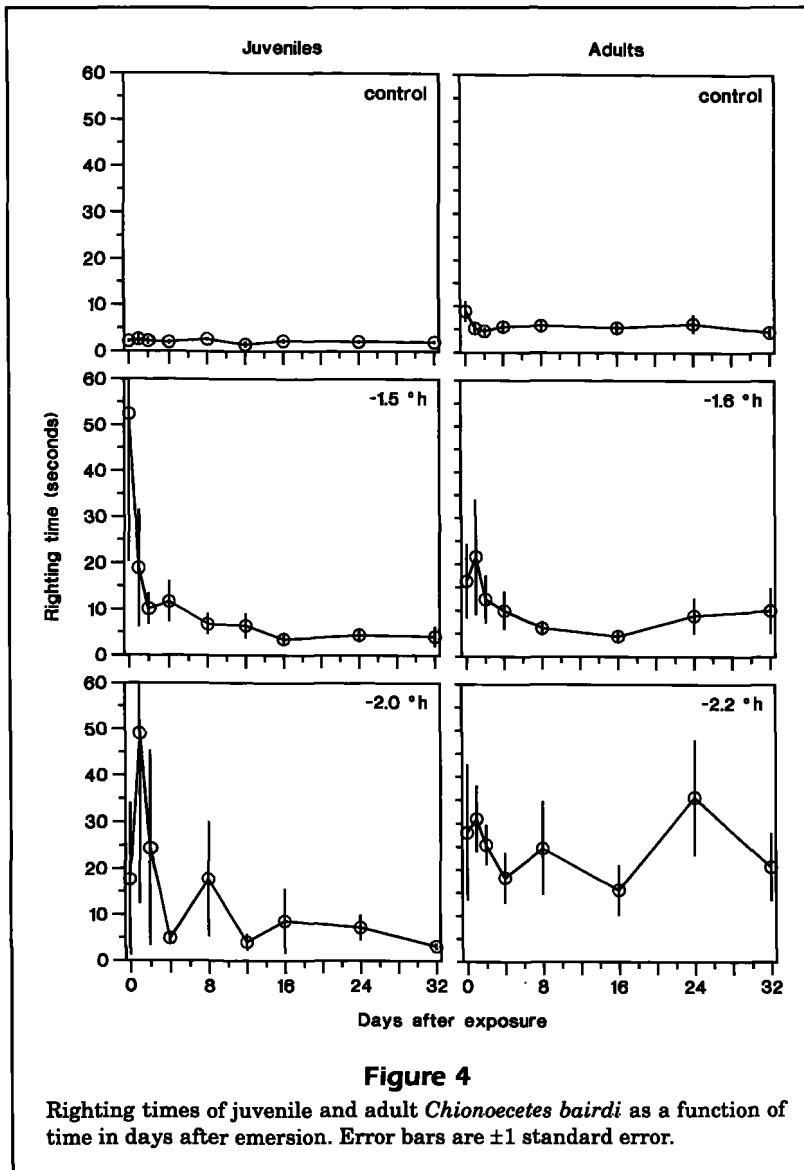
trusion (4 May ±7 days) may also have been changed by exposure, but again the statistical results were inconclusive (P_{linear}=0.011, $P_{lack\ of\ fit}$=0.700, r^2=0.16, n=41). Exposure did not affect the percentage of Tanner crabs extruding eggs (93%, P_{linear}=0.730, r^2=0.03, n=6).
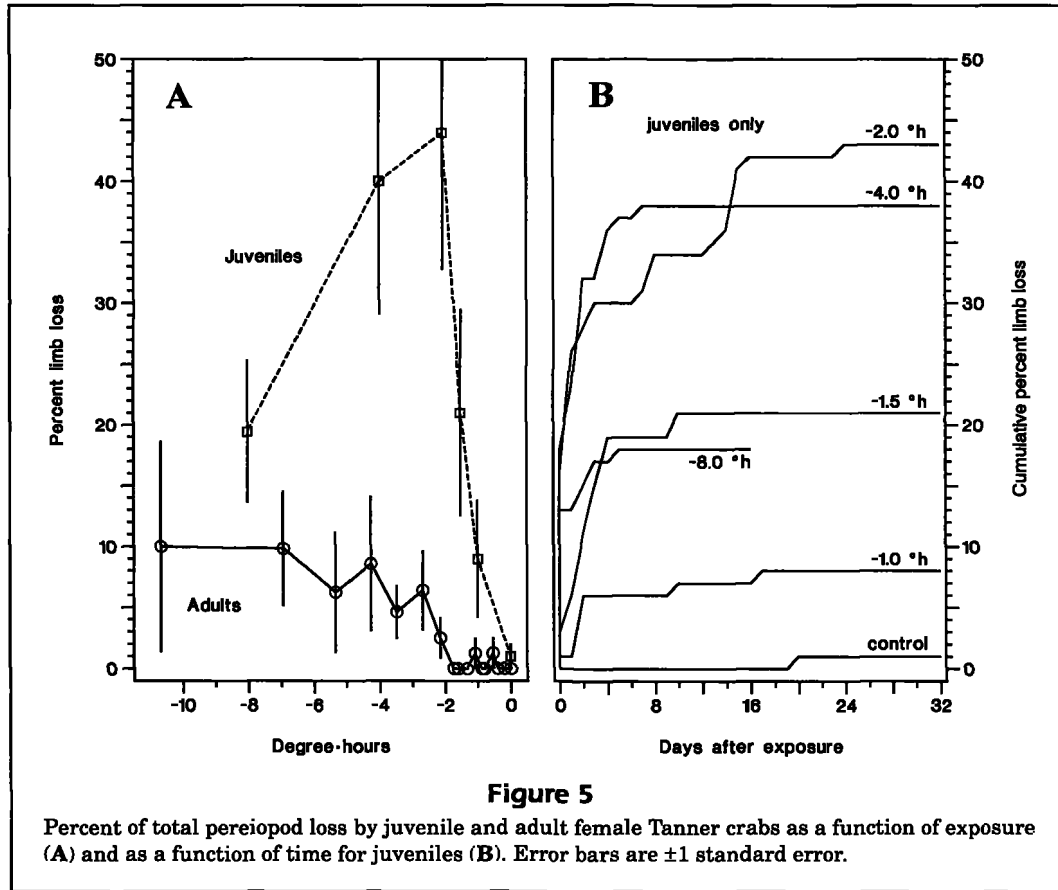
Discussion

