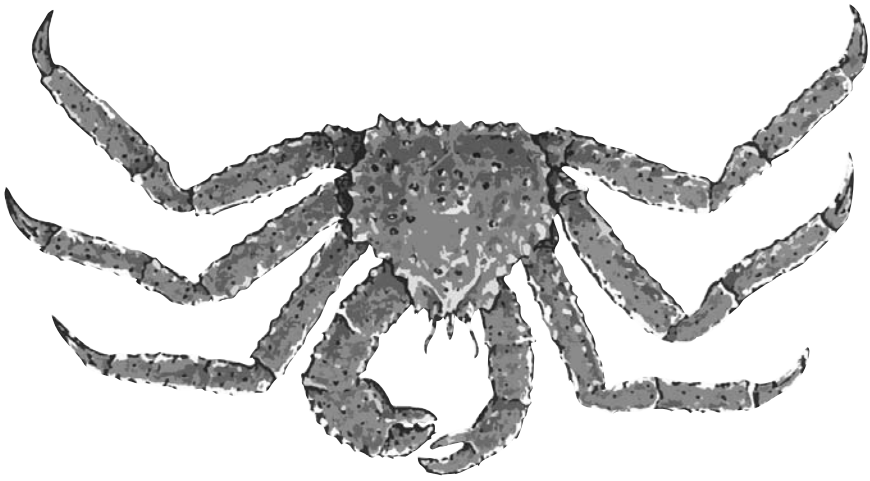

CRABS IN COLD WATER REGIONS:
BIOLOGY, MANAGEMENT, AND ECONOMICS

A.J. Paul, Earl G. Dawe, Robert Elner, Glen S. Jamieson,
Gordon H. Kruse, Robert S. Otto, Bernard Sainte-Marie,
Thomas C. Shirley, and Douglas Woodby, Editors

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About the Symposium

Crab is one of the world's most valuable marine consumables, especially to Alaska. So it is not surprising that the topic of crab has been addressed more often than any other by the Lowell Wakefield Symposium series, each time at the request of resource managers and researchers. Crab2001, Crabs in Cold Water Regions: Biology, Management, and Economics, held January 17-20, 2001 in Anchorage, Alaska, was the sixth crab symposium in the series (1982, 1984, 1985, 1989, 1995, and 2001). The year for the Crab2001 symposium had been "selected" six years earlier by participants at the 1995 Wakefield symposium on high latitude crabs.

The symposium was organized and coordinated by Brenda Baxter, University of Alaska Sea Grant Program, with the assistance of the organizing committee. Committee members are: Earl Dawe, Department of Fisheries and Oceans, Canada; Glen Jamieson, Department of Fisheries and Oceans, Canada; Gordon Kruse, University of Alaska Fairbanks, School of Fisheries and Ocean Sciences (formerly of Alaska Department of Fish and Game); Bob Otto, U.S. National Marine Fisheries Service, Alaska Fisheries Science Center; A.J. Paul, University of Alaska Fairbanks, Institute of Marine Science; and Dave Witherell, North Pacific Fishery Management Council.

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The Lowell Wakefield Symposium Series

The University of Alaska Sea Grant College Program has been sponsoring and coordinating the Lowell Wakefield Fisheries Symposium series since 1982. These meetings are a forum for information exchange in biology, management, economics, and processing of various fish species and complexes as well as an opportunity for scientists from high latitude countries to meet informally and discuss their work.

Lowell Wakefield was the founder of the Alaska king crab industry. He recognized two major ingredients necessary for the king crab fishery to survive—ensuring that a quality product be made available to the consumer, and that a viable fishery can be maintained only through sound management practices based on the best scientific data available. Lowell Wakefield and Wakefield Seafoods played important roles in the development and implementation of quality control legislation, in the preparation of fishing regulations for Alaska waters, and in drafting international

agreements for the high seas. Toward the end of his life, Lowell Wakefield joined the faculty of the University of Alaska as an adjunct professor of fisheries where he influenced the early directions of the university's Sea Grant Program. This symposium series is named in honor of Lowell Wakefield and his many contributions to Alaska's fisheries. Three Wakefield symposia are planned for 2003-2005.

Proceedings Acknowledgments

This publication presents 53 symposium papers. Each full-length paper was reviewed by two peer reviewers, extended abstracts had one review each, and papers were revised according to recommendations by associate editors who generously donated their time and expertise: A.J. Paul, Earl G. Dawe, Robert Elner, Glen S. Jamieson, Gordon H. Kruse, Robert S. Otto, Bernard Sainte-Marie, Thomas C. Shirley, and Douglas Woodby.

The first two papers, by T.C. Shirley and B.G. Stevens, and the last, by S.D. Zaklan, were not presented at the symposium; the editors chose to include them in the book. Thanks go to the authors of all 53 contributions.

Many thanks to the following people who reviewed one or more manuscripts for this book: Klaus Anger, Dave Armstrong, Celine Audet, David Barnard, Jim Blackburn, Jim Boutillier, Forrest Bowers, Ryan Burt, Larry Byrne, Alan Campbell, John Clark, J. Crain, Paula Cullenberg, Braxton Dew, Bill Donaldson, Rejean Dufour, Bob Elner, Darryl Felder, Richard Forward, Caleb Gardner, Skip Gish, Don Gunderson, David Hankin, Gretchen Harrington, Marcel Hebert, S.Y. Hong, Luke Jadamec, Glen Jamieson, Stephen Jewett, B. Alan Johnson, Knut Jørstad, Jiro Kittaka, Tom Kline, Kooichi Konishi, Gordon Kruse, Andrew Levings, Gustavo Lovrich, Patsy A. McLaughlin, Tony Mecklenburg, G.A. Messick, Bob Miller, Adam Moles, Frank Morado, Mikio Moriyasu, Holly Moore, Hiroyuki Munehara, Jiro Nagao, Peter Ng, Chuck O'Clair, Steinar Olsen, Wongyu Park, A.J. Paul, Judy Paul, Doug Pengilly, Ian Potter, Martin Robinson, Amelie Rondeau, Christopher Rooper, Gregg Rosenkranz, Janet Rumble, Mary Schwenzfeier, Tom Shirley, Shareef Siddeek, Barry Smith, Brad Stevens, Jan Sundet, Kathy Swiney, Arnie Thomson, Shelly Tallack, Dave Taylor, Donn Tracy, Oliver Tully, Al Tyler, Sherry Tamone, Federico Tapella, John Tremblay, Dan Urban, Peter van Tamelen, Julio Vinuesa, Ivan Vining, Elmer Wade, Jonathon Warrenchuk, Leslie Watson, Greg Workman, Hiroshi Yamaguchi, Zane Zhang, and Jie Zheng.

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Correct Spelling and Publication Date for the Golden King Crab (*Lithodes aequispinus* Benedict, 1895)

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Introduction

The date of publication of the species description of the golden king crab *Lithodes aequispinus* Benedict, 1895 and the spelling of the specific name have been sources of confusion for some time for authors. A publication date of 1894 has been incorrectly used, and the specific name has been incorrectly spelled as *aequispina*.

The source of confusion concerning the publication date is readily obvious: the volume of the *Proceedings of the United States National Museum* (Benedict 1895) containing the description of the golden king crab is a collection of separate articles having different publication dates. Although the year 1895 is listed on the title page of the volume, that date pertains to the entire volume and not to the individual articles, some of which were published in 1894. The crux of the issue is probably that Benedict's article has "1894" printed in its running head, as the volume covers the proceedings for that year. However, the table of contents of the volume lists the publication date for Benedict's article as January 29, 1895. Copies of each article in the proceedings volumes were published as separates in advance of publication of the completed volumes (Smithsonian Institution 1947).

The source of confusion over the spelling of the specific name of golden king crab is less obvious. The species was described originally as *Lithodes aequispinus,* and no valid reason exists to change the spelling of the specific name. Although Benedict (1895) erred in assigning a masculine ending to a feminine Latin noun (spina), there is no indication that this was an inadvertent error (Patsy A. McLaughlin, Chair of the American Fisheries Society Decapod Subcommittee, pers. comm.). Yet, Bouvier (1896) changed Benedict's *Lithodes aequispinus* to *L. aequispina.* The current edition of

the *International Code of Zoological Nomenclature* (ICZN 1999) is unambiguous on this point: Article 32.2 "The original spelling of a name is the 'correct original spelling,' unless it is demonstrably incorrect as provided in Article 32.5." In section 32.5.1 "Inadvertent errors . . . must be corrected." However, "incorrect transliteration or latinization . . . are not to be considered inadvertent errors" and therefore *not* to be corrected. The original spelling given by Benedict stands because it is not demonstrably incorrect under Article 32.5.

The errors in spelling and date were continued in commonly accepted taxonomic references: Macpherson's 1988 *Revision of the Family Lithodidae Samouelle, 1819 (Crustacea, Decapoda, Anomura) in the Atlantic Ocean,* and the American Fisheries Scientific Publication 17, *Common and Scientific Names of Aquatic Invertebrates of the United States and Canada* (Williams et al. 1989). An annotation will appear in the new edition of the AFS publication, stating that the species was incorrectly cited as *Lithodes aequispina* in the first edition, as was the date of publication as 1894 (Patsy A. McLaughlin, Chair of the American Fisheries Society Decapod Subcommittee, pers. comm.).

Thus, the correct scientific name and publication date for the golden king crab is *Lithodes aequispinus* Benedict, 1895.

Acknowledgments

Patsy A. McLaughlin, Chair of the American Fisheries Society Decapod Subcommittee, is thanked for details on Bouvier's errors and her communications with Smithsonian taxonomists. Catherine W. Mecklenburg, Point Stephens Research, obtained the volume of the *Proceedings of the United States National Museum* and clarified use of Latin and the *International Code of Zoological Nomenclature*. Susan Shirley, Alaska Department of Fish and Game, is thanked for editing.

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Checklist of Alaskan Crabs

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Alaska has long been known for its crab fisheries. The king crab fishery is perhaps the most famous and valuable of these, pound for pound, although the snow crab fishery has produced both the greatest landings and the greatest revenue in recent years. However, there are many more crab species in Alaskan waters, some of which support incidental or small fisheries, and others that will never support commercial fishing due to their size or scarcity. On the occasion of the symposium, Crabs in Cold Water Regions: Biology, Management, and Economics, devoted to the study of crabs, and occurring in Alaska, it seemed appropriate to consider exactly what constitutes an "Alaskan crab."

The following checklist (Table 1) was assembled from a review of publications on intertidal and subtidal marine species in Alaskan waters, loosely defined as anything within 200 nautical miles of the Alaskan coastline, including islands. Species on the list have been documented to occur in Alaskan waters in a published reference. The exceptions are six species collected from Patton Seamount, and not yet published, but which probably also occur on seamounts and on the continental slope closer to shore. Among them, the long clawed spider crab (*Macroregonia macrochira*) has not previously been observed north of 49ºN, but was found on Patton Seamount in the Gulf of Alaska at 54.5ºN, and probably ranges across the entire North Pacific seafloor below 1,000 m.

The list (Table 1) is ordered alphabetically by family, then by genus and species. The present list contains 11 families and 80 species of crabs that have been identified in Alaskan waters. Among these, 28 species are hermit crabs (family Paguridae), 18 are stone crabs (family Lithodidae, including king crabs), 14 are spider crabs (family Majidae, including snow and Tanner crabs), and 6 are pea crabs (family Pinnotheridae). The squat lobsters (family Galatheidae) and pinchbugs (family Chirostylidae) are included because they are anomurans, like the Paguridae and Lithodidae. Perhaps more will be discovered in the near future.

Latin names denoted with [a] are tentative identifications. The common names are those accepted and published by the American Fisheries Society

Table 1. Checklist of Alaskan crabs.

Scientific name	Common name	Source
Atelecyclidae		
Erimacrus isenbeckii (Brandt, 1848)	hair crab	2
Telmessus cheiragonus (Tilesius, 1815)	helmet crab	5, 7
Cancridae		
Cancer gracilis Dana, 1852	graceful rock crab	5, 7
Cancer magister Dana, 1852	Dungeness crab	5, 7
Cancer oregonensis (Dana, 1852)	pygmy rock crab	5, 7
Cancer productus Randall, 1839	red rock crab	7, 9
Chirostylidae		
Chirostylus perarmatusa Haig, 1968	Pacific red pinchbug[b]	8
Galatheidae		
Munida quadrispina Benedict, 1902	pinch bug[b]	5
Munidopsis albatrossaea Pequegnat & Pequegnat, 1973	Albatross squat lobster[b]	8
Grapsidae		
Hemigrapsus nudus (Dana, 1851)	purple shore crab	7
Hemigrapsus oregonensis (Dana, 1851)	yellow shore crab	7
Lithodidae		
Acantholithodes hispidus (Stimpson, 1860)	fuzzy crab[b]	5
Cryptolithodes sitchensis Brandt, 1853	umbrella crab	7
Cryptolithodes typicus Brandt, 1849	butterfly crab	3
Dermaturus mandtii Brandt, 1849	wrinkled crab[b]	4
Hapalogaster grebnitzkii Schalfeew, 1892	soft crab[b]	5
Hapalogaster mertensii Brandt, 1849	hairy crab	7
Lithodes aequispinus (Benedict, 1895)	golden king crab	5
Lithodes couesi Benedict, 1895	scarlet king crab	5
Lopholithodes foraminatus (Stimpson, 1859)	brown box crab[b]	3, 5
Lopholithodes mandtii Brandt, 1849	box crab[b]	3, 5
Oedignathus inermis (Stimpson, 1860)	paxillose crab[b]	7
Paralithodes camtschaticus (Tilesius, 1815)	red king crab	5
Paralithodes platypus Brandt, 1850	blue king crab	5
Paralomis multispinus (Benedict, 1895)	spiny paralomis[b]	8
Paralomis verrilli (Benedict, 1895)	Verill's paralomis[b]	8
Phyllolithodes papillosus Brandt, 1849	flatspine triangle crab	5
Placetron wosnessenskii Schalfeew, 1892	scaled crab	5
Rhinolithodes wosnessenskii Brandt, 1849	rhinoceros crab	5
Majidae		
Chionoecetes angulatus Rathbun, 1924	triangle Tanner crab	5
Chionoecetes bairdi Rathbun, 1924	Tanner crab	5
Chionoecetes opilio (Fabricius, 1788)	snow crab	5
Chionoecetes tanneri Rathbun, 1893	grooved Tanner crab	5
Chorilia longipes Dana, 1851	longhorn decorator crab	3
Hyas coarctatus Leach, 1815	Arctic lyre crab	5
Hyas lyratus Dana, 1815	Pacific lyre crab	5
Macroregonia macrochira Sakai T., 1978	long clawed spider crab[b]	8
Mimulus foliatus Stimpson, 1860	foliate kelp crab	7, 9

Scientific name	Common name	Source
Oregonia bifurca Rathbun, 1902	splitnose crab[b]	8
Oregonia gracilis Dana, 1851	graceful decorator crab	5
Pugettia gracilis Dana, 1851	graceful kelp crab	7, 10
Pugettia producta (Randall, 1839)	northern kelp crab	7
Scyra acutifrons Dana, 1851	sharpnose crab	7, 9
Paguridae		
Discorsopagurus schmitti (Stevens, 1925)	tubeworm hermit[b]	4
Elassochirus cavimanus (Miers, 1879)	purple hermit	5, 6
Elassochirus gilli (Benedict, 1892)	Pacific red hermit	5, 6, 9
Elassochirus tenuimanus (Dana, 1851)	widehand hermit[d]	6
Labidochirus splendescens (Owen, 1839)	splendid hermit	5, 6
Pagurus aleuticus (Benedict, 1892)	Aleutian hermit	6
Pagurus armatus (Dana, 1851)	armed hermit	5
Pagurus beringanus (Benedict, 1892)	Bering hermit[b]	6, 7
Pagurus brandti (Benedict, 1892)	sponge hermit	5
Pagurus capillatus (Benedict, 1892)	"Dirty Harry"[c]	6
Pagurus caurinus Hart, 1971	greenmark hermit	6
Pagurus confragosus (Benedict, 1892)	knobbyhand hermit	6
Pagurus cornutus (Benedict, 1892)	hornyhand hermit	5, 6
Pagurus dalli (Benedict, 1892)	whiteknee hermit	6
Pagurus granosimanus (Stimpson, 1859)	grainyhand hermit	7
Pagurus hemphilli (Benedict, 1892)	maroon hermit	10
Pagurus hirsutiusculus (Dana, 1851)	hairy hermit	6, 10
Pagurus kennerleyi (Stimpson, 1864)	bluespine hermit	6
Pagurus mertensii Brandt, 1851		6
Pagurus ochotensis Brandt, 1851	Alaskan hermit	6
Pagurus rathbuni (Benedict, 1892)	longfinger hermit	5, 6
Pagurus samuelis (Stimpson, 1857)	blueband hermit	9
Pagurus setosus (Benedict, 1892)	setose hermit	6
Pagurus stevensae Hart, 1971	Stevens hermit	6
Pagurus tanneri (Benedict, 1892)	longhand hermit	5, 6
Pagurus townsendi (Benedict, 1892)		6
Pagurus trigonocheirus (Stimpson, 1858)	fuzzy hermit	5, 6
Pagurus undosus (Benedict, 1892)	Pribilof hermit	5, 6
Pinnotheridae		
Fabia subquadrata Dana, 1851	grooved mussel crab	7
Pinnixa faba (Dana, 1851)	mantle pea crab	7
Pinnixa littoralis Holmes, 1894	gaper pea crab	7
Pinnixa occidentalis Rathbun, 1893	western pea crab[b]	7
Pinnixa schmitti Rathbun, 1918	Schmitt pea crab	7
Pinnixa tubicola Holmes, 1894	tube-dwelling pea crab[b]	7
Porcellanidae		
Pachycheles rudis Stimpson, 1859	thickclaw porcelain crab	4
Petrolisthes eriomerus Stimpson, 1871	flattop crab	7
Xanthidae		
Lophopanopeus bellus (Stimpson, 1860)	blackclaw crestleg crab	7

[a]Tentative identification.

[b]Species lacking AFS common name; common name listed here was used by the source cited.

[c]Name commonly used by staff at the NMFS Kodiak Fisheries Research Center laboratory.

[d]Widehand is correct; name in ref. 1 is likely a typographic error.

[1], except for species lacking common names (denoted with [b]), where a name was created by the source cited. Many of the common names, especially for hermit crabs, were codified by Kessler [5] and subsequently accepted by the AFS. Names commonly used by staff at the NMFS Kodiak Fisheries Research Center laboratory are denoted by [c].

I encourage others to examine, revise, and add species to this list as they are identified, and I thank all those who have done so already.

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Setal Stage Duration of Female Adult Dungeness Crab (*Cancer magister*)

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Extended Abstract

The Dungeness crab, *Cancer magister*, supports a significant commercial fishery between northern California and southeastern Alaska. Dynamics of female *C. magister* molting patterns and their relation to growth and reproduction have been the subject of several studies (Wild 1980; Mohr and Hankin 1989; Hankin et al. 1989, 1997). The universal staging methods of Drach (1939) and Drach and Tchernigovtzeff (1967) have not, however, previously been applied to adult *C. magister*. Hatfield (1983) described various stages of the molt cycle of *C. magister* larvae (megalopae), but her description of setal stages and stage durations does not apply to juveniles or adults.

Adult female *C. magister* have a distinct annual molting period with most activity occurring from February through May in northern California (Hankin et al. 1989). For crustaceans with distinct annual molting periods, setal molt staging can, in principle, be used to predict molting destiny of individual crabs prior to the annual molting season. Setal stages can only be used for this purpose; however, if it is determined that beyond a specific molt stage molting is an "inevitable event" (e.g., a threshold stage after which the crab must later molt). To be a reliable indicator of molting destiny, the expected number of days from entrance of this specific stage until molting must exceed the duration of the annual molting period (Mohr and Hankin 1989). If a sample were collected immediately prior to the annual molting season, then crabs staged at such a point or beyond would be predicted to molt whereas other animals would not.