Extreme exposure to cold air was lethal to Tanner crabs. It is also possible that thermal shock caused when the crabs were returned to water following exposure was also damaging. Following sublethal exposure, crabs exhibited a slowed righting response, autotomy of pereiopods, depressed feeding rates (adults), and weight loss or reduced weight gain (juveniles).

Temperature and duration of treatment were both critical factors in determining how aerial exposure affected Tanner crabs. In a similar experiment with king crabs, the response of crabs to exposure was clearly observed when exposure was defined as the product of temperature and the length of exposure time (Carls and O'Clair, 1990). The use of this composite variable worked well with the current data set. However, our approach may not be generally applicable (for discussion see Carls and O'Clair, [1990]).

Design of this experiment precluded independent analysis of temperature and time factors. However, either factor may be predicted as a function of the other. For example, at –10°C, 10% of juvenile crabs may be killed by an 8-minute exposure, and 50% may be killed by a 20-minute exposure. Similarly, a 10-minute exposure would impair righting in 50% of juvenile crab at –7°C. Predicted times and temperatures were calculated from degree-hours causing death (LC) or from effective degree-hours causing cessation of righting (EC) estimates (Tables 2 and 3); temperature multiplied by time (units are Celcius and hours) matched the LC or EC estimates. Predictions of adult and juvenile Tanner crab response are summarized in Figure 10 and Appendices. In our example (Fig. 10), short-term effects are predicted by ability to right immediately after exposure; impaired crabs may be subject to increased predation at this time. Long-term effects are pre-
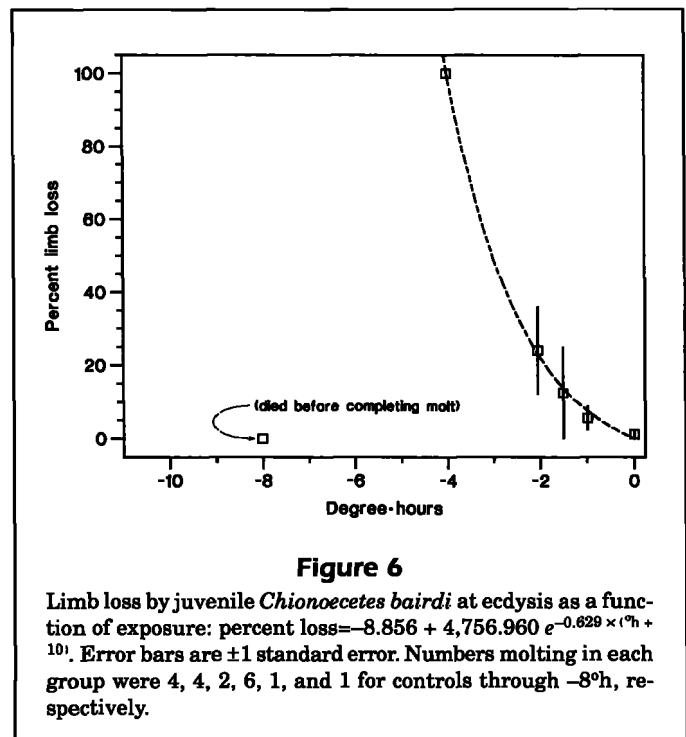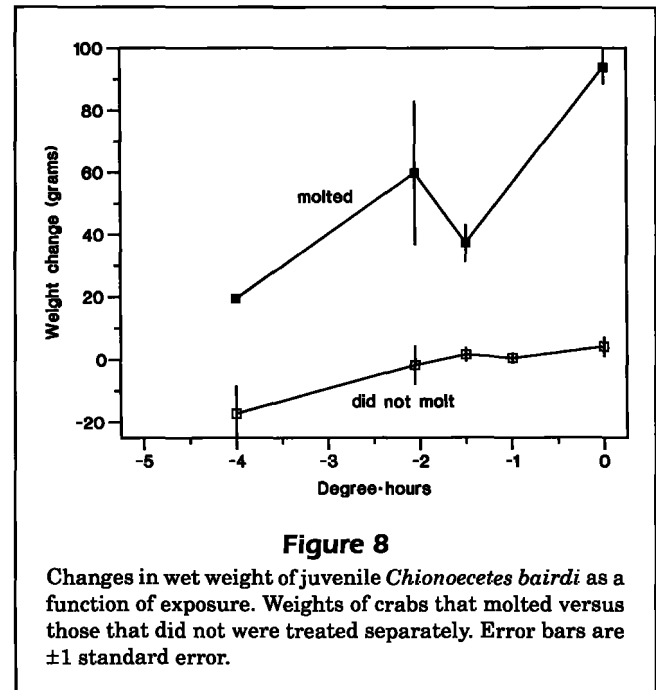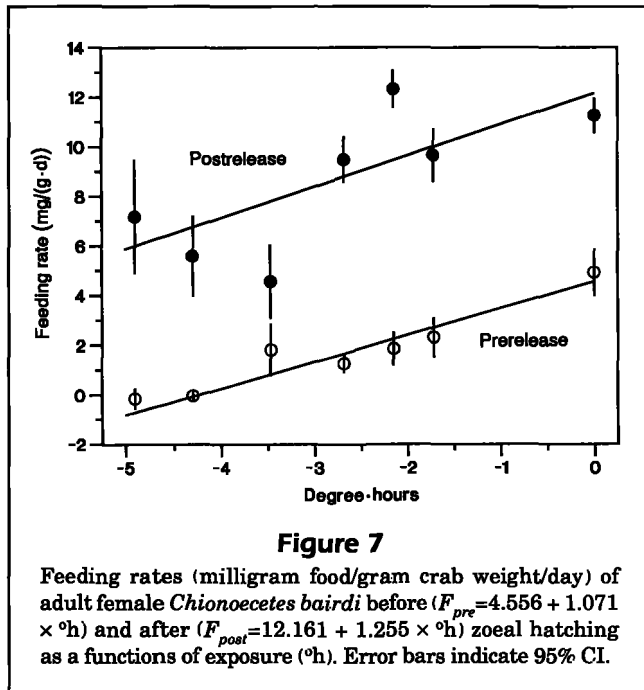

Figure 4

Righting times of juvenile and adult *Chionoecetes bairdi* as a function of time in days after emersion. Error bars are ±1 standard error.

Figure 5

Percent of total pereiopod loss by juvenile and adult female Tanner crabs as a function of exposure (A) and as a function of time for juveniles (B). Error bars are ±1 standard error.

dicted by mortality after exposure-induced death ceased.

Mortality of adult Tanner crabs was significantly greater below –3°h and vigor was reduced below –2°h compared with control crabs. Exposures that are this severe probably occur infrequently on the fishing grounds except during winter in the northern Gulf of Alaska and the Bering Sea. Data are lacking on the time incidentally captured crabs remain on deck before being released, but duration probably varies widely. Larger vessels employing assembly-line techniques may process crabs more rapidly than do smaller vessels. Poor handling of culls combined with prolonged exposure may further reduce survival of incidentally caught crabs.

Crabs captured incidentally during trawling are probably stressed more than those caught in pots. Stevens (1990) reported trawl tows ranging up to 6.4 hours and retention times of Tanner crabs up to 17 hours; the median lethal holding time for Tanner crabs was 8.3 hours. Net type influenced survival, and injuries were present in a greater proportion of dead than of live crabs (Stevens, 1990).

Figure 6

Limb loss by juvenile *Chionoecetes bairdi* at ecdysis as a function of exposure: percent loss=–8.856 + 4,756.960 $e^{-0.629 \times (°h + 10)}$. Error bars are ±1 standard error. Numbers molting in each group were 4, 4, 2, 6, 1, and 1 for controls through –8°h, respectively.

Figure 7

Feeding rates (milligram food/gram crab weight/day) of
adult female *Chionoecetes bairdi* before (F_{pre}=4.556 + 1.071
× °h) and after (F_{post}=12.161 + 1.255 × °h) zoeal hatching
as a functions of exposure (°h). Error bars indicate 95% CI.

Figure 8

Changes in wet weight of juvenile *Chionoecetes bairdi* as a
function of exposure. Weights of crabs that molted versus
those that did not were treated separately. Error bars are
±1 standard error.

Mortality and injury due to aerial exposure have
been reported for other commercially harvested de-
capod crustaceans. For example, king crabs were af-
fected by exposure to cold air, but were less sensitive
than Tanner crabs (Carls and O'Clair, 1990). The
western rock lobster, *Panulirus cygnus*, was signifi-
cantly affected by ≥15 minutes exposure to warm air
(27–35°C); recapture rates were lower than for un-
exposed controls, and the probability of mortality due
to predation rose (Brown and Caputi, 1983).