Aiken (1973) used pleopods on the American lobster, *Homarus americanus*, to describe premolt development and determined that molt preparation could become arrested during setal stage D-0, with stage D-1′ being the earliest stage at which molting appeared "inevitable." O'Halloran and O'Dor (1988), using maxilliped exopodites in the snow crab, *Chionoecetes opilio*, also found that D-1′ was the earliest stage at which molting appeared inevitable. In this study, we used Drach and Tchernigovtzeff's (1967) staging method to describe progression of premolt development, estimated the error in stage assignments, and estimated duration of individual molt stages.

Using the general scheme of Drach and Tchernigovtzeff (1967), we were able to identify intermolt stages (A1-C4) and premolt stages (D-0, D-1′, D-1″, D-1‴, and > D-2) of adult female *C. magister* based on setal development of branchial epipods (Table 1). One notable difference between our observations and those of Drach and Tchernigovtzeff (1967) is the absence of a "cone" in the setal lumen during the late C4 stage. The cone was only apparent in C. magister at stage D-0, when retraction of the epidermis revealed a cone partially within the bulbous base of the seta (Fig. 1).

We assessed the reliability of molt stage assignments by making three independent assignments of molt stage for a sample of 69 appendages. For each appendage, the "average" molt stage assigned was the most frequently assigned molt stage (i.e., 3 out of 3, or 2 out of 3 independent stagings) or the intermediate stage if an appendage received 3 different stage assignments. For the *k*th molt stage an index of the error in assignment of that stage, I_k, was calculated using a modification of Beamish and Fournier's (1981) formula for estimation of error in aging fish:

$$I_k = \frac{1}{N_k} \sum_{j=1}^{N_k} \left(\frac{1}{R} \sum_{i=1}^{R} X_{ij} \right)$$

where N_k is the number of appendages given average stage k, R is the number of times each appendage was staged, and X_{ij} is the ith stage assignment of the jth appendage:

(1) $X_{ij} = 0$ if stage X_{ij} is the same as the "average" stage (= k) of the jth appendage; or

(2) $X_{ij} = 1$ if stage X_{ij} is different than the "average" stage of the jth appendage.

(Molt stage assignments were never more than one substage away from the average stage, k, over the three independent stagings.)

If all N_k appendages were each given three different assignments in three sessions, then I_k would take on a maximum value of 1. If, instead, all N_k appendages were given identical assignments in all sessions, then I_k would take on its minimum value of 0. These indexes of errors in molt

Table 1. General crustacean molt stage descriptions following Drach and Tchernigovtzeff (1967) and molt stages defined for female *Cancer magister*. Descriptions indicate the earliest characteristics observed for individual molt stages.

Drach and Tchernigovtzeff (1967)		This study	
Stages	Description	Stages	Description
A1-C4	No subcuticular development[a]	A1-C4	Same as D & T[c]
D-0	Start of premolt, indicated by separation of epidermis from cuticle	D-0	Same as D & T
D-1′	Setogenesis begins with an invagination forming under the old setae	D-1′	Same as D & T
D-1″	Invagination of setae at maximum depth	D-1″	Same as D & T
D-1‴	Cuticle formation within the setae. Barbules on setae present	D-1‴	Same as D & T
D-2	Cuticle formation between developing setae, with some secretion of procuticle	≥ D-2	Cuticle formation between developing setae
D-3[b]	Ecdysial suture cracks under finger pressure		
D-4[b]	Ecdysial suture has split open		

[a]Stages of development from A1-C4 are classified by other means.
[b]Stages cannot be classified using the branchial epipod.
[c]Drach and Tchernigovtzeff (1967).

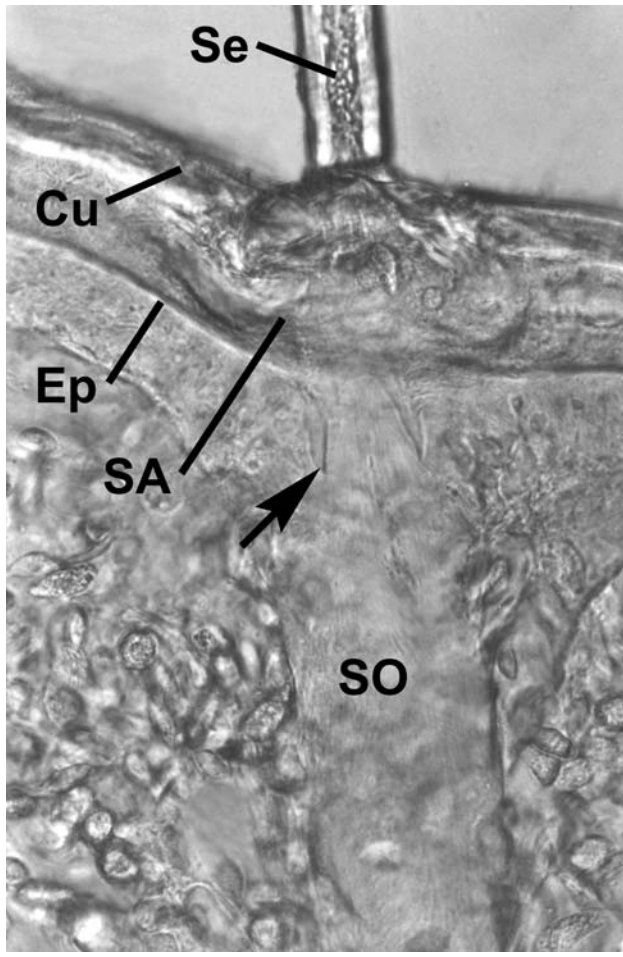

Figure 1. Photograph (40×) of the branchial epipod (gill cleaner) anterior margin displaying molt stage D-0, characterized by the following: separation of the new epidermis (Ep) from the cuticle (Cu); setal organ (SO) well developed; and base of the cone (arrow) pulling away from the setal articulation (SA). Tip of cone is well within the bulbous base of the seta.

Table 2. Analysis of variance of fitted days to molt model for female *Cancer magister* held at the Humboldt State University Marine Laboratory, Trinidad, California.

Variables	d.f.	Total sum of squares	Mean square	*F*-value	*P*-value
Molt stage	4	40,939.34	1,0234.83	43.01	<0.0001
Date staged	1	1,299.06	1,299.06	5.46	0.02
Carapace width	1	1,928.89	1,928.89	8.11	0.006
Residuals	76	17,846.00	237.95		

stage assignments could not be calculated for stages D-1‴ and ≥ D-2 due to inaccessibility of crabs with those stages at the time of the experiment. Calculated errors in assignment of stages were 0.13, 0.18, and 0.19 for stages A1-C4, D-0, and D-1‴ respectively, but 0.06 for stage D-1″. To our knowledge this is the first time that reliability in assignments of molt stages has been calculated.

In laboratory experiments we determimed the molt stage of 102 crabs prior to and during the annual molting season and then held these crabs until they molted, thus generating "days to molt" data for crabs with a known initial premolt stage. Multiple regression (MR) was used to determine the possible influence of molt stage, date the crab was staged, carapace width, holding temperatures (~10-12ºC or 14-16ºC), or any interactions between these variables on days to molt. Our results indicated that molt stage, carapace width, and date staged were significant, while temperature and all interactions were nonsignificant (Table 2). When the order of entry of carapace width and date staged in the MR were switched, date staged remained significant (P <0.001) while carapace width was nonsignificant (P = 0.72). This aspect of the MR results was due to the high correlation between carapace width and date staged (P = 0.68); smaller sized crabs (carapace width) tend to molt earlier during the molting season than larger sized crabs (Hankin et al. 1997). It may be that the duration of individual premolt stages and of the complete premolt process is slightly less for smaller crabs.

Using the method described by Hankin (2002), we estimated the mean duration of individual premolt stages from laboratory "days to molt" data. Estimated durations of premolt stages were 9.5 days (D-0), 48.6 days (D-1′), –0.75 days (D-1″), 16.5 days (D-1‴), and 19.7 days (≥ D-2), for a total estimated expected duration from the beginning of premolt stage D-1′ until molting of 84 days. The unrealistic estimate of –0.75 days for stage D-1″ may possibly be explained by its descriptive characteristic of "maximum invagination of the setae." This is only a single point-in-time characteristic

that would take a relatively short time to progress to the next stage. We therefore propose that stage D-1″ is not a legitimate stage and should be considered only as an endpoint of stage D-1′ leading into stage D-1‴.

Although experimental data thus showed that molting destiny of individual crabs could be predicted up to 84 days in advance of actual molting, the typical duration of the molting season for female Dungeness crabs in northern California is approximately 120 days, substantially longer than the "notification time" achieved via molt staging. Molt stage description and estimation of durations may still, however, have a utility in further understanding physiological processes involved in molting.

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Estimating Intermolt Duration in Giant Crabs (*Pseudocarcinus gigas*)

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Abstract

Estimates of intermolt duration of giant crabs, based on tag-recapture methodology, are used in evaluating management options. However, several shortcomings of tag-recovery data have been noted, including the low number of tags inserted in legal-sized animals and the long periods of time-at-large which require an unusually long intermolt duration. This led to the evaluation of alternative methods to estimate intermolt duration. Reproduction in female giant crabs occurs in annual cycles, although females occasionally "skip" a reproductive season and do not become ovigerous; it has been noted previously that this appears to be associated with molting. Thus the proportion of females that do not participate in reproduction may indicate the proportion molting. We tried this approach with a sample of 342 females and measured the number that were "skipping" a reproductive season by computerized tomography scanning (CT-scanning) of their ovaries prior to the extrusion of eggs. From the inferred proportion molting, intermolt duration was estimated at 9 years for mature size classes; however, 95% confidence limits were broad (6.8-13.1 years). This estimate does, however, corroborate those previously reported from studies in which tag and recapture methods were employed. Radiometric aging (^{228}Th/ ^{228}Ra) of carapaces was also undertaken with the focus of this work on testing an assumption of the method, rather than describing the intermolt duration of a population. We tested the assumption that there is negligible exchange of radionuclides during intermolt in the exoskeleton, which is critical for reliable estimation of intermolt. SEM images of the internal structure of the exoskeleton indicated that exchange of material within the exoskeleton was unlikely and the majority of radiometric assays were consistent with this observation. Radiometric age was estimated

by gamma spectroscopy, which allowed rapid analysis compared to previously reported methodology. This rapid processing may facilitate broader application of radiometric aging to crustacean research.

Introduction

Giant crabs (*Pseudocarcinus gigas*) are fished across southern Australia in a small fishery based on high value live product. The fishery developed only within the last decade, with negligible catch prior to 1991 (Gardner 1998a). As a result, management is rudimentary in comparison to more established fisheries in the region, notably that for the southern rock lobster (*Jasus edwardsii*). Although considerable research has been expended on giant crabs, more information is required on their biology, including growth. Growth influences most basic fisheries analyses, such as yield- and egg-per-recruit analyses, and is thus a high priority area for research.

General observations on molting of giant crabs were reported by Levings et al. (1996). They reported that males molt more frequently than females, molting occurs in cycles longer than 1 year, and females produce broods over a range of instars (that is, there is no terminal molt to maturity).

Growth in crustaceans is a function of both the increase in size at molt (molt increment) and the frequency of molting (intermolt duration). Molt increment in giant crabs has been estimated using data collected through field based tag-recapture work with methods discussed by Levings et al. (1996). McGarvey et al. (1999; and R. McGarvey, South Australian Research and Development Institute, West Beach, Adelaide, South Australia, pers. comm.) modeled molt increment from the 350 recaptures in this data set that had molted at least once and quantified significant differences in spatial patterns among both sexes in four states. They noted that estimates of intermolt duration from tag recoveries require larger sample sizes than for quantifying the distribution of molt increments. This is because of the uncertainty around the time prior to the last molt for each crab tagged or recaptured.

Estimates of mean female intermolt by R. McGarvey et al. (pers. comm.) ranged from 4.5 years for immature females of 120 mm carapace length (CL) to 15 years for mature females of 180 mm CL. These estimates were based on a discrete normal likelihood estimator, mean intermolt period modeled as a quadratic polynomial of premolt length. The analysis pooled all recaptures over a 5-year period from across southern Australia, as there were insufficient data to differentiate regional trends. This analysis of tag-recapture data for intermolt duration by McGarvey et al. (1999) has been used in assessing management of the Australian giant crab fishery, notably showing that the current legal minimum length for females is conservative, protecting about 50% of virgin population egg production. However, several shortcomings of tag recovery data from commercial fisheries in giant crabs are noted. For instance, although most of the Australian catch is taken in Tasmania, only 14 recaptures that had molted were

recorded from this state, with only 2 of these from males. Limitations of tagging for estimating intermolt duration of giant crabs are threefold: (1) Because giant crabs are high value and numbers captured are low, tags inserted in the course of commercial fishing operations have been placed almost solely in giant crabs that are protected and must therefore be legally returned to the sea. These are crabs below the legal minimum length of 150 mm CL, and ovigerous females. Tags have thus rarely been placed in legal size animals. (2) The unusually long intermolt duration of giant crabs requires corresponding long times-at-large. (3) Uncertainty remains, as with all tag-recovery intermolt period estimators, about the time back to the most recent molt prior to first capture.

We assessed three alternative methods for study of growth in giant crabs: (1) inferring the proportion of the population molting based on the proportion of females participating in reproduction; (2) radiometric aging of the exoskeleton; and (3) lipofuscin aging. Although lipofuscin aging is a relatively new technique, it has been studied intensively and methods are described in detail elsewhere (Sheehy 1992, Wahle et al. 1996, Sheehy et al. 1998). Consequently, in this paper we focus on the first two methods, which have been applied less widely.

Reproductive State of Females

Female giant crabs produce clutches of eggs in annual cycles with females extruding eggs in late autumn that hatch in spring, although not all females participate in egg production each year (Levings et al. 1996, Gardner 1997). "Skipping" of reproduction by females may occur in years before or after molting, based on observations in tank trials and also through comparing fouling state of shells with ovigerous state of females (Gardner 1998b, McGarvey et al. 1999). This relationship between molting and skipping of reproduction implies that a measure of intermolt duration could be obtained from the proportion of females skipping reproduction in any 1 year. For instance, if half the population were found to skip reproduction in any 1 year, it would suggest that molting occurred every 2 years.

Radiometric Aging

Research on the radiometric aging of calcified biological structures has been undertaken sporadically for several decades with several studies focused on crustaceans (Bennett and Turekian 1984, Le Foll et al. 1989, Nevissi et al. 1996). The application of radiometric aging to crustaceans is based on the incorporation of radium (^{228}Ra) with calcium into the exoskeleton after molting; this radium thereafter decays to thorium (^{228}Th). Several methods to measure nuclear decay in biological samples have been described including alpha-spectroscopy, thermal ionization mass spectrometry, and gamma-spectroscopy (Bennett and Turekian 1984, Reyss et al. 1995, Andrews et al. 1999). Various methods differ in the accuracy of their age estimation and also in time and expense required to process samples;

however, the fundamental principle for the estimation of age through nuclear decay sequences remains consistent. An aspect of radiometric aging that has caused greater concern among many biologists is the validity of assumptions made in radiometric age determination. These were outlined by Nevissi et al. (1996) as: "(1) during molting virtually all the calcium and associated nuclides are lost by the animal; (2) the carapace is calcified rapidly after molting, so that (3) addition or removal of radionuclides during the intermolt period is negligible."

Similar assumptions to those outlined by Nevissi et al. (1996) exist with all applications of radiometric aging for biological samples, yet they are seldom tested. Fenton et al. (1990) showed that an assumption of constant accumulation of ^{226}Ra into otoliths of a finfish, the blue grenadier (*Macruronus novaezelandiae*), was violated and thus radiometric aging could not be applied. Le Foll et al. (1989) used radiometric techniques to estimate the age of crustacean exoskeletons of known age, which provided a test of the extent of any addition or removal of radionuclides during the intermolt. Although they found reasonable agreement, some discrepancies were noted at extremes. We also examined the assumption of negligible addition or removal of radionuclides during the intermolt period in giant crabs by comparing age estimates for inner, middle, and outer layers of the carapace.

Methods

Proportion of Females Reproducing

A total of 342 female giant crabs were collected in April 1998 by a commercial fisher from areas adjacent to Bicheno off Tasmania's east coast. Sizes were from 92 to 208 mm CL, with the majority of animals ($N = 327$) larger than the size at 50% onset of maturity for this region, approximately 135 mm CL (Levings et al. 2001). This sample was collected prior to females extruding their eggs, which typically occurs in May (Gardner 1997). Fishers confirmed that no ovigerous females had been observed along the coast during the month of April. Samples were collected prior to oviposition to avoid bias in the ratio of reproductively active to inactive females, as ovigerous females have reduced catchability (Gardner 1998a).

The proportion of females in this sample that were reproductively active in the current year was assessed by the extent of ovarian development. Ovaries and spermathecae were viewed nondestructively using a GM™ computerized tomography scanner (CT-scanner; Gardner et al. 1998). Forty specimens were individually tagged and retained in tanks for a further 2 months until after oviposition to validate the ovarian classifications from the CT-scans. Ten animals were held in each 4 m^3 tank, which were equipped with flow-through seawater supply and a sand substrate, approximately 150 mm deep, to assist in oviposition.

The proportion of females without developing ovaries was used as an indicator of the proportion molting by calculating the ratio of females without

developing ovaries relative to those with developing ovaries. Confidence limits of this estimate were obtained by bootstrapping using 10,000 simulations.

Test of Assumptions of Radiometric Aging

Six male giant crabs were captured from areas adjacent to Bicheno off Tasmania's east coast by a commercial fisher. Each specimen had shell with heavy wear (carapace-condition 3 in Gardner [1997]) and ranged between 199 and 223 mm CL. Large males were selected for this component due to their thick carapaces, which facilitated separation of the shell into different layers and the collection of large amounts of material. Radiometric analyses were by gamma spectroscopy, which is more rapid with larger samples.

The potential for addition or removal of radionuclides during the intermolt period was initially investigated by viewing the internal structure of the exoskeleton. Scanning electron microscopy (SEM) images were acquired in environmental mode with an ElectroScan™ ESEM2020 using water vapor as the imaging gas. The specimen chamber pressure was maintained at 5.0 torr.

Testing of the extent of exchange of radionuclides during the intermolt period by radiometric analysis was based on the hypothesis that material exchange would not occur uniformly through the exoskeleton. If exchange of radionuclides occurred between the exoskeleton and internal tissues, then we would expect younger age estimates from inner layers. Likewise, if exchange occurred with the environment, then age estimates from outer layers would be younger than those from the middle or inner layers.

Radiometric analysis was by gamma spectroscopy which avoided the chemical ingrowth stages described by Nevissi et al. (1996), although the principle of estimation through the analysis of the $^{228}Th/^{228}Ra$ ratio remained the same. Samples of the exoskeleton were prepared for analysis by grinding with hand-held grinder (Dremmel™) using a rotating tungsten steel bit. This was intended to separate material into coarse inner, middle, and outer layers of the exoskeleton, rather than anatomical layers of the integument. Samples were ground further in a standard ring mill prior to radiometric analyses, then weighed accurately into 55 ml Petri dishes to completely fill the dish. Due to the absence of any prolonged gaseous stage in the decomposition chain, processing did not involve any steps of prolonged sealing. Samples were measured on a high-resolution Compton suppression gamma-ray spectrometer (Canberra Industries, Meriden, USA). The spectrometer consisted of an n-type high-purity germanium (HPGe) coaxial detector with relative efficiency of 50% surrounded by a sodium iodide (NaI) annular guard detector and removable NaI "plug" detector. The detector assembly was housed in a graded lead shield. Data analysis was performed using GENIE2000 software developed by Canberra Industries (Meriden, USA).