We do not know what physiological mechanism(s)
caused the abnormal events during ecdysis that of-
ten resulted in death. O'Brien et al. (1986) induced
apolysis (the separation of integumentary tissues
from the exoskeleton during proecdysis) in several
species of brachyurans by packing crabs in ice.
Apolysis occurred within one hour in most cases and
was not caused by death (O'Brien et al., 1986).
O'Brien et al. (1986) did not observe ecdysis in their
experimental crabs; therefore, the effect of apolysis
on the timing, duration, and success of ecdysis in
crabs is not known. In the present experiment, al-
though mortality occurred during ecdysis in juvenile
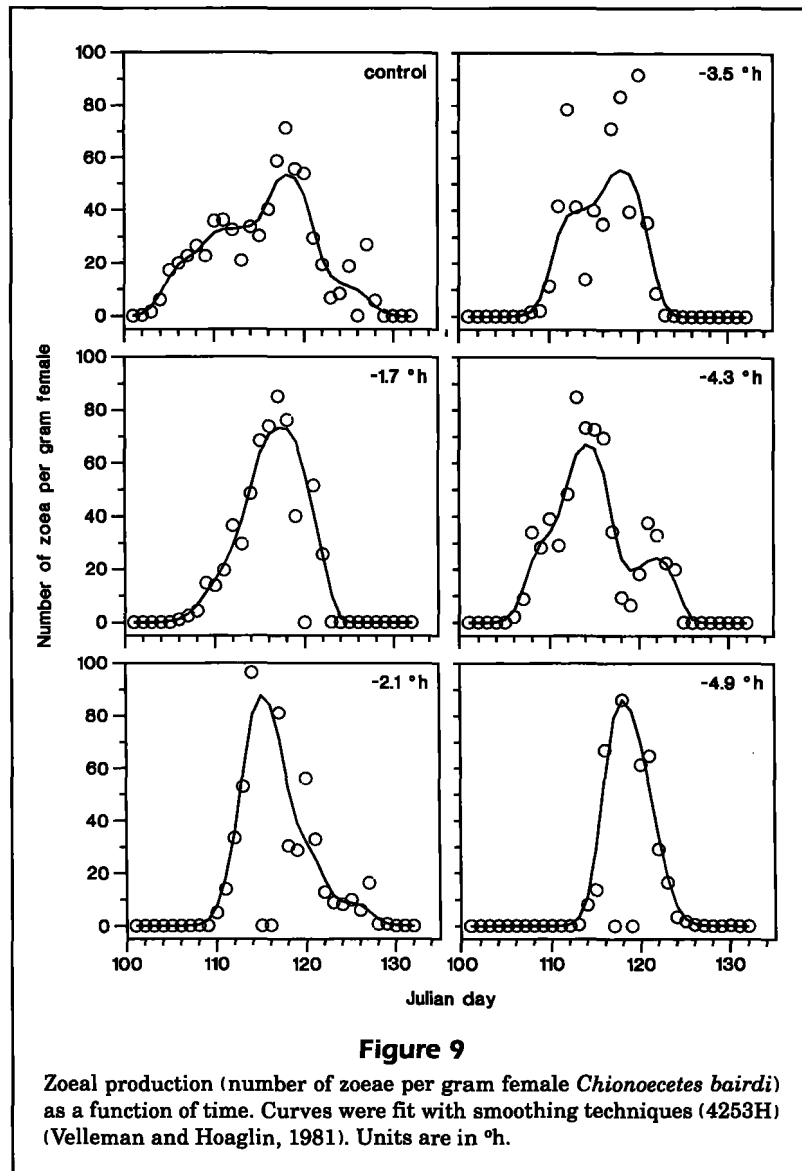crabs, the timing of ecdysis was not affected.

Evaporative water loss during exposure probably
did not contribute significantly to the effects we ob-
served. The fact that warmer exposures, such as the
32-minute exposure at +5°C, caused little or no ef-
fect supports this supposition. Similar observations
were made for king crab (Carls and O'Clair, 1990).
In a study by Taylor and Whiteley (1989), the lob-

ster *Homarus gammarus vulgaris*, which rarely
comes in contact with air in its natural environment,
was exposed to air at 15°C for up to 14 hours. Water
loss, inferred from the constancy of most hemolymph
ion concentrations, was minimal (Taylor and
Whiteley, 1989). Oxygen delivered to *H. gammarus*
tissues was substantially reduced, and CO_2 accumu-
lated, but levels returned rapidly to normal after a
14-hour exposure. Lactate levels increased, but el-
evation of bicarbonate ions increased the buffering
capacity of the hemolymph. Because exposures did
not exceed 32 minutes, it is unlikely that reduced
oxygen directly caused Tanner crab mortality in our
experiment. However, at low air temperatures, gills
may have been damaged by frost, thus impairing
respiratory gas, metabolite, and ion exchange after
the crabs were returned to the water.

The ability of crabs to right themselves proved to be
a sensitive measure of crab viability. Righting response
data collected immediately after exposure correlated
strongly with less-immediate responses such as mor-
tality and growth. Pereiopod loss also impaired righting.

Pereiopod autotomy in adult crabs was a function
of exposure. Mortality may have influenced the au-
totomy response curve for juvenile crabs: during se-
vere exposure, crabs apparently died before autotomy
could take place.