The activity of ^{228}Ra was determined by measuring its daughter ^{228}Ac at 911 keV and the activity of ^{228}Th was determined by its progeny ^{212}Pb at

238 keV (Reyss et al. 1995). The age of the specimen was then determined according to the following equation:

Age of carapace at death = (*Isotopic Age*) – (*time between death and measurement*)
where:

$$Isotopic\ Age = -4.12 \times \mathrm{Ln}\left[1 - 0.669 \times \frac{(Activity\ of\ ^{228}Th)}{(Activity\ of\ ^{228}Ra)}\right]$$

Isotopic Age is in years.

Results

Proportion of Females Reproducing

Retention of a subsample of 40 individually tagged female crabs in tanks after CT-scanning confirmed that the 35 females classed as possessing developing ovaries went on to extrude eggs, while the remaining 5 females with ovaries classed as undeveloped did not extrude eggs. This step validated the use of CT-scanning of ovaries for estimating the proportion of the sample that would reproduce in the current year.

Only two females did not appear to have mated, based on the appearance of the spermathecae; each of these were relatively small (92 and 142 mm CL). The proportion of females that were reproducing in the current year was lowest in smaller size categories, although stabilized in size classes greater than 140 mm CL (Fig. 1). The mean proportion of females that were not reproducing for all size classes greater than 140 mm CL pooled was 11%, which equates to approximately 1 in 9 ($N = 327$). Assuming the apparent link between molting and skipping reproduction holds true, this implies an intermolt period of 9 years for female giant crabs greater than 140 mm CL.

Estimates obtained by this indirect method of estimating intermolt duration appear affected by the constraining upper limit of 100% maturity of females. That is, random error around the estimate of the proportion reproducing appears to have a large influence on the estimate of intermolt duration. This is shown by the bootstrapped estimates of inferred intermolt duration which have a broad range (Fig. 2; lower 95% confidence limit = 6.81 years, upper = 13.08 years).

Test of Assumptions of Radiometric Aging

The validity of the assumption of no addition or removal of radionuclides during intermolt was initially assessed by viewing samples of the carapace in cross section using SEM. General structure of the exoskeleton was similar to that described by Stevenson (1985) with the epicuticle, pre-ecdysal procuticle, and principal layer of the procuticle calcified and formed of laminae parallel with the surface (Fig. 3A). Fine canals of around 2 μm in diameter run perpendicular to the surface and appeared to be associated

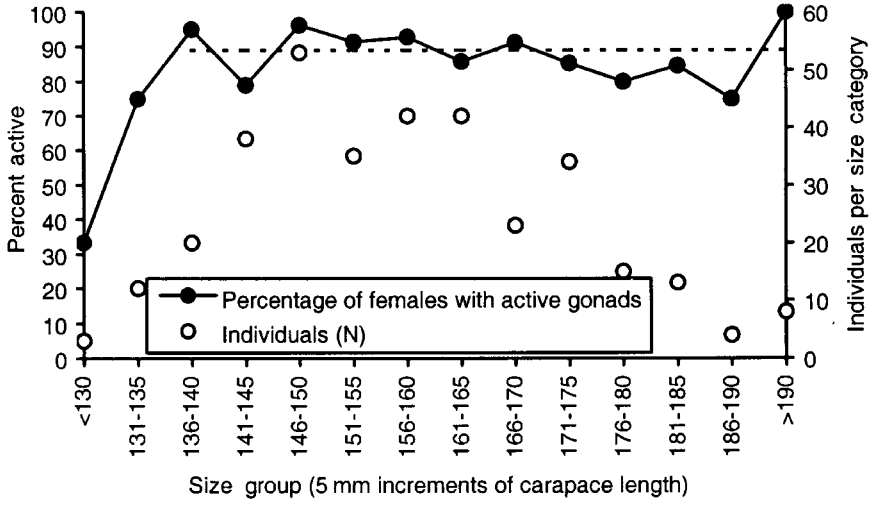

Figure 1. The proportion of females with ovaries classed as active in relation to carapace length. Classification of ovaries as active or inactive was based on CT-scans. Mean proportion of females greater than 140 mm CL participating in reproduction in the year of sampling was 89% (dashed line).

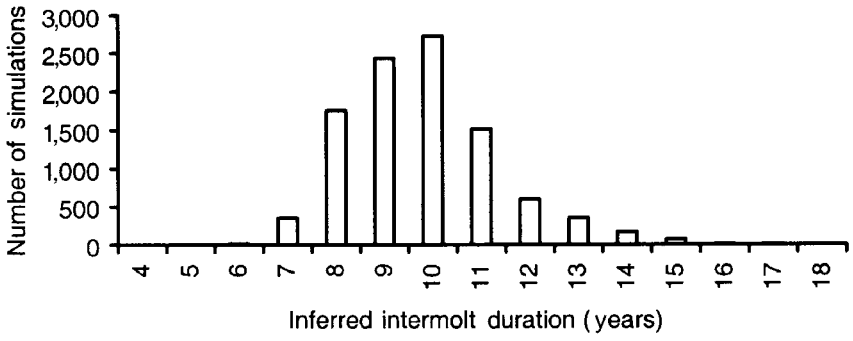

Figure 2. Bootstrapped simulations of the inferred intermolt duration based on the proportion of females without developing ovaries.

with tegumental glands (Fig. 3B). No structures that suggest that material is exchanged within the carapace were present, such as the canaliculi involved in cycling of mammalian bone (Junqueira and Carneiro 1983).

Radiometric results presented here are preliminary as they are based on only 18 analyses (3 layers for each of 6 crabs; Fig. 4) and further analyses are in progress. Estimates for these individuals ranged between 2 and 5 years. Although the sample size is small, there appears to be no significant difference in age estimates between layers in most specimens. This suggests that there was no material exchanged within the carapace during intermolt. In contrast, different age estimates between layers were observed in two specimens (numbers 1 and 4). There was no systematic pattern between these sets of analyses; in one case the oldest estimate was from the outer layer, while the youngest estimate was from the outer layer in the other.

Discussion

The methods assessed here may contribute to our understanding of intermolt duration based on tag-recapture data. Measurement of the proportion of females reproducing produced intermolt duration estimates of around 9 years, although confidence limits were broad (ranging from 6.8 to 13.1 years). This estimate of intermolt duration corroborates that obtained from tagging data (McGarvey et al. 1999) and provides support for the conclusion of an exceptionally long intermolt duration in female giant crabs. The robust carapace of giant crabs, which can exceed 4 mm in thickness, also testifies to a protracted intermolt period.

The use of the proportion of females participating in reproduction to estimate intermolt could only be applied to species meeting a specialized set of criteria. These criteria include a well-defined reproductive season and the linking of molting to the reproductive cycle so that the two events are mutually exclusive. Estimates will have greater precision where the proportion of animals that are participating in reproduction does not approach the 0% or 100% bounds. This implies greatest precision where molting occurs every 2 or 3 years (closer to 50% of animals molting each year), rather than the more protracted intermolt of giant crabs which led to broader confidence limits around estimates.

Radiometric estimates of male intermolt period also corroborate data obtained through tagging. Our estimates from individual analyses of crabs, which all had worn carapaces, ranged between 2 and 5 years while McGarvey et al. (1999) estimated intermolt from tagging data to be around 4 years.

We attempted to evaluate the potential for error in these estimates of radiometric age caused by exchange of material during intermolt. The microscopic structure of the exoskeleton would suggest that regular turnover of material within the exoskeleton is unlikely, which is consistent with the process of endocuticle synthesis described by Stevenson (1985) and Skinner et al. (1992). Radiometric analyses also indicated that exchange

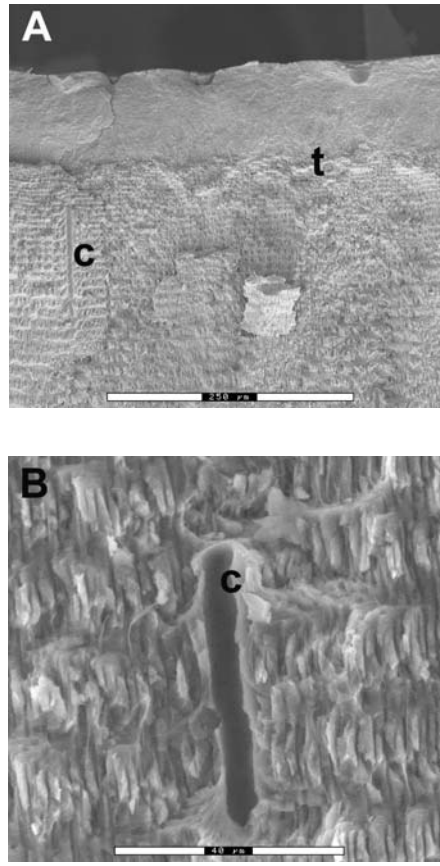

Figure 3. SEM images of the carapace of a male giant crab. Image (A) shows the transition (t) between the pre-ecdysal procuticle and the principal layer (image taken at 200×, black and white scale bar = 250 μm). Note the laminate structure with fine tegumental gland canals (c) running perpendicular to the surface. A canal (c) is shown in greater detail in image (B) (taken at 1,200×, scale bar = 40 μm).

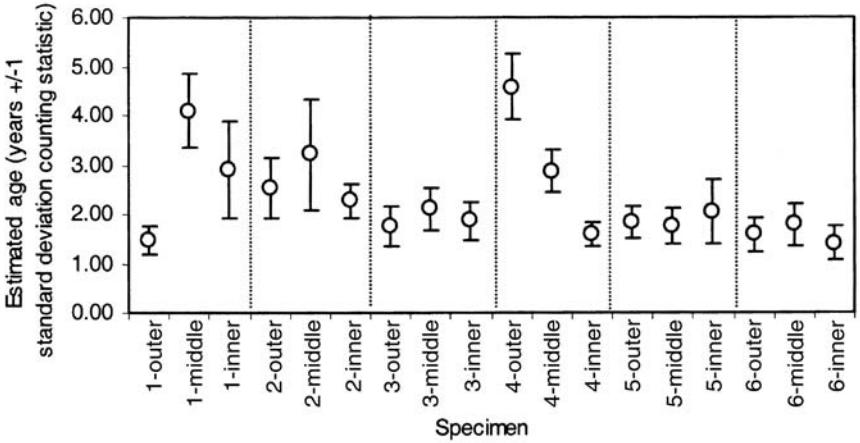

Figure 4. Radiometric estimates of shell age for inner, middle, and outer layers of the carapace of male giant crabs.

of material during intermolt does not generally occur, although results were not conclusive given that two specimens had significantly different age estimates from different layers. The lack of any consistent pattern between these two specimens indicates that the cause of the differing age estimates is more likely due to contamination of samples, rather than a biological effect. Further analyses are under way to increase the number of samples with the aim of resolving this issue.

Radiometric aging studies are often constrained by the prolonged processing times required for chemical ingrowth and measurement with total processing time in excess of one year. Consequently, the total number of analyses undertaken is generally small; Nevissi et al. (1996) reported results from five analyses, Le Foll et al. (1989) reported results from nine analyses, and Bennett and Turekian (1984) reported results from four analyses. The gamma-spectroscopic method applied here was more direct with specimen processing limited to grinding and weighing, and measurement of the $^{228}Th/^{228}Ra$ ratio determined in as little as a single day. Although this method requires specialized equipment, it offers the potential for broader application to crustacean research.

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Molting of Red King Crab (*Paralithodes camtschaticus*) Observed by Time-Lapse Video in the Laboratory

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Abstract

Molting of six red king crabs was observed and recorded on time-lapse video in January 2000. Three molted during daytime, and three at night under dark red light. A suite of 16 behaviors were exhibited during the 6 hours prior to and one hour after molting, including two behaviors not previously observed: body shaking and leg pumping. During leg pumping, the crab alternately contracted and extended the legs causing the new exoskeleton to bend and fold, thus shortening the legs to enable their extraction from the old exoskeleton. Average time required for ecdysis, from splitting the carapace to complete extrication, was 0.34 hour (20 minutes, 17 seconds).

Introduction

Among all animals, the growth process of the Arthropoda is unique because of the requirement for ecdysis, or molting of the exoskeleton. In crustaceans, this process has been fairly well studied from a metabolic and physiological point of view, as reviewed by Skinner (1985). The stages of ecdysis were initially defined by Drach (1939) based on exoskeleton hardness, then later redefined by Skinner (1962) on the basis of subcuticular cellular processes. The longest stage is the intermolt, or anecdysial period (stage C_4). During this period, molt inhibiting hormone (MIH) is secreted by the X-organ/sinus gland complex of the eyestalk, preventing ecdysis (Skinner 1985). Cessation of MIH release, usually in response to environmental stimuli, allows production and release of molting hormone (MH, or α-ecdysone) from the Y-organ, stimulating ecdysis. Molting begins with proecdysis,

during which ecdysone is released, and somatic muscles atrophy (D_0), the old exoskeleton is reabsorbed (D_1), epidermal cells enlarge and secrete a new cuticle (D_2-D_3), and astaxanthin is resorbed from the cuticle into the blood (D_4). Ecdysis (stage E) occurs when the carapace splits at the epimeral line, and the animal withdraws from the old exoskeleton. During the following stages, termed metecdysis, the epidermal cells shrink (A), muscle is synthesized (B), endocuticle is formed (C_1-C_3), and the shell hardens.

The stages of ecdysis and early metecdysis are probably the most vulnerable periods in the life of a crustacean. During this brief interval, the muscles are weakened, the animal may be trapped halfway out of the old exoskeleton, it may be blinded, and the soft new cuticle provides little protection from predators. It is therefore surprising that few studies have been conducted on the behavioral aspects of molting. For the red king crab (*Paralithodes camtschaticus*) there is evidence that adults cease feeding up to 3 weeks prior to molting, and do not resume feeding until more than a week afterwards (Zhou et al. 1998). First- through fourth-stage juvenile red king crabs spend more time in sheltered habitats than on open sand during periods of molting (B.G. Stevens, unpubl. data). However, the physical act of molting has rarely been documented.

The commercial value and size of king crabs makes them particularly worthwhile subjects for studies of molting. Predation of crabs during molting is a common subject of speculation and hyperbole among commercial fishermen. Recently molted red king crabs are occasionally found in the stomachs of large predatory fish such as Pacific cod (*Gadus macrocephalus*) and Pacific halibut (*Hippoglossus stenolepis*), leading many fishermen to blame them for the demise of local crab populations. Over geologic time scales, crustaceans must have developed adaptive behaviors which lessen the likelihood of molt-associated mortality. This study was conducted in order to better understand the behavioral aspects of molting in red king crab. Specific questions of interest were: How long does it take? When does it occur? Are specialized behaviors involved? What problems can arise during molting? And not least of all, it seemed worthwhile to record the process on video for research and educational purposes.

Materials and Methods

Red king crabs were captured by scuba divers and brought to the laboratory, where they were measured and tagged with a numbered Peterson disk tag attached to a plastic cable-tie wrapped around the third right leg. Crabs were held in two 500 liter tanks, fed twice weekly with squid, and observed daily until they showed signs of molting. About 24 hours prior to molting the abdomen began to swell, from its normal thickness at the edge of about 1-2 mm, to a thickness of about 5-10 mm. The crab was then placed into a 200 liter tank (dimensions $0.5 \times 0.5 \times 0.65$ m) containing running filtered seawater and a gravel-covered bottom. A waterproof black and white video camera was suspended in the tank so that it viewed 90%

of the tank bottom. The tank was illuminated indirectly by a white fluorescent light from 0700 to 1700, and by dark red light from 1700 to 0700 (L:D ratio of 10:14). The camera signal was recorded on a time lapse VCR (Panasonic AG6550) running in continuous 24 hour mode (actual time compression ratio was 13:1). Crabs were checked periodically to determine when molting occurred. If the crab had not completed molting within 24 hours, the tape was rewound and restarted.

Recorded videotapes were converted to an MPEG type digital video file, and analyzed using "The Observer Video-Pro" software (Noldus Corporation, Netherlands). Individual behavior codes were assigned to keyboard characters, so that the computer recorded the behavior code, video frame number, and time (to the nearest 0.1 second) whenever a key was pressed. Independent variables recorded were species, sex, tag number, and date and time that the time-lapse recording was started. Behavioral observations were of two types: events and states. Events (Table 1) were short discrete behaviors for which only the start time was recorded. Some events had modifiers describing the event. States (Table 2) were longer-lasting but nonoverlapping behaviors, which lasted until the next behavioral state occurred. Events could occur within states. Descriptions of the events, states, and modifiers are listed in Tables 1 and 2.

Most crabs were in the observation tank for more than a day before molting, although some molted within a few hours. For this reason, the length of observation varied for each crab. In order to standardize as much as possible, only the last 6 hours of the time-lapse video prior to molting was analyzed for most crabs. This period is about equivalent to the duration of molt stage D_4.

Results

Videotaped observations were made for six crabs in January of 2000. Two crabs were females, and four were males; sizes ranged from 82 to 102 mm carapace length (CL; Table 3). Although "Leg out," "Abdomen," and "Molt" with their associated modifiers were used to describe specific stages of the molting process, they are not behaviors per se. Shove, Tilt, Rest, Rock, Push, Walk, Move legs, Rotate, and Stand/sit are normal behaviors that are used in other contexts besides molting; they were probably associated with finding a "comfortable" place and position in which to begin molting and may not be part of the molting process itself. Pump body and Pump legs were behaviors that were strictly associated with the act of ecdysis and did not occur in any other context. Shaking, although it began up to 6 hours prior to molting, is not a behavior exhibited by crabs at any other time, and was never observed prior to this study.

Figures 1A and 1B illustrate the behaviors of two crabs from 5 hours before molting to about 1 hour after. These two were selected because of their similarity in general behavior pattern, length of observation time, and similarity to mean data (see Fig. 2). The following is a general description

Table 1. Behavioral events observed during red king crab molting observations.

Events	Description	Modifiers	Modifier description
Leg out	Crab extracts tip of dactyl completely from old shell.	Right, left	
Abdomen	Abdominal portion of exoskeleton detaches from body.		
Tilt	Crab tilts anterior carapace while sitting or standing.	Up, down	
Shove	Crab shoves body forward abruptly.	Forward, backward	
Molt	Specific events in the molting sequence.	Split	Back of carapace splits at epimeral line.
		Halfway	Crab has backed out so that the two largest spines in the center of the carapace are revealed.
		All out	Tip of rostrum has been removed from the old shell.
		Finish	Last part of crab, usually a leg, sometimes the abdomen, has separated from the old shell.

Table 2. Behavioral states recorded during red king crab molting observations.

State	Description
Rest	Crab resting quietly with no movement except antennules.
Shake	Crab shakes body rapidly, like shivering.
Rock	Crab rocks body back and forth.
Push	Crab pushes against side of tank, usually forward.
Move legs	Crab extends and retracts legs, without moving body.
Walk	Crab walks around tank.
Rotate	Crab rotates around body axis.
Pump body	Crab contracts and expands body in effort to dislodge old carapace.
Pump legs	Crab contracts and extends legs while extracting from old shell.
Stand/sit	Crab lowers body to tank floor, or rises up on legs.
View	Crab out of camera range, obscuring view.

Table 3. Statistics of observation data on molting red king crabs: sex and size of crabs, date and time of molting, and duration of molting and observations.

Crab number	Sex	CL (mm)	Molt date	Time start observation	Time finished molting	Molt duration	Observed duration
3187	F	90.4	1/21/00	08:59:08	15:11:01	00:16:57	06:30:40
7071	F	84.0	1/13/00	16:18:30	03:04:46	00:26:33	11:41:29
7075	M	101.6	1/12/00	12:31:05	13:31:11	00:11:12	01:30:27
7078	M	86.2	1/16/00	15:52:15	21:20:42	00:32:18	07:03:19
7121	M	86.0	1/19/00	10:34:47	15:35:49	00:14:23	07:12:15
7123	M	82.0	1/11/00	14:19:53	20:00:41	02:21:30	05:45:19
Mean		89.6			18:47:22	00:20:17[a]	06:37:15

[a]Excluding crab 7123.

Times are expressed as hh:mm:ss.

of behaviors, based on these six observations. Up to 4 hours prior to molting, the crabs spend much of their time walking, turning, and resting in the observation tank, as if trying to find a suitable place in which to begin molting. Between 4 and 2 hours prior to molting, walking becomes less frequent, and the crab begins occasionally shaking and moving its legs around between bouts of resting. From 1 to 2 hours before molting, shaking and pushing become more frequent. In the last 30 minutes prior to molting, the crab becomes relatively quiescent, showing little movement. At this time, pumping of the body may begin. The observable act of ecdysis begins when the carapace splits. From then until molting is completed, the crab engages in vigorous pumping of body and legs. The legs are usually the last parts to be withdrawn, and they come out in close proximity to each other. The abdominal exoskeleton is usually the last part to detach completely from the new shell. After completion of molting, the crab rests on the bottom and moves its legs around.

The most unique behavior observed was that of leg pumping. During this process the leg and newly formed shell actually compress and fold. To withdraw the leg, the crab contracted its leg muscles, which caused the leg to fold and shorten up and pull out of the old exoskeleton about 1 cm per contraction. Then the leg was extended, lengthening it and pushing the crab out of and away from the old shell. On the merus, the largest leg segment, folding usually occurred about 2 cm proximal to the merus-carpus joint. Repeated contraction and lengthening act like a ratchet to remove the crab from the old exoskeleton. Leg pumping and folding were observed in all crabs. Such movement is only possible due to the softness of the new shell.

Among these six crabs, three molted in mid-afternoon during daylight (white light on), two in early evening, and one in early morning (Table 3);

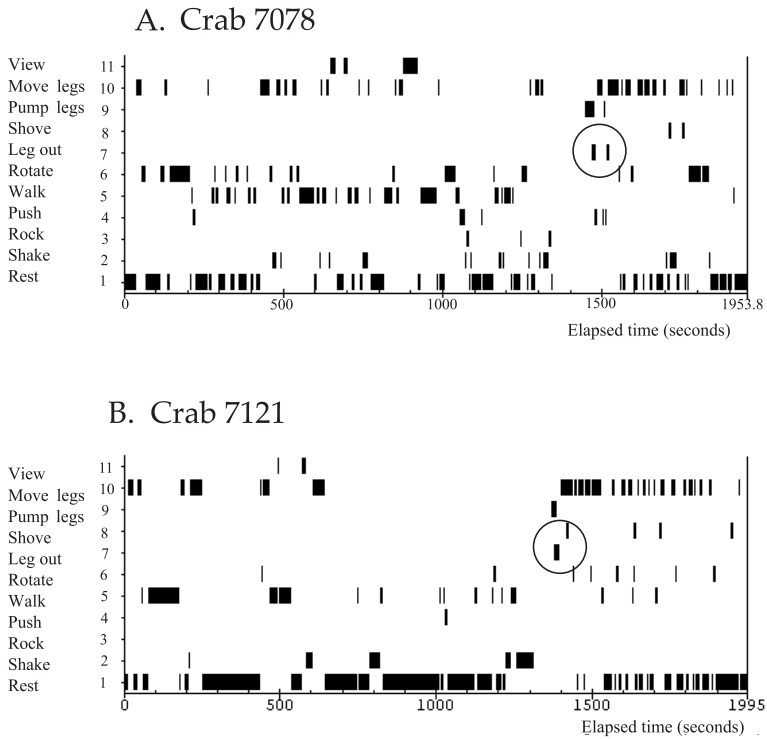

Figure 1. Behavior plots for molting in two red king crabs. Time spent in each behavioral state is shown as a continuous dark horizontal bar. Events are marked by brief vertical lines. Ecdysis is most closely associated with removal of legs from the carapace, noted as eight sequential events (circled).

the latter three molted in the subjective nighttime (i.e., with the red light on). The average time of day that molting occurred was 18:47. The amount of time they were observed averaged 6.62 hours, and ranged from 1.5 to 11.68 hours. The time required to finish molting, from splitting of the carapace to complete extrication, ranged from 0.18 hour (11 minutes) to almost 2.5 hours. Excluding the longest time, mean molting time was 0.34 hour (20 minutes, 17 seconds). Within the time frame observed, on average crabs spent 35% of the time resting; about 15% shaking; a total of 26% pumping the body, walking or moving legs; and the remainder of the time pushing, rotating, rocking, standing up/sitting down, or pumping legs (Fig. 2).

Two crabs had difficulty disengaging themselves from the old exoskeleton. Crab 7078, a male, required about 10 minutes more than average to remove the last leg (fourth right) from the shell. This crab was

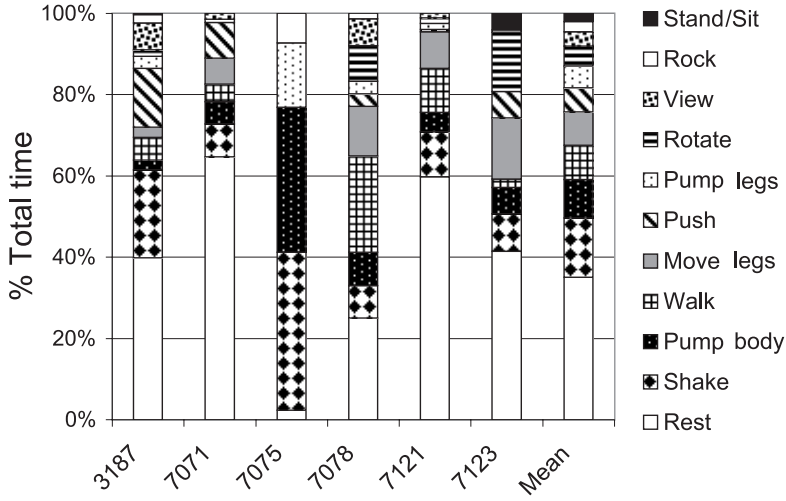

Figure 2. Proportion of time that crabs spent exhibiting different behaviors, for each individual crab observed, and averaged over all six crabs. Most common behavior was resting, followed by shaking. Pumping body, walking, and moving legs averaged 26% of the total time.

missing the second and third legs on that side and may not have been able to generate enough leverage to push itself away with only the right cheliped. However, this is such a small variation in overall behavior that it shows up only as a slightly delayed "leg out" in the behavior plot (Fig. 2). Crab 7123, another male, required over 2 hours to complete molting because the abdominal covering did not detach itself completely until that time, although the carapace and legs were all extricated.

Discussion

These observations indicate that red king crabs (and probably others) utilize a full suite of behaviors to assist them in the molting process. Among these are two behaviors not previously documented: shaking and leg pumping. Shaking is probably used by the crab to help free itself from attachment to the old exoskeleton. Leg pumping is apparently a mechanism for extracting itself from the old shell.

Matsuura and Takeshita (1976) observed molting by 5 laboratory-reared king crabs. They noted that abdominal swelling occurred at least 1 day before molting, and that complete molting required 3-10 minutes (mean = 5). In my study, molting took about twice as long (11-20 minutes) but this difference may depend on the definitions of starting and ending times, and the accuracy with which those times were recorded. Videotaped observations

are more accurate because the observer does not have to look away to record the time of an event, and the videotape can be reviewed for accuracy.

Molting of crustaceans is under hormonal control but may be entrained to synchronize with an external environmental cue. Molting of larval American lobsters (*Homarus americanus*) to the postlarval stage is synchronized with the light:dark cycle; it generally occurs within 10 hours after the onset of darkness whether in a natural or reversed daylight cycle, regardless of scotophase length (Waddy and Aiken 1999). Molting becomes asynchronous within 3 days after exposure to constant light or darkness, and can be reinstated stepwise over 4 days. Molt timing of American lobsters is also dependent on temperature; molting occurs earlier in the season when water temperatures are warmer (Tremblay and Eagles 1997). Molting in the shore crab (*Carcinus maenas*) is circatidal; adult females collected from mating pairs during low tide molted at the expected time of high tides in the laboratory (Abello et al. 1997), and wild-caught glaucothoe molted to the first crab stage at times of expected high tide (Zeng et al. 1997).

In this study, half (3 of 6) of the crabs molted during daytime, and half in the subjective nighttime. This sample size is not large enough to make a general statement about the time of molting. Although crabs were exposed to a L:D cycle of about 10:14 (from artificial lighting in the laboratory, longer than available daylight in January) prior to observation, whether they retain their entrained natural rhythm after several months in the laboratory is unknown.

In the confined environment of a laboratory tank, molting crabs usually move away from others, but are often cannibalized soon after molting (personal observation). If loss of legs increases the time required to extricate itself from the old shell, such crabs may be more vulnerable to cannibalism or predation during this extended period of vulnerability. In the case of crab 7078, its vulnerable period (30 minutes) was 50% longer than average (20 minutes). Leg loss is a common effect of the sorting and discard process in commercial fisheries (Stevens 1990, MacIntosh et al. 1996); thus, one previously unrecognized effect of handling-induced leg loss is potentially increased vulnerability to predation during subsequent molts.

Reference to trade names in this paper does not imply endorsement by the National Marine Fisheries Service.

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Growth of Red King Crabs from the Central Aleutian Islands, Alaska

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Abstract

Growth per molt and molting probability were estimated from male red king crabs *Paralithodes camtschaticus* that were tagged and released during the 1970s by Alaska Department of Fish and Game (ADFG) biologists in the Adak Island to Amlia Island area within the Adak (Aleutians) Management Area, Alaska. There were 14,742 tagged crabs released, of which 1,385 were recovered by fishermen during commercial red king crab fisheries, and by subsequent pot surveys by ADFG. Measurement error and growth per molt in carapace length (CL) were estimated using mixture model analyses. Crabs tagged and released in different years had different growth rates, from an average growth of approximately 8 mm CL to 16 mm CL in a single year. The molting probability also varied between years, though high molting probabilities were estimated for crabs less than 115 mm CL, and low molting probabilities were estimated for crabs greater than 155 mm CL, for all years.

Introduction

Accurate life history information is necessary for proper management of commercial marine fisheries. Knowledge of various aspects of growth, such as size at age and annual growth rate, is some of the most important information desired (Powell 1967). Growth parameters have become especially important with increased use of catch-based models (i.e., catch-at-age and catch-at-length models) to estimate population size and trends (Zheng et al. 1995, Collie and Kruse 1998).

Past studies and analyses of growth per molt in king crabs have not investigated annual growth variability and used graphical methods to specify growth. Most of the growth per molt and molting probability analyses have been conducted by combining several mark-recapture surveys or a single survey. Moreover, measurement error has only been subjectively distinguished from true growth in past studies (Weber and Miyahara 1962, Powell 1967, Weber 1974).

Table 1. Release and recovery periods, the numbers of red king crabs tagged and recovered, and the number of red king crabs released as new-shell and used in these analyses.

Release periods	Number of crabs tagged	Recovery periods	Number of crabs recovered	Number of new-shell crabs used
Feb-Mar 1970	2,543	Oct 1970-Mar 1971[a]	263	239
Apr, Dec 1971	3,410	Nov-Dec 1971-1973[b]	329	297
Feb 1973	4,054	Nov-Dec 1973, Jan-Mar 1975[c]	614	497
1974-1977	4,735	1975, 1978-1979	179	53
Total	14,742		1,385	1,086[d]

[a] Also includes one recovery in February 1970 and one recovery in January 1973.

[b] Also includes one recovery in February 1973, two recoveries in January 1975, and one recovery in March 1975.

[c] Also includes one recovery in February 1974, one recovery in September 1974, one recovery in November 1977, and one recovery in March 1978.

[d] A total of 70 old-shell crabs were used in this analysis from the combined years 1970, 1971, 1973-1977.

The purpose of this report is to estimate growth per molt and molting probabilities by capture year for new- and old-shell male red king crabs during 1971-1977 in the area between Adak and Amlia islands. We used probability distribution mixture models to estimate the mean and standard deviation of growth, the mean and standard deviation of measurement error, and the proportion of molting crabs.

Methods

A total of 14,742 male red king crabs were tagged from 1970-1977 in the area from Adak Island to Amlia Island, Alaska (Table 1). Of those, 1,385 crabs were recovered, primarily by fishermen during subsequent red king crab commercial fisheries in the Adak (Aleutians) Management Area, and were measured by ADFG staff when the crabs were delivered to processing plants. Fishermen were encouraged to return all tagged crabs even if the crabs were less than the minimum legal size (sublegal). A few tagged crabs were also recovered in subsequent pot surveys performed by ADFG. Carapace length (CL), shell condition, date, and location were recorded at the time of release and on recovery. The carapace length was measured using Vernier calipers from the posterior margin of the right eye orbit to the midpoint of the posterior margin of the carapace and recorded to the nearest millimeter (Wallace et al. 1949). The growth of an individual crab was calculated by subtracting the CL when the crab was initially caught and tagged from the CL when it was recaptured. Shell condition was classified as either new-shell or old-shell (Blau 1990).

The data from recovered male crabs were divided into five samples for analysis based on shell condition at release and year of release (Table 1). Crabs were separated by shell condition because past studies indicate new- and old-shell red king crabs have different growth rates and molting probabilities (Weber and Miyahara 1962, McCaughran and Powell 1977, Schmidt and Pengilly 1990, Zheng et al. 1995). The recovery of tagged males released in new-shell condition in each of 1970, 1971, and 1973 provided sample sizes sufficient to analyze separately by year of release. However, due to the low number of tag recoveries of crabs tagged and released in new-shell condition during 1974-1977 these data were pooled for analyses, as were the data from males tagged and released in old-shell condition during 1970, 1971, and 1973-1977. Due to the larger sample sizes, we concentrated our investigation more on the crabs released in new-shell condition during 1970, 1971, and 1973.

Growth per molt was calculated by estimating the parameters of a mixture model. A mixture model is a composite of two or more probability distributions. We estimated a composite of two or more normal distributions, with the mean of each normal distribution representing the expected growth per molt. The formula for a mixture model representing a composite of three normal distributions is:

$$f(x) = \pi_1\Phi_1(\mu_1,\sigma_1) + \pi_2\Phi_2(\mu_2,\sigma_2) + (1 - \pi_1 - \pi_2)\Phi_3(\mu_3,\sigma_3)$$

where

$\Phi(\mu, \sigma)$ = a normal density function with mean μ and standard deviation σ,

π_1 = weight given to Φ_1,

μ_1 = mean of normal density function Φ_1,

σ_1 = standard deviation of normal density function Φ_1,

π_2 = weight given to Φ_2,

μ_2 = mean of normal density function Φ_2,

σ_2 = standard deviation of normal density function Φ_2,

μ_3 = mean of normal density function Φ_3, and

σ_3 = standard deviation of normal density function Φ_3.

The parameters π_1, μ_1, σ_1, π_2, μ_2, σ_2, μ_3, and σ_3 were estimated in this mixture model. The mixture model for a composite of two normal distributions is identical to the three normal distributions mixture model except that only one weight parameter and only two normal distribution parameters are specified.

In the context of our estimation of growth per molt, $\Phi_1(\mu_1, \sigma_1)$ represents the distribution of measurement error that can occur at the time of tagging and recovery of crabs that did not molt, and π_1 represents the proportion in a sample of recovered crabs that did not molt. The second

and third normal distributions $\Phi_2(\mu_2, \sigma_2)$ and $\Phi_3(\mu_3, \sigma_3)$ represent the growth in a single molt and in two molts, respectively, plus independent measurement error that can occur at the time of release and recovery. The weights π_2 and $(1 - \pi_1 - \pi_2)$ represent the proportions in a sample of recovered crabs that molted and grew one and two times, respectively.

Maximum likelihood estimates of the mixture model were computed by minimizing the negative log likelihood (Venables and Ripley 1994). The functions used to estimate the mixture model parameters were written in the statistical package/language S-Plus (MathSoft 1998) by Venables and Ripley (1994). Parameter standard error calculations were calculated from the information matrix generated by the minimization estimate of Venables and Ripley (1994). Histograms of the growth data were used to provide guidance on the number of normal distributions that were likely present. When more than one model was possible, convergence to a unique solution and comparability of the parameter estimates to published estimates of red king crab growth were used to evaluate the best model.

The mixture model results were compared to the growth of recovered crabs to identify crabs that had not molted (i.e., the apparent "growth" represented measurement error) and crabs that had molted or grown prior to recovery. The male red king crabs that were at large for approximately 1 year (8-14 months) and had lived through one "molting season" were given a binary attribute "0" if they were classified as not having molted and "1" if they were identified as having molted and grown.

A logit model was fit to molting probability versus carapace length. The form of the logit model (MathSoft, Inc. 1997) was:

$$p = \frac{e^{\alpha+\beta x}}{1+e^{\alpha+\beta x}}$$

where

x = carapace length of a red king crab at release,

p = probability of molting in one year for red king crabs of carapace length x, and

α and β are logit model parameters to be estimated.

A generalized linear model (glm) function in S-Plus (MathSoft 1998) was employed to estimate the parameters of the logit model. The carapace lengths where 10%, 50%, and 90% of the crabs will have molted was estimated from the logit model.

Results

Scatterplots of apparent growth in carapace length for recovered males released in new-shell condition indicated most of the smaller crabs (<120 mm CL) molted at least once, but few large crabs (>155 mm CL) molted.

Little or no dependency of growth on size at release was evident in the scatterplots.

The mixture model parameters for the crabs released in new-shell condition during 1970 were estimated using a two-normal-distributions model (Fig. 1a), whereas the mixture model parameters for the crabs released in 1971 and 1973 were each analyzed using a three-normal-distributions model (Figs. 1b and 1c). The pooled new-shell and old-shell samples were both analyzed using a two-normal-distributions model.

The estimated parameters for the different mixture models varied by year (Table 2). Estimates of the portion of crabs within a sample that did not molt ranged from 0.19 for males released as new-shells in 1971 to 0.84 for males released as new-shells in 1970. The estimated average growth from one molt was similar for crabs released in new-shell condition during 1970 (10.6 mm CL) and during 1973 (10.8 mm CL). The estimated average growth from a single molt for crabs released in new-shell condition during 1971 was 15.7 mm CL, indicating a possibly higher growth of molting crabs between 1971 and 1972 than during the other molting seasons. The average growth from a single molt estimated from the pooled new- and old-shell samples was considerably lower (8.3 mm and 8.8 mm CL respectively) than the estimates from the other samples. To compare the growth from one molt between sample years and shell condition, 95% confidence intervals were estimated for the mean of the first growth-per-molt. The 95% confidence interval for new-shell crabs of 1970 was 9.5-11.6 mm, for 1971 it was 15.3-16.1 mm, for 1973 it was 10.1-11.6 mm, and for 1974-1977 it was 6.7-9.9 mm, with old-shell being from 7.3 to 10.4 mm. This shows that new-shell growth for the first molt was not significantly different between 1970 and 1973, but the growth from 1971 was different. Also, though marginal, the combined new-shell 1974-1977 growth for the first molt was not significantly different from 1970, but was significantly different from 1971 and 1973. The old-shell growth for the first molt was only significantly different from the 1971 new-shell growth.

Average growth from two molts was estimated as 26.7 mm CL from the sample of males released as new-shells in 1971 and 28.0 mm CL from the sample of males released as new-shells in 1973 (Table 2). Estimated mean measurement error for each sample was within 1 standard error of 0.0 mm CL, and the standard deviation of measurement error was estimated to be less than 1.0 mm CL in each sample (Table 2).

A change in carapace length of ≥5 mm was used as an indication of growth. From the mixture model analysis, the probability that a ≥5 mm change was due to measurement error was less than 0.001 for all years and shell conditions, indicating a difference in carapace length of 5 mm or more was not due to measurement error. The probability of crabs at release size molting within 8-14 months after release, as estimated by the logit model, varied among samples (Table 3, Fig. 2). All models indicated high probabilities (>0.9) of molting within 8-14 months for males ≤118 mm CL, and low molting probabilities (<0.1) for males ≥154 mm CL (Table 4).