Aerial exposure reduced weight gain in juvenile
crabs and caused weight loss in juveniles that did
not molt. However, wet weights of the adult crabs
(all anecdysial) did not vary with exposure. This ab-

Figure 9

Zoeal production (number of zoeae per gram female *Chionoecetes bairdi*) as a function of time. Curves were fit with smoothing techniques (4253H) (Velleman and Hoaglin, 1981). Units are in °h.

sence of weight changes in the adults is puzzling because feeding rates were significantly depressed by exposure. Growth of adult western rock lobsters was reduced by exposure (Brown and Caputi, 1985).

Body size, shape, and volume may be important factors in predicting crab response to cold-air exposure. Results of the present experiment support this hypothesis: smaller crabs (juveniles) were more sensitive to exposure than were larger crabs (adults). Additionally, adult Tanner crabs were more sensitive to exposure than were larger king crabs (Carls and O'Clair, 1990), but unknown interspecific factors may have influenced this difference. An experiment involving a broad size range of conspecific individuals is needed to test whether sensitivity to exposure is size-dependent in crabs.

Surprisingly, aerial exposure did not measurably affect the developing larvae of exposed females unless the female died. Surviving crabs produced normal zoeae. Moreover, the timing of larval release, larval swimming ability, and viability were not affected by exposure. Longer-term larval responses, such as survival past the first molt and zoeal growth, were not examined. Exposure may have reduced hatching success (by <1%) of the Tanner crab larvae and possibly may have affected the timing of egg extrusion, but these responses did not vary strongly. Schlieder (1980) reported a 13% reduction in hatching success in the stone crab, *Menippe mercenaria*, compared with controls when the crabs were exposed to air at 27–33°C for two hours. Hatching success was reduced further by a five-hour exposure and by autospasy (Schlieder, 1980).

In summary, although environmental conditions as severe as those tested are uncommon on the fishing grounds during fishing operations (except in the central and northern Bering Sea), low-temperature aerial exposure during fishing operations can adversely affect incidentally captured crabs. Exposure to cold air reduced crab vigor and feeding rates, caused limb autotomy, and killed the crabs in severe situations. Progeny died if exposure to cold air killed females brooding them, otherwise larvae were not measurably affected. Prompt return of incidentally caught Tanner crabs to the sea, especially during extremely cold weather, should reduce adverse effects of exposure to cold air.

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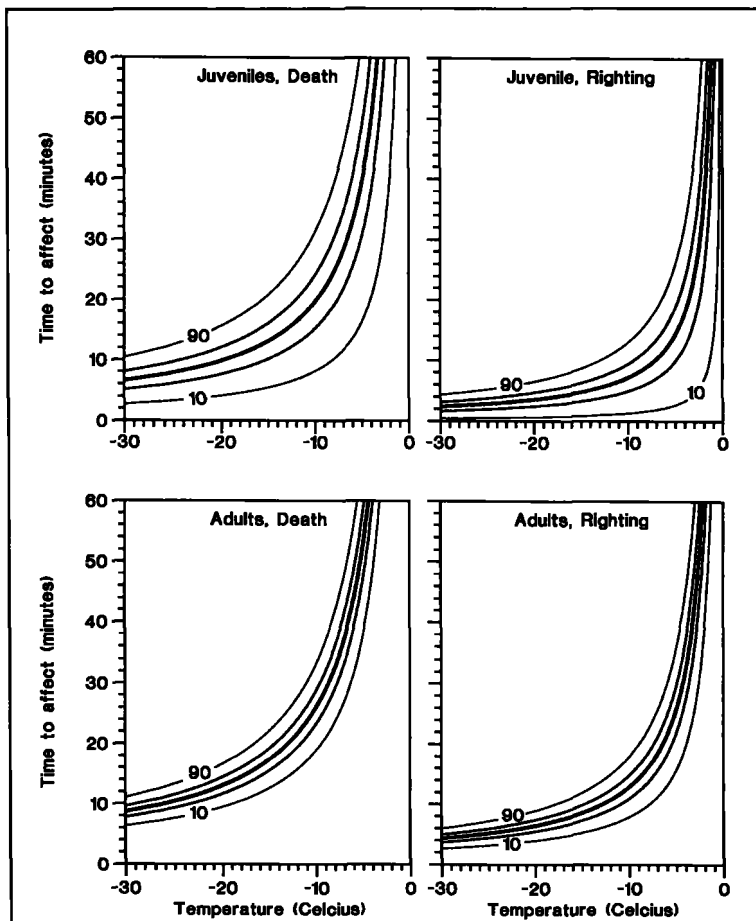
Figure 10

Predicted time in minutes required to cause death or impair righting of juvenile and ovigerous female *Chionoecetes bairdi* following exposure to cold air. Mortality predictions are based on cumulative mortality through day 16; no deaths were observed in the ensuing 16 days. Righting predictions are based on responses immediately after exposure; there was a tendancy for righting times to improve after exposure, but improvements were generally not statistically significant.