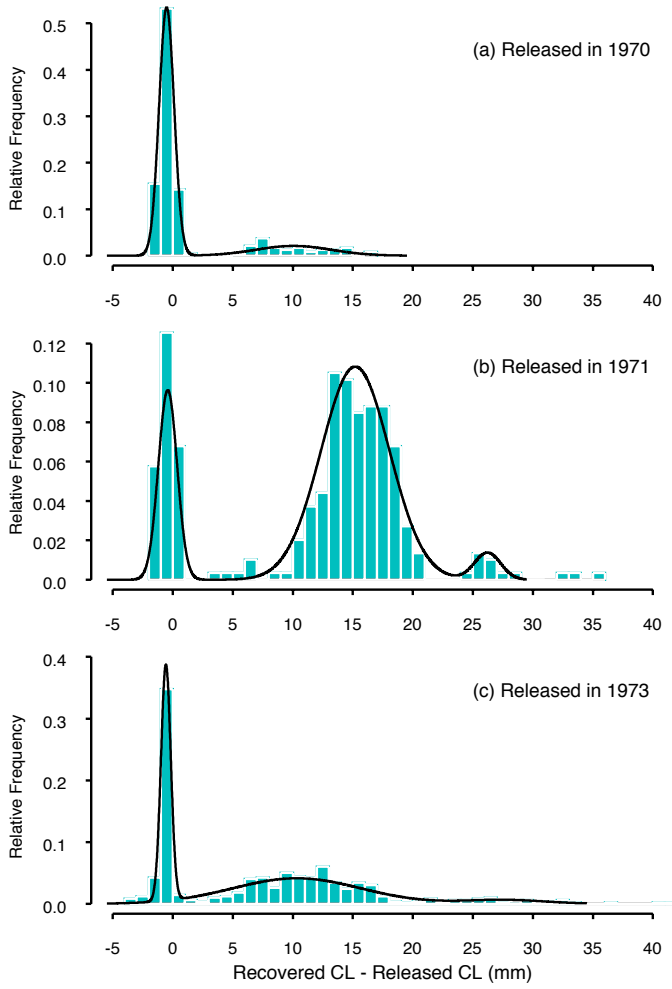

Figure 1. Histogram of the difference between recovered and released carapace length, with the estimated mixture model for new-shell male red king crabs released in 1970 (a), 1971 (b), and 1973 (c).

Table 2. Mixture model parameter estimates (with associated standard error in parentheses) of proportion molting, and mean and standard deviation (S.D.) of growth for male red king crabs tagged during 1970, 1971, and 1973-1977 in the Adak Island to Amlia Island area of the Adak (Aleutians) Management Area, Alaska.

Male crabs sampled	New-shell 1970	New-shell 1971	New-shell 1973	New-shell 1974-1977	Old-shell 1970,1971, 1973-1977
No molts					
Proportion	0.84 (0.024)	0.19 (0.024)	0.39 (0.023)	0.69 (0.065)	0.34 (0.063)
Mean[a]	–0.01 (0.044)	0.08 (0.112)	–0.07 (0.033)	0.13 (0.151)	0.03 (0.134)
S.D.[b]	0.62 (0.032)	0.78 (0.082)	0.41 (0.030)	0.90 (0.107)	0.58 (0.108)
Single molt					
Proportion	0.16 (0.024)	0.77 (0.026)	0.55 (0.025)	0.31 (0.065)	0.66 (0.063)
Mean	10.56 (0.514)	15.70 (0.202)	10.83 (0.382)	8.29 (0.807)	8.81 (0.781)
S.D.	3.13 (0.386)	2.85 (0.147)	5.35 (0.337)	2.99 (0.628)	4.69 (0.542)
Double molt					
Proportion	NA	0.04 (0.049)	0.06 (0.047)	NA	NA
Mean	NA	26.72 (0.354)	28.04 (0.893)	NA	NA
S.D.	NA	1.09 (0.248)	3.41 (0.592)	NA	NA

[a]Mean of measurement error.

[b]Standard deviation of measurement error.

Table 3. Logit parameter estimates, slope (a) and intercept (b), and their standard errors (S.E.) for new-shell male red king crabs released in 1970, 1971, 1973, and pooled 1974-1977, and old-shell male red king crabs released in 1970, 1971, and 1973-1977 pooled.

Year	Shell condition	Slope (β) estimate	Slope (β) S.E.	Intercept (α) estimate	Intercept (α) S.E.
1970	New	–0.205	0.0327	26.66	4.433
1971	New	–0.234	0.0373	33.54	5.202
1973	New	–0.202	0.0186	27.67	2.583
1974-1977	New	–0.124	0.0464	16.82	6.619
1970, 1971, 1973-1977	Old	–0.180	0.0555	25.59	7.908

Once again, the sample of males released as new-shells during 1971 stands out, with molting probabilities >90% for crabs up to 134 mm CL. In contrast, the other three samples of males released as new-shells indicated that the probability of molting within 8-14 months for crabs released at 130-137 mm CL was ≥50%. The old-shell crabs also had a relatively large size (130 mm CL) for a 90% molting probability.

Discussion

Although dependent on shell condition and year of release, the average growth from a single molt estimated for male red king crabs located in the area from Adak Island to Amlia Island in this study is similar to that estimated for red king crabs in other areas of Alaska. The estimates of growth per molt of the males released as new-shells during 1970 and 1973 (10.6 mm and 10.8 mm CL, respectively) are similar to estimates for male red king crabs in Norton Sound (10.5-12.7 mm CL; Powell et al. 1983), and within the range for red king crabs of Bristol Bay (10.0-20.0 mm CL; Weber 1974). The males released as new-shells during 1971 had an average growth per molt of 15.7 mm CL, which is similar to the average estimated growth per molt of 15.1-16.0 mm CL for Bristol Bay male red king crabs (Weber and Miyahara 1962). That estimate is also similar to growth-per-molt estimates of Kodiak male red king crabs: 16.0 mm CL (11.0-19.8 mm CL, depending on area and year; ADFG, Kodiak, unpubl. data, 1974-1981); 17.0 mm (Powell 1967); 16.5 mm (Stevens 1956); and 16.4-18.2 mm CL (Schmidt and Pengilly 1990). However, none of our crab growth-per-molt estimates were as high as those estimated for crabs in Chiniak Bay, Kodiak Island, during 1959 at 19.7 mm (Powell 1967) or Bristol Bay from 1955-1965 at

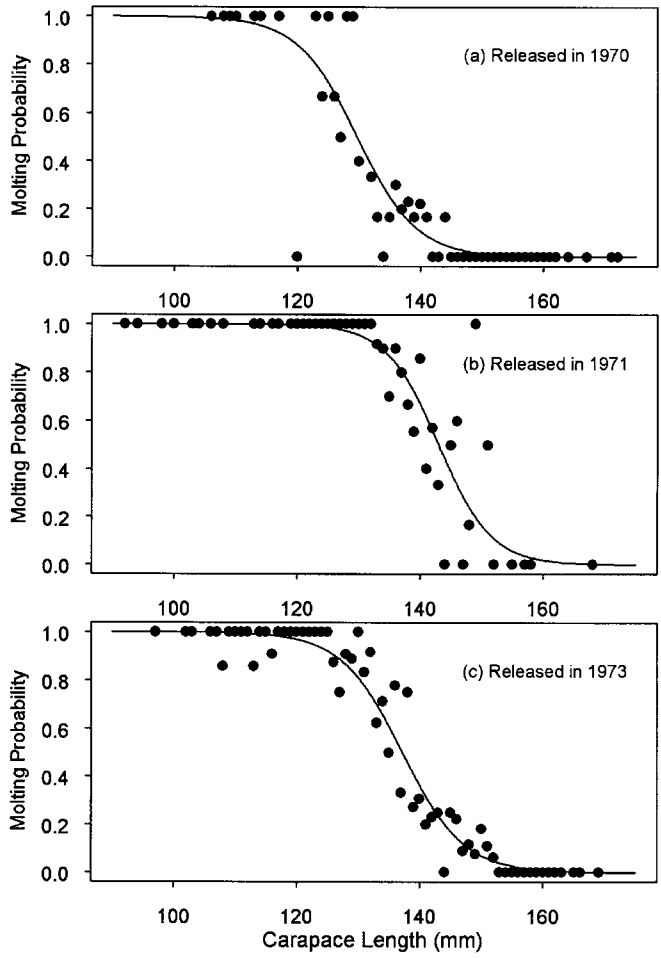

Figure 2. Released carapace length versus the molting probability observed in the sample, along with the estimated logit model for male red king crabs at large approximately 1 year (8-14 months) released in 1970 (a), 1971 (b), and 1973 (c).

Table 4. Logit estimates of carapace lengths where 10%, 50%, and 90% of the male red king crabs would molt for new-shell crabs released in 1970, 1971, 1973, and pooled 1974-1977, and old-shell male red king crabs released in 1970, 1971, and 1973-1977 pooled.

Year	Shell condition	Carapace length of 90% molt (mm)	Carapace length of 50% molt (mm)	Carapace length of10% molt (mm)
1970	New	119	130	140
1971	New	134	143	152
1973	New	126	137	148
1974-1977	New	118	136	154
1970, 1971, 1973-1977	Old	130	142	154

17.5 mm (Weber 1974). Additionally, no studies have estimated an average growth per molt for new-shell red king crabs as low as the 8.3 mm, estimated for the pooled (1974-1977) new-shell red king crabs in our study. In general, growth per molt of male red king crabs in the Adak Island to Amlia Island area appears to be lower than that in Bristol Bay or Kodiak.

Few studies (Powell et al. 1983) have compared growth per molt by year, due either to low recovery rates (Powell 1967) or because growth per molt at size was assumed to be constant between years (Weber and Miyahara 1962, Weber 1974). However, our analysis shows that there can be considerable variation among years in growth per molt at size (Fig. 2). There also seemed to be interannual differences in Bristol Bay, although that was attributed to differences in size distributions (Weber and Miyahara 1962, Weber 1974). Furthermore, when annual growth is combined for several years interannual variation can be overshadowed by one or two high recoveries from tagging studies. For example, in Weber's (1974) analysis, 54% of the recoveries of crabs tagged over 7 years (1955-1961) were from two release years (1957 and 1958). One implication of annual variability in growth per molt is that length-based population assessment models (Zheng et al. 1995) could be biased if they are dependent upon a growth-per-molt parameter estimated from only one year or combined-years data.

We also found variation between years in the molting probability by carapace length. From the logit parameters estimated by McCaughran and Powell (1977) for molting probabilities at size for male Kodiak red king crabs (a varying from 25.4 to 29.3 and a β of –0.17), the carapace length at which 50% of the crabs molt within one year would range from 149 mm CL to 172 mm CL. That indicates that male Kodiak red king crabs are more likely to molt within 1 year, at carapace lengths from 120 mm CL to 150 mm CL, than are similar-sized crabs from the central Aleutian Islands.

Both the growth per molt and molting probability estimates could have been influenced by recapture bias because most tag recoveries were collected by the fishing fleet. Sublegal crabs may have been recovered less often than legal-sized crabs. Hence, growth of males released as sublegals may be over-represented because if a sublegal crab did not molt, thus retaining its sublegal classification, it was less likely to be reported since it would not be legal to keep under normal circumstances. However, the tagging studies that provided growth-per-molt estimates of male red king crabs in other areas of Alaska also relied upon king crab commercial fisheries for tag recoveries.

Differences between years observed in the growth per molt and molting probabilities in the Adak Island to Amlia Island area could be due to changes in environmental conditions or spatial variability. Favorable environmental conditions could likely lead to greater growth and higher molting probabilities. However, we have found no data to indicate any major difference in temperature or other environmental conditions. The samples collected in the Adak Island to Amlia Island area were all from the same general area (Blau 1993), so any differences were not likely due to spatial differences.

Finally, we note the utility of mixture models in estimating growth-per-molt parameters of crabs. The value of the mixture-model approach is that it allows for estimating parameters of measurement error and growth from one or more molts without any a priori specification of the range of values that represent no molts (measurement error), one molt, or multiple molts.

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Estimating Natural Mortality of King Crabs from Tag Recapture Data

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Abstract

Natural mortality (*M*) is used as a surrogate for the maximum sustainable yield level of fishing mortality in determining limit and target reference points under precautionary management for the Bering Sea and Aleutian Islands (BSAI) crab stocks. Precise *M* estimates are needed to improve stock-assessment models as well as computer-simulation models for evaluating alternative harvest strategies. In the federal crab fishery management plan for the BSAI areas, an annual *M* of 0.3 for Tanner and snow crabs (*Chionoecetes*) and 0.2 for king crabs (*Lithodes* and *Paralithodes*) were adopted. We attempted to determine plausible *M* values for BSAI golden, red, and blue king crab stocks by employing an optimization routine that minimized the differences between observed and expected effective tagged populations based on 1990s tag-release-recapture data. The age-based-Virtual Population Analysis (VPA) *M* estimator produced an annual *M* of 0.38 for male golden king crabs in the Aleutian Islands and 0.54 for male red king crabs in Bristol Bay. The annual *M* estimated by the multinomial maximum likelihood method for St. Matthew Island combined sexes blue king crabs was 0.19. The length-based-VPA *M* estimator was annually variable and ranged from 0.02 to 1.62 for the Bristol Bay red king crab males. The red king crabs *M* estimates appeared high considering its longevity.

The simplified assumptions made for the length-based analysis cast doubt on the variable *M* estimates. Type A error was high among all experiments, but was estimated from the models and hence did not affect *M* estimates.

Introduction

The instantaneous natural mortality (*M*) is an important parameter in Bering Sea and Aleutian Islands (BSAI) crab stock assessment and management (NPFMC 1999). The analysis and data are poor for most BSAI crab stocks; consequently, *M* is used as a surrogate for the maximum sustainable yield level of fishing mortality (F_{MSY}) in determining limit and target reference points under precautionary management (Restrepo et al. 1998).

Although *M* of BSAI crabs is likely to vary by size, age (Hirschhorn 1966, Balsiger 1974, Reeves and Marasco 1980, Reeves 1988, Greenberg et al. 1991), or year (Zheng et al. 1995a), finding a constant or average *M* reflecting the longevity of the species is directly relevant to current crab stock assessment and management, and helps to obtain a direct estimate of F_{MSY}. Although *M* may not frequently equal F_{MSY}, one could establish a relationship between *F* and *M* to obtain an optimum yield (Siddeek, ADFG, unpubl.). Thus, estimation of *M* appears to be a useful exercise, although a difficult one, for heavily exploited stocks such as BSAI crabs. Therefore, in this paper we attempted to estimate *M* for Aleutian Islands golden king crab (*Lithodes aequispinus*), Bristol Bay red king crab (*Paralithodes camtschaticus*), and St. Matthew Island blue king crab (*P. platypus*) using tag-recapture data with a suite of optimization techniques.

Tag-recapture data have been used in the past to estimate *M* and many other parameters of BSAI crab stocks. Hirschhorn (1966) and Balsiger (1974) used data from the 1950s and 1960s tag-recaptures with effort data to estimate size-specific annual *M* for Bristol Bay red king crab males in the size range 80-179 mm carapace length (CL). The estimates varied from 0.001 to 0.93 for the size range 80-169 mm CL with *M* increasing by size (Balsiger 1974). Other size-specific *M* estimates based on trawl survey data ranged from 0.08 to 1.21 for the size range 85-169 mm CL, but smaller crabs (<125 mm CL) had higher natural mortality (Reeves and Marasco 1980, Reeves 1988, Greenberg et al. 1991, Zheng et al. 1995a). Zheng et al. (1995a) reviewed those estimates and concluded that a curve of *M* might be bowl-shaped when plotted by length and varied over time. Although sound statistical methodologies have been employed in a number of tag-recapture and trawl-survey data analyses (e.g., Balsiger 1974), they suffer from the confounding effect of both *M* and the catchability coefficient (*q*) in the estimation process. Siddeek (1989, 1991) developed an optimization technique based on Pope's (1972) cohort (or virtual population analysis, VPA) formulas for estimating *M* using tag-recapture data, obtained under either variable or constant intervening *F* without fishing effort. We adopted this method in this paper to reduce the confounding error on *M* estimation. We formulated a new length-based VPA *M* estimator following

Zheng et al.'s (1995a) length-based model for crab populations. We also applied the multinomial maximum likelihood estimator (Seber 1982, Hampton 2000) to experiments for which a VPA *M* estimator could not be applied. We used the 1990s tag-recapture data to assess the natural mortality pattern in recent years.

Materials and Methods

Tag Releases

The Alaska Department of Fish and Game (ADFG) conducted tagging surveys of Bristol Bay red king crabs in 1990, 1991, and 1993 (Watson 1992, Pengilly and Watson 1992, Watson and Pengilly 1994); St. Matthew Island blue king crabs in 1995 and 1998 (Blau 1996, Blau and Watson 1999); and Aleutian Islands golden king crabs in 1991 and 1997 (Blau and Pengilly 1994, Blau et al. 1998) by chartered commercial crab vessels (Table 1). (Adak and Dutch Harbor areas were combined and are now Aleutian Islands.) These tagging experiments were conducted during summer months before the fishing season started. Recaptures were used for refinement of trawl survey population size estimates, estimation of exploitation rates, establishment of relative population indexes, and estimation of growth and mortality parameters.

Rectangular, king crab pots were used to capture crabs for tagging in all surveys with the exception of the 1991 golden king crab survey in the Aleutian Islands where smaller, conical pots were used. Tagging location, date, and fishing depth were recorded for each pot retrieved. Upon pot retrieval, carapace length of crabs was measured to the nearest millimeter, shell condition recorded, tagged, and released on or adjacent to the capture location. Isthmus-loop tags (spaghetti or Floy tags) were used to tag crabs (Gray 1965) larger than 80-90 mm CL. Internal, passive integrated transponder (PIT) tags were also used on some legal-sized (>152.4-mm carapace width (CW)) blue king crabs during the 1995 St. Matthew Island survey, but recovery rates were so poor that data were excluded from current analysis (Blau 1996). The carapace length of each crab was measured from the posterior margin of the right eye orbit to the midpoint of the posterior margin of the carapace with Vernier calipers (Wallace et al. 1949). The exoskeletal condition on each crab was categorized either as new-shell (1), old-shell (2), or very old-shell (3) based primarily on the degree of scratching on the coxae (Wallace et al. 1949). Sublegal or legal size for males was determined by measuring carapace width (the straight-line distance across the carapace, including the adjacent outer spines) using fixed measuring sticks set at 5.5 inches (139.7 mm CW) for blue king crabs, 6.0 inches (152.4 mm CW) for golden king crabs, and 6.5 inches (165.1-mm CW) for red king crabs. Tag recoveries were recorded by onboard observers at sea and by ADFG dockside samplers at various crab processing plants.

Table 1. Crab tag release-recapture experiments screened for natural mortality estimation.

a. Dutch Harbor golden king crab

Sex/size class	Number tagged in 1991	Numbers recovered				
		1991	1992	1995	1997	Total
Legal males	590	64	19	1	0	84
Sublegal males	658	14	15	1	1	31
Mature females	285	0	0	0	0	0
Juvenile females	37	0	0	0	0	0
Total	1,570	78	34	2	1	115

b. Adak golden king crab

Sex/size class	Number tagged in 1991	Number recovered						
		1991	1992	1994	1995	1997	Un-known	Total
Legal males	672	27	10	0	0	0	1	38
Sublegal males	1,691	26	13	3	1	1	1	45
Males size unknown	2	0	0	0	0	0	0	0
Mature females	613	2	1	1	0	0	0	4
Juvenile females	253	0	0	0	0	0	0	0
Total	3,231	55	24	4	1	1	2	87

c. Aleutian Islands golden king crab

Sex/size class	Number tagged in 1997	Number recovered				
		1997	1998	1999	2000	Total
Legal males	2,957	596	193	52	9	850
Sublegal males	4,704	243	303	189	79	814
Females	2,138	42	22	14	8	86
Total	9,799	881	518	255	96	1,750

d. Bristol Bay red king crab

Sex/size class	Number tagged in 1990	Number recovered			
		1990	1991	1992	Total
Legal males	2,418	251	6	2	259
Sublegal males	955	23	3	0	26
Total	3,373	274	9	2	285

Table 1. (Continued.) Crab tag release-recapture experiments screened for natural mortality estimation.

e. Bristol Bay red king crab

Sex/size class	Number tagged in 1991	Number recovered					
		1991	1992	1993	1996	1997	Total
Legal males	5,416	377	106	36	1	2	522
Sublegal males	2,155	61	49	15	1	0	126
Total	7,571	438	155	51	2	2	648

f. Bristol Bay red king crab

Sex/size class	Number tagged in 1993	Number recovered				
		1993	1996	1997	1998	Total
Legal males	4,171	1,136	6	1	4	1,147
Total	4,171	1,136	6	1	4	1,147

g. St. Matthew Island blue king crab

Sex/size class	Number tagged in 1995	Number recovered				
		1995	1996	1997	1998	Total
Legal males	2,296	217	175	99	29	520
Mature females	421	18	1	0	1	20
Total	2,717	235	176	99	30	540

Development of M Estimator

1. VPA-Based Optimization Function

Siddeek (1989) developed an age-based VPA *M* estimator with the following assumptions:

1. *M* was constant among different tagging experiments.

2. *SR* was the product of tagged population initial survival proportion (*S*) and recapture reporting proportion (*R*). *S* was the proportion of tagged animals survived after immediate tagging-related death and tag shedding, and *R* was the proportion of reporting of tag-recaptures. 1-*SR* was known as Ricker's (1975) Type A error. SR_j for *j*th tag release-

recapture experiment (hereafter referred to as experiment) was normally distributed with a common mean and standard deviation.

3. Two groups of experiments considered for optimization had suffered different magnitudes of annual instantaneous total mortality (Z).

4. Numerous releases were made in each experiment to conform to deterministic mortality process and to minimize dependence between successive recaptures.

We modified some of the above assumptions to suit the current tag-recapture data analysis as follows:

1. SR_j for jth experiment within a group of experiments was distributed log normally with a common mean and standard deviation. Compared to commercial catches, tag recaptures were few and lognormal error structure reduced heteroscedasticity of SR variance.

   The assumption of a common mean ln(SR) for a selected group of experiments is plausible because we chose the group members to have the same species, season of tagging, type of tag, and condition of handling. Furthermore, we arbitrarily grouped the experiments by trial estimated closer SR_j values.

2. At least two experiments with different magnitudes of Z were available. Although one experiment would be sufficient to determine M from the minimization functions 7 and 16 developed in the subsequent sections, nevertheless, following Silliman's [1943] approach of solving two simultaneous equations with varying total mortality and effort for a unique M solution, we used at least two experiments with different Z (hence different F) values in the minimization functions for M estimation.

   The SR_j for jth experiment was estimated by the following steps:

$$N_{jt+1} = N_{jt}e^{-M} - C_{jt}e^{-(1-y_j)M} \tag{1}$$

and

$$N_{jt} = N_{jt+1}e^{M} + C_{jt}e^{y_jM} \tag{2}$$

where

N_{jt+1} = tagged population number from jth experiment at the start of $t+1$th time period (duration of a time period was set to one year) after release,

C_{jt} = observed number of tag recaptures from jth experiment during tth time period after release,

M = constant annual instantaneous natural mortality of the tagged population during tth time period after release, and

y_j = time fraction in years from the mid-date of jth tag releases to mid- or start date of the first fishing season.

Following Pope (1972),

$$SR_j = \frac{1}{N_{j0}}[C_{j0}e^{y_j M} + C_{j1}e^{y_j M + M} + \ldots + C_{jt}e^{y_j M + tM} + \ldots + N_{jn}e^{nM}] \quad (3)$$

N_{jn} was estimated using the following relation:

$$N_{jn} = \frac{C_{jn}Z_n}{F_n(1 - e^{-Z_n})} \quad (4)$$

where

Z_n = annual instantaneous total mortality of the tagged population during the last tag recovery time period after release, n, and

F_n = annual instantaneous fishing mortality of the tagged population during the last tag recovery time period after release, n.

The Z_n (and hence F_n by subtracting a given M value from Z_n) to tune the VPA to estimate SR_j for jth experiment was determined by fitting a linear regression to the natural log of the Baranov's catch equation (i.e., modified from equation [18] with constant F, M, Z, y_j, and δ) as follows:

$$\ln(C_{jt+1} + 1) = \ln[(F \times SR_j \times N_{j0} / Z)(1 - e^{-Z\delta})] - My_j - tZ \quad (5)$$

where

ln = natural logarithm.

The minimization function (7) to estimate M from observed tag recapture data (C_{jt}) was formulated by the following steps:

$$SR_j = S\mathrm{R}e^{\varepsilon_j} \quad (6)$$

where

SR_j = estimated product of initial survival and reporting proportions for jth experiment, and

ε_j = a normal random error with a mean of zero and standard deviation σ,

ln(SR) = expected (mean) value of ln(SR_j); and

$$\sum_{j=1}^{k}[\ln(SR_j) - \ln(SR)]^2 \tag{7}$$

where

k = number of experiments in the selected group.

We opted to formulate the minimization function based on SR_j rather than C_{jt} because errors in N_{jt} (and hence SR_j) estimates shrink during the backward computation process as the number of time steps of calculation increases (Pope 1972). Ln(SR_j) and ln(SR) can be considered as a form of observed and expected ln(SR). Note that SR_j has the accumulation of all observed catches and similarly we may think of SR to have the accumulation of all expected catches.

The above was an age-based approach, which could be extended to a length-based form used in crab population modeling. Following Sullivan et al. (1990) and Zheng et al. (1995a),

$$[N_{l_{ji}t+1}] = [P_{l_{ji}l'}][m_{l_{ji}t}][A_{l_{ji}t}] \tag{8}$$

where

[ ] = matrix sign,

$$A_{l_{ji}t} = (N_{l_{ji}t} + O_{l_{ji}t})e^{-M_t} - C_{l_{ji}t}e^{-(1-y_j)M_t} \tag{9}$$

$N_{l_{ji}t}$ = new-shell tagged populations of length class l_{ji} in jth experiment during the tth time period after release,

$C_{l_{ji}t}$ = number of tag recoveries of length class l_{ji} in jth experiment during the tth time period after release,

$O_{l_{ji}t}$ = old-shell tagged populations of length class l_{ji} in jth experiment during the tth time period after release,

$$O_{l_{ji}t} = [(N_{l_{ji}t} + O_{l_{ji}t})e^{-M_t} - C_{l_{ji}t}e^{-(1-y_j)M_t}](1 - m_{l_{ji}t}), \tag{10}$$

$m_{l_{ji}t}$ = molting probability of crabs in length class l_{ji} in jth experiment during the tth time period after release,

M_t = annually variable instantaneous natural mortality of crabs in length class l_{ji} in jth experiment during the tth time period after release, and

$P_{l_{ji}l'}$ = probability of crabs in length class l_{ji} in jth experiment growing to length class l' The annual growth increment (x) was assumed to have a gamma distribution as follows:

$$P_{l_{ji}l'} = \frac{\int_{l'_1-\tau_{l_{ji}}}^{l'_2-\tau_{l_{ji}}} gamma(x / \alpha_{l_{ji}}, \beta)dx}{\sum_{i=1}^{n_j} \int_{l'_1-\tau_{l_{ji}}}^{l'_2-\tau_{l_{ji}}} gamma(x / \alpha_{l_{ji}}, \beta)dx}, \tag{11}$$

$$gamma(x / \alpha_{l_{ji}}, \beta) = \frac{x^{\alpha_{l_{ji}}-1} e^{-\frac{x}{\beta}}}{\beta^{\alpha_{l_{ji}}} \Gamma(\alpha_{l_{ji}})}, \tag{12}$$

where

n_j = number of length classes in the jth experiment,

l'_1 and l'_2 = lower and upper limits, respectively, of the receiving length class l',

β = a parameter of the gamma distribution,

$$\alpha_{l_{ji}} = G_{l_{ji}} / \beta, \text{ and} \tag{13}$$

$G_{l_{ji}}$ = mean annual growth increment per molt for the length class l_{ji} in jth experiment with a middle carapace length $\tau_{l_{ji}}$ just before molting.

The mean annual growth increment was assumed to be a linear function of the molting class mid-length as follows:

$$G_{l_{ji}} = a + b\tau_{l_{ji}}, \tag{14}$$

where

a and b = constants.

We assumed M_t to be length invariant for the current tag-recapture analysis. For simplicity, we also assumed all recaptures were new shells. Therefore, the term $O_{l_{jit}}$ in equation 9 and the entire equation 10 were ignored in the current analysis. See the discussion section for justification.

The terminal population abundance vector $N_{l_{ji}n}$ for experiment j was estimated using equation 4 for each size group i with a constant Z_n estimated from equation 5 and F_n calculated from Z_n by subtracting a given M value. This population size vector was projected backward by one step by inverse matrix multiplication to obtain the previous time-step population size vector as follows:

$$[N_{l_{jit}}] = [m_{l_{jit}}]^{-1}[P_{l_{jil'}}]^{-1}[N_{l_{jit+1}}]e^{M} + [C_{l_{jit}}]e^{y_j M} \tag{15}$$

Equation 15 was derived by combining equations 8 and 9, ignoring $O_{l_{ji}t}$. Repeated inverse matrix multiplication with observed $C_{l_{ji}t}$ and given other parametric values led to the estimation of effective number of tagged crabs released at length group l_{ji} for jth experiment, $SR_{l_{ji}} \times N_{l_{ji}0}$, and then $SR_{l_{ji}}$ for each length group l_{ji}. Then the minimization function for M estimation was formulated as follows:

$$\sum_{j=1}^{k} \sum_{i=1}^{n_j} [\ln(SR_{l_{ji}}) - \ln(SR)]^2 \tag{16}$$

where

n_j = number of length classes in the jth experiment, and

k = number of experiments in the selected group of experiments.

It is also possible to use a single tagging experiment to estimate M by minimizing the function (16). In that case, $k = 1$.

2. Multinomial Likelihood M Estimator

A maximum likelihood method was developed to estimate M from some tagging experiments, which were not suited for the VPA procedure. It was derived assuming that the observed tag recapture data set $<C_{jt}>$ from jth experiment had the following multinomial distribution (see page 274 of Seber [1982] and Hampton [2000] for the derivation):

$$f(\langle C_{jt} \rangle) = \frac{(SR_j \times N_{j0})!}{(\prod_{t=1}^{T} C_{jt}!)(SR_j \times N_{j0} - \sum_{t=1}^{T} C_{jt})!} \left(1 - \frac{\sum_{t=1}^{T} \hat{C}_{jt}}{SR_j \times N_{j0}}\right)^{SR_j \times N_{j0} - \sum_{t=1}^{T} C_{jt}} \prod_{t=1}^{T} \left(\frac{\hat{C}_{jt}}{SR_j \times N_{j0}}\right)^{C_{jt}} \tag{17}$$

where

T = total number of tag recovery periods for jth experiment,

C_{jt} = observed number of tag recaptures during tth year after release from jth experiment,

$\hat{C}_{jt}$ = expected number of tag recaptures during tth year after release from jth experiment,

$$\hat{C}_{jt} = SR_j \times N_{j0} e^{-\sum_{k=1}^{t-1} (F_k \delta_k + M) - My_{jt}} \frac{F_t}{Z_t} (1 - e^{-Z_t \delta_t}) \tag{18}$$

y_{jt} = time fraction in years from the mid date (considering only month and day) of jth tag release to the start date of the tth fishing season, and

δ_k = fishing period during kth year after release as a fraction of a year.

The negative log of the multinomial likelihood function to be minimized for M estimation from a single experiment j was then – ln f($<C_{jt}>$):

$$A - (SR_j \times N_{j0} - \sum_{t=1}^{T} C_{jt}) \ln(1 - \frac{\sum_{t=1}^{T} \hat{C}_{jt}}{SR_j \times N_{j0}}) - \sum_{t=1}^{T} C_{jt} \ln(\frac{\hat{C}_{jt}}{SR_j \times N_{j0}}), \qquad (19)$$

where

A = a constant independent of estimating parameters.

It is also possible to use multiple experiments to estimate M by modifying the above negative log-likelihood function to $-\sum_{j=1}^{k} \ln f(\langle C_{jt} \rangle)$, assuming a common M and SR among k experiments.

Results

Although tag releases and recoveries were categorized as legal and sublegal (Table 1), we did not differentiate them for M estimation because there were overlaps in size ranges of recaptures over the years. We arbitrarily selected those tagging experiments that produced over 4.5% total returns for parameter estimation. Recovery rates ranging from 5% to 20% were normal in open population tagging experiments and have been used for M estimation (e.g., 12-13% for tunas [Hampton 2000]; 5-17% for shrimp [Siddeek 1991]). We used the age-based-VPA M estimator whenever we had at least two sets of tagging experiments with different Z, similar SR, and a sufficiently large number of releases, and used the multinomial likelihood M estimator for those experiments that could not be grouped under the above criteria.

We estimated an average Z using equation 5 for each experiment to constrain the M estimate for the selected group of experiments such that $M+F <$ upper 95% confidence limit of the lowest Z in the group. The Z estimate was also used to select a pair of M and terminal F to estimate SR_j by VPA in the process of minimization. The M was incremented systematically by a small step from 0.01 to Z, the corresponding terminal F was estimated by subtracting it from Z, and the minimization routine was run for each incremented start M and corresponding terminal F values to obtain the best M estimate at the global minimum of the minimization function. A VBA program was written to use the Excel solver routine to determine M. For Z and M estimation, we grouped the tag-recaptures into yearly intervals. The natural log of recaptures plus one (to take care of zero recaptures) vs. the time period for each set of releases is shown in Fig. 1 and the

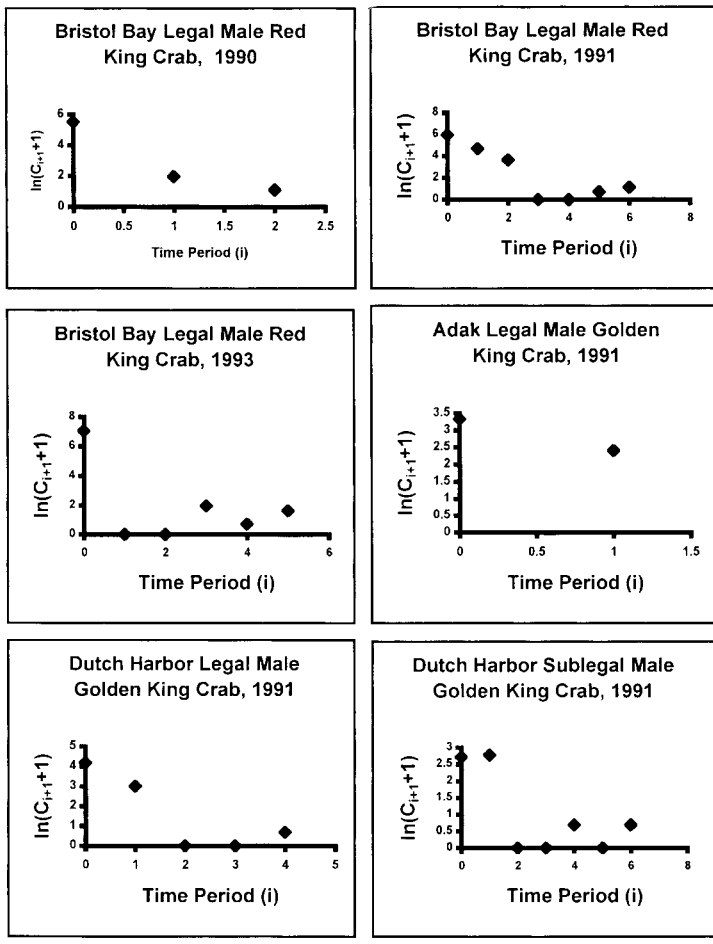

Figure 1. Natural log of recaptures vs. time period for instantaneous total mortality (Z) estimation to initiate virtual population analysis for optimization. Data from Bristol Bay red king crab males, Aleutian Islands golden king crab males, and St. Matthew Island blue king crab males and females experiments selected for optimization are shown in the figure.

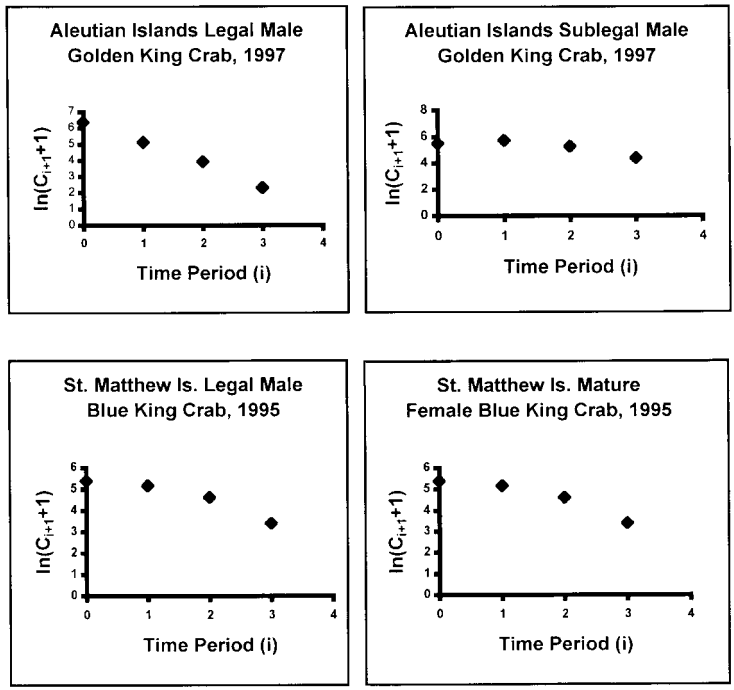

Figure 1. (Continued.)

average Z estimates are given in Table 2. A few experiments have fairly constant Z values shown by linear relationships with nonsignificant fits (Aleutian Island golden crab legal males; Bristol Bay red king crab legal and sublegal males; and St. Matthew Island blue king crab legal males). The annual Z ranged from 0.38 to 1.33 for golden king crab males for the recovery period 1991 to 2000, from 0.66 to 2.22 for red king crab males for the recovery period 1990 to 1998, and 0.65 and 0.74 for blue king crab males and females, respectively, for the recovery period 1995 to 1998.

We restricted our analysis to determining a constant M value for most of the selected groups of experiments. We grouped the available experiments into golden, red, and blue king crab males; and blue king crab females. Furthermore, we performed optimization on subsets of experiments from each major group with subsets selected based on closer SR_j values. Because only one legal male and one female tagging experiment with over 4.5% total returns were available for St. Matthew Island blue king crabs and the number of female releases were not large enough (<1,000) for VPA M estimator, we used the multinomial likelihood estimator to determine M for each of these experiments as well as both experiments together, as-

Table 2. Instantaneous total mortality (*Z*) estimates for various crab species for input to VPA *M* estimator.

Experiment group (year of release)	Number released (recovery %)	*Z*	95%C.I.	R^2_{adj}	*N*	*P*-value
1. Golden king crab, males						
Adak legal (1991)	672 (5.5)	0.93	—	—	2	—
Dutch Harbor legal (1991)	590 (14.2)	1.00	–0.25 to 2.24	0.58	5	0.08
Dutch Harbor sublegal (1991)	658 (4.7)	0.39	–0.1 to 0.88	0.35	7	0.1
Aleutian Islands legal (1997)	2,957 (28.8)	1.33	1.02 to 1.64	0.99	4	0.003
Aleutian Islands sublegal (1997)	4,704 (17.3)	0.38	–0.36 to 1.13	0.56	4	0.16
2. Red king crab, males						
Bristol Bay legal (1990)	2,418 (10.7)	2.22	–7.82 to 12.25	0.77	3	0.22
Bristol Bay legal (1991)	5,416 (9.6)	0.93	0.21 to 1.65	0.63	7	0.02
Bristol Bay sublegal (1991)	2,155 (5.8)	0.91	0.23 to 1.58	0.72	6	0.02
Bristol Bay legal (1993)	4,171 (27.5)	0.66	–1.08 to 2.4	0.02	6	0.35
3. Blue king crab						
St. Matthew legal male (1995)	2,296 (22.6)	0.65	–0.03 to 1.33	0.84	4	0.05
St. Matthew mature female (1995)	421 (4.8)	0.74	–1.26 to 2.75	0.34	4	0.25

VPA = virtual population analysis; C.I. = confidence interval; R^2_{adj} = adjusted R^2 (see Zar 1984), and N = number of [ln (C_{jt+1}+1), t] pairs per experiment considered for the regression (see equation 5).

suming that *M* and *SR* did not vary by sex. We used the jackknife procedure by dropping one experiment at a time to remove bias and construct 95% confidence intervals on the *M* estimate. The jackknife procedure has a greater advantage over bootstrap on tag-recapture data analysis because it helps to identify influential experiments on the overall *M* estimate (Mooney and Duval 1993).