Appendix Table 1

Predicted time in minutes required to cause death of the listed percentage of adult *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based lethal responses (LC10, LC30, . . . LC90) estimated on day 16.

Temperature	10%	30%	50%	70%	90%	Temperature	10%	30%	50%	70%	90%
−1.0	189	233	260	288	332	−16.0	12	15	16	18	21
−2.0	95	116	130	144	166	−17.0	11.1	13.7	15.3	16.9	19.5
−3.0	63	78	87	96	111	−18.0	10.5	12.9	14.5	16.0	18.4
−4.0	47	58	65	72	83	−19.0	9.9	12.3	13.7	15.2	17.5
−5.0	38	47	52	58	66	−20.0	9.5	11.6	13.0	14.4	16.6
−6.0	32	39	43	48	55	−21.0	9.0	11.1	12.4	13.7	15.8
−7.0	27	33	37	41	47	−22.0	8.6	10.6	11.8	13.1	15.1
−8.0	24	29	33	36	41	−23.0	8.2	10.1	11.3	12.5	14.4
−9.0	21	26	29	32	37	−24.0	7.9	9.7	10.9	12.0	13.8
−10.0	19	23	26	29	33	−25.0	7.6	9.3	10.4	11.5	13.3
−11.0	17	21	24	26	30	−26.0	7.3	9.0	10.0	11.1	12.8
−12.0	16	19	22	24	28	−27.0	7.0	8.6	9.6	10.7	12.3
−13.0	15	18	20	22	26	−28.0	6.8	8.3	9.3	10.3	11.9
−14.0	14	17	19	21	24	−29.0	6.5	8.0	9.0	9.9	11.4
−15.0	13	16	17	19	22	−30.0	6.3	7.8	8.7	9.6	11.1

Appendix Table 2

Predicted time in minutes required to cause death of the listed percentage of juvenile *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based lethal responses (LC10, LC30, . . . LC90) estimated on day 16.

Temperature	10%	30%	50%	70%	90%	Temperature	10%	30%	50%	70%	90%
−1.0	81	152	196	241	311	−16.0	5.1	9.5	12.3	15.0	19.5
−2.0	41	76	98	120	156	−17.0	4.8	8.9	11.5	14.2	18.3
−3.0	27	51	65	80	104	−18.0	4.5	8.4	10.9	13.4	17.3
−4.0	20	38	49	60	78	−19.0	4.3	8.0	10.3	12.7	16.4
−5.0	16	30	39	48	62	−20.0	4.1	7.6	9.8	12.0	15.6
−6.0	14	25	33	40	52	−21.0	3.9	7.2	9.3	11.5	14.8
−7.0	12	22	28	34	44	−22.0	3.7	6.9	8.9	10.9	14.2
−8.0	10	19	25	30	39	−23.0	3.5	6.6	8.5	10.5	13.5
−9.0	9	17	22	27	35	−24.0	3.4	6.3	8.2	10.0	13.0
−10.0	8	15	20	24	31	−25.0	3.2	6.1	7.8	9.6	12.5
−11.0	7.4	13.8	17.8	21.9	28.3	−26.0	3.1	5.8	7.5	9.3	12.0
−12.0	6.8	12.7	16.4	20.1	26.0	−27.0	3.0	5.6	7.3	8.9	11.5
−13.0	6.2	11.7	15.1	18.5	24.0	−28.0	2.9	5.4	7.0	8.6	11.1
−14.0	5.8	10.8	14.0	17.2	22.2	−29.0	2.8	5.2	6.8	8.3	10.7
−15.0	5.4	10.1	13.1	16.0	20.8	−30.0	2.7	5.1	6.5	8.0	10.4

Appendix Table 3

Predicted time in minutes required to impair righting response of the listed percentage of adult *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based on righting responses (EC10, EC30, . . . EC90) estimated immediately after exposure.

Temperature	10%	30%	50%	70%	90%	Temperature	10%	30%	50%	70%	90%
-1.0	79	109	129	148	179	-16.0	4.9	6.8	8.0	9.3	11.2
-2.0	39	55	64	74	89	-17.0	4.6	6.4	7.6	8.7	10.5
-3.0	26	36	43	49	60	-18.0	4.4	6.1	7.2	8.2	9.9
-4.0	20	27	32	37	45	-19.0	4.1	5.8	6.8	7.8	9.4
-5.0	16	22	26	30	36	-20.0	3.9	5.5	6.4	7.4	8.9
-6.0	13	18	21	25	30	-21.0	3.7	5.2	6.1	7.0	8.5
-7.0	11	16	18	21	26	-22.0	3.6	5.0	5.9	6.7	8.1
-8.0	10	14	16	19	22	-23.0	3.4	4.8	5.6	6.4	7.8
-9.0	9	12	14	16	20	-24.0	3.3	4.6	5.4	6.2	7.5
-10.0	8	11	13	15	18	-25.0	3.1	4.4	5.1	5.9	7.2
-11.0	7.1	9.9	11.7	13.5	16.3	-26.0	3.0	4.2	5.0	5.7	6.9
-12.0	6.5	9.1	10.7	12.3	14.9	-27.0	2.9	4.0	4.8	5.5	6.6
-13.0	6.0	8.4	9.9	11.4	13.8	-28.0	2.8	3.9	4.6	5.3	6.4
-14.0	5.6	7.8	9.2	10.6	12.8	-29.0	2.7	3.8	4.4	5.1	6.2
-15.0	5.2	7.3	8.6	9.9	11.9	-30.0	2.6	3.6	4.3	4.9	6.0

Appendix Table 4

Predicted time in minutes required to impair righting response of the listed percentage of juvenile *Chionoecetes bairdi* at indicated temperatures (°C). Calculations are based on righting responses (EC10, EC30, . . . EC90) estimated immediately after exposure.

Temperature	10%	30%	50%	70%	90%	Temperature	10%	30%	50%	70%	90%
-1.0	13	49	71	93	129	-16.0	0.83	3.05	4.45	5.84	8.07
-2.0	7	24	36	47	65	-17.0	0.78	2.87	4.19	5.50	7.59
-3.0	4	16	24	31	43	-18.0	0.74	2.71	3.95	5.19	7.17
-4.0	3.3	12.2	17.8	23.4	32.3	-19.0	0.70	2.57	3.75	4.92	6.79
-5.0	2.7	9.8	14.2	18.7	25.8	-20.0	0.66	2.44	3.56	4.67	6.45
-6.0	2.2	8.1	11.9	15.6	21.5	-21.0	0.63	2.33	3.39	4.45	6.15
-7.0	1.9	7.0	10.2	13.4	18.4	-22.0	0.60	2.22	3.23	4.25	5.87
-8.0	1.7	6.1	8.9	11.7	16.1	-23.0	0.58	2.12	3.09	4.06	5.61
-9.0	1.5	5.4	7.9	10.4	14.3	-24.0	0.55	2.04	2.97	3.90	5.38
-10.0	1.3	4.9	7.1	9.3	12.9	-25.0	0.53	1.95	2.85	3.74	5.16
-11.0	1.2	4.4	6.5	8.5	11.7	-26.0	0.51	1.88	2.74	3.60	4.96
-12.0	1.1	4.1	5.9	7.8	10.8	-27.0	0.49	1.81	2.64	3.46	4.78
-13.0	1.0	3.8	5.5	7.2	9.9	-28.0	0.47	1.74	2.54	3.34	4.61
-14.0	0.9	3.5	5.1	6.7	9.2	-29.0	0.46	1.68	2.45	3.22	4.45
-15.0	0.88	3.26	4.74	6.23	8.60	-30.0	0.44	1.63	2.37	3.12	4.30