The *M* estimate ranged from 0.38 to 0.57 for golden king crab males, from 0.54 to 0.70 for Bristol Bay red king crab males, and was 0.19 for combined sexes of St. Matthew Island blue king crabs (Table 3). The 95% confidence limits for each species were overlapping with an upper limit <1.8. The confidence limits were wide because of small sample size (few experiments per group). The coefficient of variation (C.V.) of *SR* varied for different subgroups of experiments for golden king and red king crab males. The lowest values of C.V. and minimum error sum of squares (SSQ) for the group estimate as well as for individual jackknife estimates provided a way to select plausible *M* values. For example, removing the 1991 Adak experiment for jackknife estimation from group 1 experiments for golden king crab produced the lowest SSQ for that group. Hence, we did not consider *M* values of those groups having Adak releases. Similarly, the removal of the 1993 Bristol Bay experiment for red king crab resulted in the lowest SSQ for that group. Therefore, any *M* estimates from groups containing that experiment were not considered. Probable reasons for the abnormal behavior of the above two experiments are given in the discussion section. Based on the above selection criteria, an *M* of 0.38 for Aleutian Island golden king crab males was selected as the best. The best *M* value of 0.54 for the Bristol Bay red king crab male was, however, high considering its maximum life expectancy, which could range from 21 to 24 years (Matsuura and Takeshita 1990, Stevens et al. 2000). Matsuura and Takeshita (1990) observed an average maximum life span of 21 years for male Japanese red king crabs reared in the laboratory and speculated that for females maximum age might be lower. We could not use the same criteria for blue king crabs because the estimation method for these groups was different from others (i.e., multinomial likelihood estimator with an arbitrarily selected, but feasible, *SR* value that produced the lowest SSQ was used as opposed to the age-based-VPA estimator), and only one tag-recapture experiment was available for each sex. The *M* estimate by sex for blue king crabs was much lower than those for the other species (<0.1), casting doubt on the estimates, but an acceptable estimate of 0.19 was obtained for the combined sexes.

Thus, *M* estimates for Aleutian Island golden king crab males appear to be reasonable considering its longevity. The expected recaptures for *M* and *SR* estimates based on the age-based-VPA *M* estimator also matched closely to those of observed recaptures for this group of experiments (Fig. 2).

We used the length-based-VPA *M* estimator (equations 8 to 16) on Bristol Bay red king crab males, restricting M_t to be invariant of length, but not year. Because we could not get the finer classification of new-shell and

Table 3. Estimates of natural mortality (*M*) under constant *M* assumption for various crab species.

Experiment group (year of release)	Number released (recovery %)	SR_j	Estimate for the group				Jackknife bias removed *M*	Jackknife 95% C.I. of *M*	Remarks
			C.V. of *SR* (%)	SSQ	*SR*	*M*			
1. Golden king crab, male									
Adak legal (1991)	672 (5.5)	0.168	52.8	1.22	0.346	0.573	0.573	–0.66 to 1.80	VPA minimization
Dutch Harbor legal (1991)	590 (14.2)	0.254							
Dutch Harbor sublegal (1991)	658 (4.7)	0.337							
Aleutian Islands legal (1997)	2,957 (28.8)	0.508							
Aleutian Islands sublegal (1997)	4,704 (17.3)	0.681							
2. Golden king crab, male									
Adak legal (1991)	672 (5.5)	0.135	25.3	0.145	0.182	0.484	0.485	–0.56 to 1.53	VPA minimization
Dutch Harbor legal (1991)	590 (14.2)	0.228							
Dutch Harbor sublegal (1991)	658 (4.7)	0.196							
3. Golden king crab, male									
Aleutian Islands legal (1997)	2,957 (28.8)	0.398	0.0	3.28×10^{-19}	0.398	0.375			VPA minimization
Aleutian Islands sublegal (1997)	4,704 (17.3)	0.398							

SR_j = the product of initial survival and reporting for jth experiment; SSQ = minimized value of the optimization function; C.V. = coefficient of variation; C.I. = confidence interval; VPA = virtual population analysis; MLH = multinomial maximum likelihood.

[a]Chosen at min. SSQ

Table 3. (Continued.) Estimates of natural mortality (*M*) under constant *M* assumption for various crab species.

Experiment group (year of release)	Number released (recovery %)	SR_j	Estimate for the group: C.V. of *SR* (%)	Estimate for the group: SSQ	Estimate for the group: *SR*	Estimate for the group: *M*	Jackknife bias removed *M*	Jackknife 95% C.I. of *M*	Remarks
4. Red king crab, male									
Bristol Bay legal (1990)	2,418 (10.7)	0.130	48.3	0.597	0.192	0.697	0.697	–0.23 to 1.63	VPA minimization
Bristol Bay legal (1991)	5,416 (9.6)	0.206							
Bristol Bay sublegal (1991)	2,155 (5.8)	0.145							
Bristol Bay legal (1993)	4,171 (27.5)	0.351							
5. Red king crab, male									
Bristol Bay legal (1990)	2,418 (10.7)	0.124	17.6	0.0607	0.126	0.54	0.54	–0.42 to 1.50	VPA minimization
Bristol Bay legal (1991)	5,416 (9.6)	0.152							
Bristol Bay sublegal (1991)	2,155 (5.8)	0.107							
6. Blue king crab									
St. Matthew legal male (1995)	2,296 (22.6)								
St. Matthew mature female (1995)	421 (4.8)	0.25[a]		990.0		0.188			MLH

SR_j = the product of initial survival and reporting for jth experiment; SSQ = minimized value of the optimization function; C.V. = coefficient of variation; C.I. = confidence interval; VPA = virtual population analysis; MLH = multinomial maximum likelihood.

[a]Chosen at min. SSQ

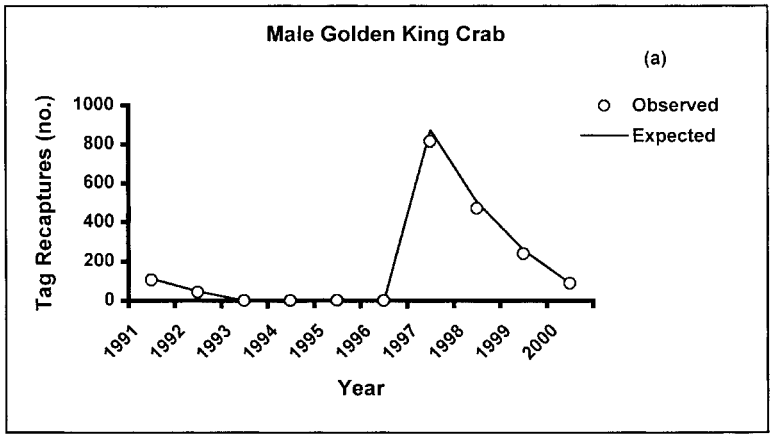

Figure 2. Observed vs. expected recaptures based on estimated constant annual natural mortality (M) for Aleutian Islands golden king crab males.

old-shell tag recaptures, we assumed all of them to be new-shell and the molting probability at each 5-mm CL size interval to be one and constant over the whole recapture period. We selected the Bristol Bay tagging experiments because auxiliary parameters necessary for length-based assessment were available for this stock from other studies. We used an a value of 13.14, a β value of 0.018 from Zheng et al. (1997a) in the linear growth equation (14) and changed the β parameter from 0.05 to 3 by small steps to optimize the minimization function (16). Although growth constants and molting probabilities could have been estimated from the minimization function we did not attempt to do so. This was because there were not large enough releases; the time series of recapture data were short; and few recaptures were recorded in most of the time periods in the selected set of experiments to reliably estimate a large number of parameters. We initiated the back calculation process for optimization by estimating the terminal tag population abundance at each size group, I_{ji}. For this purpose, we used equation 4 with the lowest 95% upper confidence of Z in the selected group. The optimized values of annually variable M ranged from 0.02 to 1.62 (Table 4) for a β value of 1.119. We are cautious about the results because a number of simplified assumptions had been made to apply the length-based model to the Bristol Bay data. As mentioned previously, most of the M values for red king crabs were very high to have confidence on the estimates. The length-based M estimator may have provided realistic estimates of M, if successful experiments with fairly large number of releases and long time series of recaptures were used. We are

Table 4. Estimates of natural mortality (*M*) under annually variable *M* assumption for Bristol Bay red king crab males by length-based VPA *M* estimator.

Experiment group (year of release)	Number released (recovery %)	SSQ	*SR*
Bristol Bay legal (1990)	2,418 (10.7)	$1.99 \times 10^{+2}$	0.114
Bristol Bay legal (1991)	5,416 (9.6)		

	M Estimate for the group							
	1990	1991	1992	1993	1994	1995	1996	1997
Bristol Bay legal (1990 and 1991)	0.36	1.57	0.52	0.03	1.62	1.62	1.62	0.02

SR = the product of initial survival and reporting; SSQ = minimized value of the optimization function.

currently investigating pre-1990 experiments to select any experiments with those characteristics to use in this estimator.

Discussion

Most of the Bering Sea and Aleutian Islands crab stocks are in depressed states, with reduced catches in recent years (Kruse et al. 2000), which prompted us to look into 1990s tag release-recapture data to estimate *M* among different stocks during the last decade. However, apart from Aleutian Islands golden king crab males and St. Matthew Island blue king crab combined sexes experiments, others provided unreasonably high estimates considering the life expectancy of these animals. Past estimates were also high and variable during different time periods (Table 5). The high values may have resulted for some groups of experiments for a number of reasons: (1) enhanced *M* due to under-reporting of sublegals compared to legals, affecting *R* in *SR*; (2) variable *M* between sublegals and legals; (3) delayed mass mortality on tagged population, requiring different *SR* values for the first year and thereafter; and (4) as observed in the past (Table 5), *M* values for the 1990s were indeed high. We could not get reliable estimates of *M* for females because of availability of a very few acceptable experiments and unreliability of reported recaptures because of the male-only harvesting policy.

Type A error (1–*SR*) did not adversely affect the *M* estimates because it was modeled and determined independently from *SR* by the VPA *M* estimator. Although we modeled this error in the multinomial likelihood func-

Table 5. Comparison of published and selected estimated instantaneous natural mortality (*M*) for king crabs.

Species	Remarks	Males *M* Range	Males *M* Mean	Females *M* Mean	Reference[a]
Bristol Bay red king	**Tagging**				
	135-169 mm CL	0.3-0.40	0.35		1
	135-180 mm CL	0.05-0.93	0.44		2
	1954-61, 80-169 mm CL	0.05-0.93	0.44		3
	1966-68, 80-169 mm CL	0.001-0.81	0.22		
	1990-91, 80-180+ mm CL		0.54		Current estimate
	Catch and survey data				
	95-170 mm CL	0.08-0.76	0.32		4
	1969-80, 85-134 mm CL	0.33-0.71	0.53		5
	1981-86, 85-134 mm CL	0.49-1.21	0.84		5
	Survey data				
	1977-80, 95-139 mm CL	0.07-0.48	0.21		6
	1981-89, 95-139 mm CL	0.23-0.75	0.49		6
	Modeling catch and survey data				
	95-169+ mm CL,				7
	1972-79		0.23		
	1980-84		1.04		
	1985-93		0.23		
	90-140+ mm CL,				7
	1972-80			0.47	
	1981-84			1.72	
	1985-93			0.32	
	Mean for 1972-94,				8
	95-169+ mm CL		0.29		
	90-140+ mm CL			0.47	
Kodiak red king	**Survey data**				
	1981-90		0.27		9
	>165 mm CW		0.20		10
St. Matthew blue king	**Catch and survey data**				
	1982-83, 105-139 mm CL	0.19-2.04	0.81		11
	Tagging				
	1995, 80-157+ mm CL, combined sexes		0.19	0.19	Current estimate
Pribilof blue king	**Catch and Survey Data**				
	1978-83, 140-169 mm CL	0.34-0.94	0.79		11
	>165 mm CW		0.20		10
Aleutian Islands golden king	>152 mm CW		0.20		10
	Tagging				
	1997, 80-180+ mm CL		0.38		Current estimate

CL: carapace length; CW: carapace width; +: Specified length and above.

[a]1:Cleaver 1963; 2: Hirschhorn 1966; 3: Balsiger 1974; 4: Reeves and Marasco 1980; 5: Reeves 1988; 6: Greenberg et al. 1991; 7: Zheng et al. 1995b; 8: Zheng et al. 1997b; 9: Schmidt and Pengilly 1993; 10: NPFMC 1999; 11: Otto and Cummiskey 1990.

tion, we did not estimate it through the model because of availability of a few acceptable tagging experiments for blue king crabs. However, we chose acceptable *SR* values based on lowest SSQ after trial runs of optimization on blue king crab data. Type A error was high in all experiments and ranged from 0.52 to 0.89 for golden and red king crab males. This emphasized the need for a large number of releases for plausible mortality estimation. The *M* estimates may be inflated due to continuous tag shedding, systematic tagging mortality, and emigration (Ricker's type B error). Pengilly and Watson (1992) observed that Floy tag loss from red king crabs in holding tanks was virtually nonexistent. The loss rate of tags from deepwater golden king crab was not known. Because the loss rate in their natural environment was largely unknown and difficult to model independently from *M*, we assumed Type B error to be negligible. Nearly 97% of recaptures from the 1991 Adak experiment were reported during the first two years after release and 99% of recaptures from the 1993 Bristol Bay experiment were reported during the first year after release (Table 1), suggesting an enhanced catchability on tagged population during the initial years of these experiments. This may have been due to abnormal behavior or nonrandom mixing of tagged crabs, or nonrandom distribution of effort during the first two seasons after the release and is known as Ricker's type C error. The jackknife procedure was useful to detect this type of abnormal experiments, and thus we were able to choose *M* from the group that excluded abnormal experiments.

Minimum variation among $\ln(SR_j)$ for a selected group of experiments was a critical assumption for successful optimization. The *M* estimates were selected from those groups having smaller CV of *SR* (Table 3). Thus, the constant $\ln(SR)$ assumption within the selected group was satisfied. The best estimates of *M* for golden and red king crab males were selected from groups with individual releases exceeding 2000; thus, the numerous releases assumption for deterministic mortality processes was also satisfied.

The size-specific natural mortality (M_{ij}) can be introduced in the new length-based-VPA *M* estimator and the multinomial likelihood *M* estimator (Hampton 2000) for parameter estimation. In the past, size-specific *M* estimates have been reported from tag-recapture analysis (Hirschhorn 1966, Balsiger 1974). However, we opted not to pursue along this line with the current data for the following reasons. First, because recaptures were mixed with new- and old-shell crabs, *M* within a size class may not be a constant. Due to different molting probabilities, in a given size range one could find an old crab that had not molted in a given year as well as a younger crab that had molted into that size class from a smaller size group in that year. Second, the tag recovery periods extended to a few years, 2 to 7 at most with few number of recaptures (Table 1); thus, number of data points were not sufficient to estimate a large number of parameters with precision. Third, the primary objective of this paper was to obtain an average constant *M*, if possible, for direct application to currently used crab stock

assessment and management procedures. A major drawback of size-specific M estimator is the assumption of length-invariant SR, which may not hold for experiments with a wider size range of releases. However, one may select a subset of appropriate length classes to keep SR_j fairly constant among them to obtain successful optimization.

The age-based-VPA M estimator has a greater advantage over its length-based counterpart on crab mortality estimation from tag-recapture data because a crab's complex growth process (growth is a function of molt increment and molting probability) could be ignored in the former, thus reducing the number of estimating parameters in the model. However, it requires successful experiments with numerous releases, similar SR values, and different total mortality values for plausible M estimation. On the other hand, the new length-based-VPA M estimator could be used with a single successful experiment with numerous releases and recaptures for successful optimization provided conditions specified in the previous paragraph are met.

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Estimating Molting Probabilities of Female Dungeness Crabs (*Cancer magister*) in Northern California: A Multi-Stage Latent Variable Approach

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Extended Abstract

Estimation of size-specific molting probabilities of crustaceans has often been based on indirect indicators of molting status including visual or chemical methods applied to internal or external features that reflect recent molting or molting failure. Mohr and Hankin (1989) proposed a maximum likelihood estimator of size-specific molting probabilities, based on shell condition, a postmolt indicator. The validity of the Mohr-Hankin estimator hinges upon two key assumptions: (1) a well-defined molting season of relatively short duration, and (2) high classification accuracy. Satisfying condition 1 poses little problem for some crustaceans, including the Dungeness crab. The validity of assumption 2, however, could be questionable. All postmolt indicators arguably measure molting status with error due to various causes, including at least variation among observers, time elapsed since crabs last molted, and imperfect repeatability of classifications. It is well known that the misclassification will lead to biased inferences (Chen 1989). This study aims to develop improved estimators of size-specific molting probabilities that account for the imperfections in classification of molting status.

We propose a regression model that treats postmolt indicators as surrogates for true molt status. We argue that this method addresses both analytic challenges identified above. Specifically, we propose a two-stage

procedure that first synthesizes observed information to probabilistically determine true molting status, and then analyzes the association between the true molting status and other covariates via logistic regression; for example, how premolt carapace width relates to molting probability during the upcoming season. Our approach to estimating model parameters is similar to pseudo maximum likelihood (Gong and Samaniego 1981).

We illustrate application of our estimator using postmolt shell condition and sperm plug data collected from the northern California population of adult female Dungeness crabs (*Cancer magister*). Adult female Dungeness crabs are known to exhibit a well-defined annual molting season extending from mid-February through mid-May in northern California. On the basis of visual inspection of carapace condition (degree of deterioration, fouling, and discoloration), the molting history of female crabs with respect to the previous molting season was classified into one of five classes: (1) definitely molted, (2) probably molted, (2.5) impossible to judge, (3) probably did not molt, and (4) definitely did not molt. Because molting is an essential prerequisite for females to successfully mate with males, a definitive indicator of recent mating activity, if one exists, would allow more reliable assessments of molting success than could be obtained from the shell condition data alone. A recent study (Oh 2000) has provided empirical evidence that presence (or absence) of sperm plugs within the females' vaginal tracts in Dungeness crabs is a definitive indicator of mating/molting success (or failure) for crabs with postseason carapace width (CW) greater than 120 mm (D.G. Hankin, unpubl. observations). Although presence of sperm plugs has been found to be the most reliable indicator of molting status, its use is limited by the need to sacrifice animals. In contrast, shell condition data can be inexpensively and quickly obtained and hence are more practical for the purpose of estimating molting probabilities in a large sample setting. Comparison of shell condition assessments with sperm plug data revealed that (a) essentially all class 1 crabs (≥120 mm CW) had sperm plugs; (b) essentially no class 2.5 or higher crabs had sperm plugs; and (c) class 2 crabs proved to contain a mixture of molted and nonmolted crabs (D.G. Hankin, unpubl. observations). Our analysis effectively corrects such imperfections in shell classification.

To estimate molting probabilities, we developed a four-stage fitting algorithm. In stage 1 we calculated the probability $p1$ ($p0$) that a crab is correctly classified as having (not having) molted, based on sperm plug data from a substudy. In stage 2 we estimated molting probabilities given shell condition data from field samples using Bayes' theorem, while fixing $p0$ and $p1$ at their estimates from the first stage. We also assumed that the ratio, R, of size-independent survival probabilities through the molting season for molting as compared with nonmolting crabs is known. In stage 3 we randomly assigned molting status to each crab using its estimated conditional probability of molting given its shell classification and reconstructed the premolt size distribution according to molting status using a well-defined premolt-postmolt size relationship (Mohr and Hankin 1989).

Table 1. Estimated molting probabilities from postmolt shell condition data collected in June/July of 1994 and 1998 at Clam Beach, northern California. A single size-independent survival ratio, $R = 0.70$, was used in the fitting.

	1994 (N = 1,494)		1998 (N = 1,475)	
Premolt carapace width (mm)	Estimated molting probability	95% C.I.	Estimated molting probability	95% C.I.
107.5	0.98	0.96-0.99	1.00	1.00
110.5	0.97	0.95-0.99	1.00	1.00
113.5	0.96	0.94-0.98	1.00	1.00
116.5	0.94	0.91-0.97	1.00	1.00
119.5	0.92	0.89-0.95	1.00	0.99-1.00
122.5	0.89	0.85-0.93	0.99	0.99-1.00
125.5	0.85	0.81-0.89	0.98	0.97-1.00
128.5	0.80	0.76-0.84	0.95	0.92-0.99
131.5	0.74	0.70-0.78	0.87	0.80-0.94
134.5	0.67	0.62-0.72	0.70	0.60-0.80
137.5	0.59	0.52-0.65	0.44	0.32-0.56
140.5	0.50	0.42-0.58	0.21	0.11-0.32
143.5	0.41	0.33-0.50	0.08	0.02-0.15
146.5	0.33	0.24-0.43	0.03	0.00-0.06
149.5	0.26	0.17-0.35	0.01	0.00-0.02
152.5	0.20	0.11-0.29	0.00	0.00-0.01
155.5	0.15	0.07-0.23	0.00	0.00
158.5	0.11	0.04-0.18	0.00	0.00
161.5	0.08	0.02-0.14	0.00	0.00

In stage 4, we estimated size-specific molting probabilities via logistic regression. We repeated stages 3 and 4 a large number of times to take into account the uncertainty in the randomization and variability in premolt size estimates. Finally, the results of these analyses were then combined to produce a single overall inference.

Estimated size-specific annual molting probabilities and corresponding 95% confidence intervals for female Dungeness crabs, made from 1994 and 1998 shell condition data collected at Clam Beach, northern California, are presented in Table 1. Table 1 shows a steep decline in molting probability ($\hat{p}$) from near 0.90 to near 0 over the narrow range of 131 to 144 mm premolt carapace width in 1998. Whereas the estimated molting probability for females at 144 mm remained high at 0.4 in 1994, followed

by a gradual decline to less than 0.1 at carapace widths exceeding 158 mm CW. In view of these findings, we conclude that interannual variation in size-specific molting probabilities may make a substantial contribution to between-year variation in growth and reproductive potential of female Dungeness crabs.

In summary, in this paper we developed a new approach to estimating size-specific molting probabilities for species that exhibit a well-defined molting season. By incorporating sperm plug data from the substudy for molting status calibration, the proposed method effectively diminishes the bias resulting from potential misclassification of shell condition in molting probability estimation.

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Effects of Windchill on the Snow Crab (*Chionoecetes opilio*)

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Abstract

Tens of millions of snow crabs, *Chionoecetes opilio* (Fabricius), are sorted and discarded each year during the Alaskan snow crab fishery. The fishery occurs during winter in the Bering Sea and there is a high probability that discarded crabs will be exposed to cold air temperatures and high winds (windchill) during the sorting process. A laboratory experiment was conducted to measure responses of snow crab to a range of air temperatures and wind speed to assess the effects of windchill. Male snow crabs of sizes typically discarded during the fishery were collected from the Bering Sea. A wind tunnel in a walk-in freezer simulated the windy and cold conditions on the deck of a Bering Sea crab boat. Crabs were exposed to wind speeds from 8 to 16 m per second and air temperatures from –2 to –10ºC for 5 minutes. Mortality, reduced activity in the form of a righting response, and limb loss were assessed before, immediately after, 1 day, and 7 days post-treatment. Snow crabs experienced 40-100% mortality at windchill values from –10ºC to –16ºC. Limb loss was variable, but pronounced at windchill values below –10ºC. Righting response was impaired after all but the least severe treatment. Reduced exposure time significantly reduced mortality.

Introduction

The snow crab fishery in Alaska occurs during winter months when conditions in the Bering Sea are the most severe. Sublegal-sized males (<78 mm carapace width, CW) and females must be returned to the sea; crabs deemed unmarketable such as very old-shell males, injured crabs, and small males (78-101 mm CW) are also sorted and discarded. Discarded snow crabs receive aerial exposure to harsh windchill conditions during pot retrieval and sorting.

Extreme heat loss can be fatal for any organism and is especially problematic for heterothermic crabs. Air movement accelerates heat loss, so the effects of wind must also be considered. Accelerated cooling due to the combination of cold temperatures and wind is referred to as windchill (Court 1948). Air movement disturbs the laminar insulating layer of air around an object and serves to draw heat away from that object (Court 1948).

Aerial exposure for short periods has minimal effects on snow crab fitness. In an experiment on temperature tolerance of snow crabs, crabs stored in moist air for 4 days at 3ºC or 8ºC had no mortality (McLeese 1968). Time to 50% mortality was 8.5 days at 3ºC and 1.9 days at 13ºC (McLeese 1968), demonstrating that snow crabs can survive aerial exposure to cool moist air for short periods with no mortality.

Aerial exposure to cold air temperatures affects red king crabs, *Paralithodes camtschaticus*, and Tanner crabs, *Chionoecetes bairdi*. Short duration exposure to low temperatures caused the same effects as longer exposure at higher temperatures (Carls and O'Clair 1990). Severe exposure (long duration at moderate temperatures or short duration at low temperatures) caused death in Tanner crabs and red king crabs (Carls and O'Clair 1990, 1995). Moderate exposures caused reduced vigor, limb loss, depressed feeding rates, and decreased juvenile growth in Tanner crab (Carls and O'Clair 1995). Studies that simulated capture and release indicated that handling alone does not cause significantly higher mortality in red king crabs (Zhou and Shirley 1995) and Tanner crabs (MacIntosh et al. 1996). Snow crabs, having morphology similar to Tanner crabs, may have similar responses to handling. However, laboratory handling is likely to be conservative when compared to field handling. During the fishery, snow crabs may fall from 1 meter to a hard surface as pots are tipped for unloading (Tracy and Byersdorfer 2000). Crabs can be pinched and crushed under the pot, and the mass release of many crabs through small scuppers may also cause damage.

The combined effect of wind and cold air temperature, or windchill, could be the most severe stressor on snow crabs. Red king crabs (Shirley 1999) and Tanner crabs (Shirley 1998) had dramatic responses to windchill exposure. Laboratory experiments with juvenile male Tanner crabs demonstrated that exposure to windchill values commonly encountered during the fishery resulted in mortality, limb loss, and decreased activity (Shirley 1998). Five-minute exposures to temperatures of –7ºC and wind speed of 16 m per second resulted in 90% mortality of Tanner crabs within a week.

Incidental capture of snow crabs occurs in many fisheries in the Bering Sea, but the snow crab fishery itself accounts for most of the bycatch. Between 1994 and 1999, bycatch due to the snow crab fishery ranged from 40 million to 75 million crabs per year (Table 1). Of lesser importance were groundfish trawls, groundfish fixed gear, scallop dredging, and other crab fisheries. Bycatch of snow crabs is decreasing in the groundfish fisheries and is not a major component of the total bycatch. The majority

Table 1. Bycatch of *C. opilio* in Bering Sea fisheries, 1994-1999 and estimated abundance of small males (thousands of crabs) (NPFMC 2000).

Year	Directed crab pot	Groundfish trawl, fixed gear, scallop dredge	Bycatch total	Abundance of small male opilio (<102 mm)	Bycatch as % of small males
1994	53,083	12,517	65,600	4,282,500	1.53
1995	48,734	5,396	54,130	4,086,800	1.33
1996	56,571	4,016	60,587	2,700,100	2.24
1997	75,005	6,026	81,031	1,490,800	5.44
1998	51,591	4,905	56,496	1,014,700	5.57
1999	41,666	1,965	43,631	517,000	8.44

of snow crab bycatch are small, legal-sized males (Moore et al. 2000). The legal size and marketable size of snow crabs differ; crabs in the size range between legal size (79 mm CW) and marketable size (102 mm CW) are discarded. Female snow crabs are estimated to account for less than 1% of the snow crab bycatch. Sublegal-sized male snow crabs (<79 mm CW) are estimated to account for 2% or less of the total bycatch (NPFMC 2000).

Total bycatch declined from 81 million crabs in 1997 to 43 million in 1999. However, bycatch as a percentage of the abundance of similar-sized male crabs (<102 mm CW) is increasing (Table 1), probably due to increased fishing effort as crab numbers decline. This trend is not apparent when bycatch is reported as a percentage of the estimated abundance of both sexes and all size classes of crabs (e.g., Witherell 2000). Since the majority of bycatch are male snow crabs less than 102 mm CW, percentages should reflect the estimated abundance of crabs of that size.

Sublethal effects such as autotomy and limb loss can occur when snow crabs are caught and discarded. Autotomy, the reflexive severance of an appendage, occurs naturally in snow crabs and is considered an adaptation to avoid predation (Juanes and Smith 1995). Reduction in growth, foraging efficiency, mating success, and increased vulnerability to predation and intraspecific competition are potential future costs of autotomy. Loss of a single limb was the most common injury observed in decapod populations (Juanes and Smith 1995). Snow crabs with regenerated limbs are rarely observed in the Bering Sea (R. Morrison, Alaska Department of Fish and Game, Dutch Harbor, pers. comm.). In a laboratory study of limb regeneration, no crabs over 90 mm carapace width were observed to regenerate limbs (Miller and Watson 1976). Smaller crabs regenerate limbs but require at least 2 molts for regeneration to 74% of their full length (Miller and Watson 1976). Since most of the snow crab bycatch consists of

males larger than 90 mm, limb loss can be considered permanent. Injury rates in the field were highly variable, but averaged 24% of discarded crabs (Tracey and Byersdorfer 2000).

Snow crabs of the size caught in the fishery may not regenerate limbs because the time and number of molts required is past terminal molt; molting rarely occurs beyond terminal molt. Tanner crabs, red king crabs, and American lobster (*Homarus americanus*) had a negative correlation between body size and injury (Juanes and Smith 1995). A negative correlation between body size and injury may indicate that injury reduces survival, and fewer crabs with lost limbs survive to grow to a larger size.

The objectives of this study were to determine the effects of windchill exposure (cold air temperature and wind) on mortality, limb loss, and activity (measured as a change in the righting response) for male snow crabs (*Chionoecetes opilio*) of the size typically discarded as bycatch.

Materials and Methods

This study was the first to use live *C. opilio* from the Bering Sea in a laboratory experiment. Male snow crabs of the size typically discarded by the fishery were collected (mean CW ± 1 S.D. = 96.3 mm ± 9.0 mm) from the Bering Sea in April 2000. Crabs with bitter crab disease, black mat syndrome, pepper crab, or torch disease (Jadamec et al. 1999) were not retained. Care was taken to minimize handling and exposure of the crabs to air. Crabs were maintained in flow-through seawater tanks at the Juneau Center, School of Fisheries and Ocean Sciences and the National Marine Fisheries Service, Auke Bay Laboratory. The seawater intake for both labs is at –30 m in Auke Bay; temperature and salinity variations were within the range recorded for the Bering Sea. Seawater discharge from the tanks was passed through a freshwater reservoir before being routed to the seawater return line.

Crabs were observed for 2 weeks prior to initiation of the experiment to ensure health and uniformity. Size measurements, previous damage (old injuries), shell condition, and hemolymph screening for bitter crab disease were performed on all specimens. Crabs were marked with Floy tags attached with a plastic cable tie to the merus of the fourth or fifth pereiopod. After the completion of the study, the crabs were frozen and disposed at the Alaska Department of Fish and Game tag lab.

The experiment was composed of seven experimental treatments and one control treatment with 15 replicate crabs in each treatment. Crabs were placed in tanks with one tank per treatment. Each treatment contained a sample of crab sizes with minimized variation in size between tanks.

Exposure times reflected actual sorting time measurements from the field. Crabs were exposed to treatments for 5 minutes, similar to the average maximum aerial exposure measured by observers in 1998 (Tracy and Byersdorfer 2000). Total exposure time was reduced to 2.5 minutes for two of the most severe treatments.

Windchill Treatments

Wind and cold treatments were selected using the best available weather data reflective of the Bering Sea during the crabbing season. Unfortunately, the best weather data are obtained from a National Weather Service buoy 300 miles southwest of the fishing grounds. Weather at the buoy and at the fishing grounds was assumed to be similar. Windchill treatments were performed with the following combinations of wind speed and temperature for an exposure time of 5 minutes: –2ºC and 8 m per second, –2ºC and 16 m per second, –6ºC and 8 m per second, –5ºC and 16 m per second, –10ºC and 8 m per second, and a control with no exposure. The two most severe treatments, –5ºC and 16 m per second and –10ºC and 8 m per second, were also performed with an exposure time of 2.5 minutes.

The windchill for each treatment was calculated using the National Weather Service formula:

$$Temp_{windchill} = Temp_{initial} + 0.045 \times [(5.27 \times \sqrt{Windspeed}) + 10.45 - (0.28 \times Windspeed)] \times (Temp_{air} - Temp_{initial})$$

where $Windspeed$ = mean wind speed (km/hour), $Temp_{air}$ = ambient temperature (ºC), and $Temp_{initial}$ = initial temperature of body (ºC). The initial body temperature of a crab was assumed to be the same as the holding water temperature (~6ºC).

Windchill treatments were performed in a walk-in freezer. Temperature was recorded every minute and averaged for the duration of the treatment. A squirrel cage blower was used to generate wind speeds through a wind tunnel (44 × 38 × 239 cm) made of wood and plastic sheeting. An electronic anemometer measured wind speeds within the tunnel. To minimize aerial exposure, crabs were moved to the cold room while immersed in seawater. Crabs were placed inside the wind tunnel while confined within mesh cages (43 × 33 × 23 cm, 2.5 × 3.8 cm mesh) to insure uniformity of exposure aspect. Immediately after exposure, crabs were replaced in seawater and returned to the lab.

Observations of mortality, limb autotomy, and the righting response were made for each numbered crab immediately after crabs were returned to the wet laboratory, then again after 24 hours, and after 7 days. Mortality was determined by detection of movement of the scaphognathites (gill bailers), pereiopods, mandibles, and maxillae. Functional mortality, where the crab remained moribund for extended periods, was noted. Mortality was assessed daily for 7 days post-treatment and dead crabs were removed from the tanks. Crabs that survived treatments were used to test significance of autotomy and included in the analysis of righting response. The righting response is a complex reflex requiring muscle coordination and balance and can be a sensitive measure of well-being of organisms (Shirley and Stickle 1982). Righting response was determined by placing the crabs on their dorsum and measuring the time in seconds (to a maximum

of 300 seconds) required for the crabs to right themselves. Each crab served as its own control, as the righting response of individual crabs was measured prior to and after exposure.

Statistical Analysis

The snow crabs in the experiment were captured in the wild before being transported to the laboratory for study. Some crabs may have been injured or slightly impaired during capture and transportation. The speed of the righting response is a measure of well-being, therefore crabs that had a slow initial righting response were removed from the data analysis. Any crab that did not right within 300 seconds before treatment was removed from the data analysis. The removal created unbalanced samples, but robust statistical analysis was still possible.

Statistical methods were selected as described by Kleinbaum et al. (1998) and Zar (1996). The Statview statistical program was used to perform calculations for statistical tests. Significance was tested at an alpha value of 0.05 unless otherwise noted. A chi-square test was used to test the significance of mortality differences among treatments and between the 2.5 minute and 5 minute exposure treatments. An unpaired *t*-test was used to test the significance of the differences between the mean size (measured as carapace width) for the pooled dead and live crabs. An unpaired *t*-test was also used to assess the difference between the mean amount of prior damage (scars from prior injuries) for the pooled dead and alive crabs. Logistic regression was performed to develop a model to predict mortality likelihood given exposure for 5 minutes to a certain windchill value. Logistic regression is a technique for modeling dichotomous dependent variables and uses maximum likelihood to estimate model parameters (Kleinbaum et al. 1998). A logistic classification table was used to assess the correctness of the fit of the model to the observed values. The Kruskal-Wallis test was used to test significance of treatments on limb autotomy and righting response time. Dunnett's test was used to test the significance of the exposure treatments against the control treatment.

Results

Mortality

Mortality increased with increasing windchill severity (Fig. 1). Mortality was 100% at a windchill of –16ºC (–10ºC and 8 m per second). Mortality was 80% and 40% for the –5ºC and 16 m per second and –6ºC and 8 m per second treatments, respectively (Fig. 1). No deaths occurred in the two least severe treatments or the control. Mortality differences among windchill treatments were significant (chi-square test, $P < 0.0001$, d.f. = 5). Size and prior damage did not affect mortality. There was no difference between the mean size (measured as carapace width) (*t*-test, $P = 0.354$) and the mean amount of prior damage (scars from prior autotomy) (*t*-test,

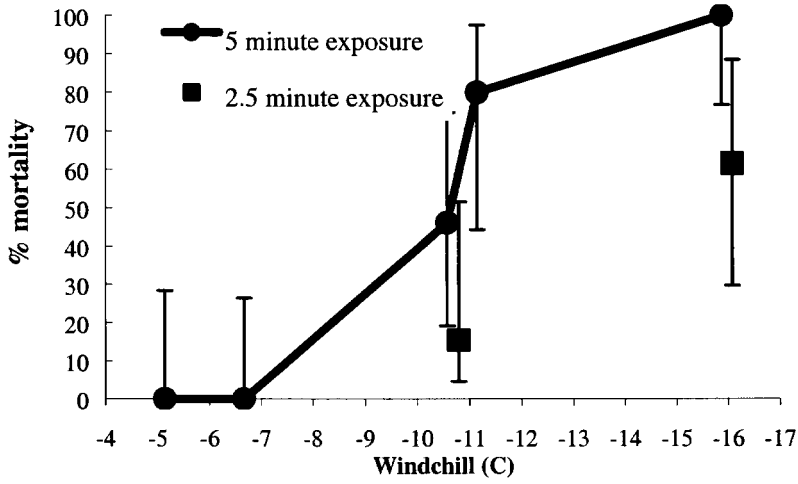

Figure 1. Percent mortality of C. opilio exposed to windchill treatments. Error bars indicate 95% confidence limits.

$P = 0.165$) for the dead and alive crabs. Shorter exposure time reduced mortality (Fig. 1). The mortality differences between the 2.5 minute and 5 minute exposure times were significantly different (chi-square $P < 0.0001$, d.f. = 1).

A logistic regression was performed to develop a model to predict the probability of mortality given exposure for 5 minutes to a certain windchill value and was significant at an alpha value of 0.1 (Fig. 2). The resulting prediction equation is:

$$pr(dead = 1) = \frac{1}{1 + \exp[-(-12.161 - 1.182 \times windchill)]}$$

For example, the probability of death for a snow crab exposed to a windchill of –10ºC for 5 minutes is 0.415. The model predicted whether a crab was alive or dead 83.3% correctly for the observed values.

Autotomy

The percent autotomy for each crab was calculated by dividing the total number of limbs lost after the treatment by the number of limbs the crab had before the treatment. Of the 120 specimens used in this study, none had regenerated limbs, and 56% had previous injuries (limb bud scars). Autotomy was measured as the proportion of limbs dropped. The arcsine transformation is recommended for proportion data (Zar 1996), but in this

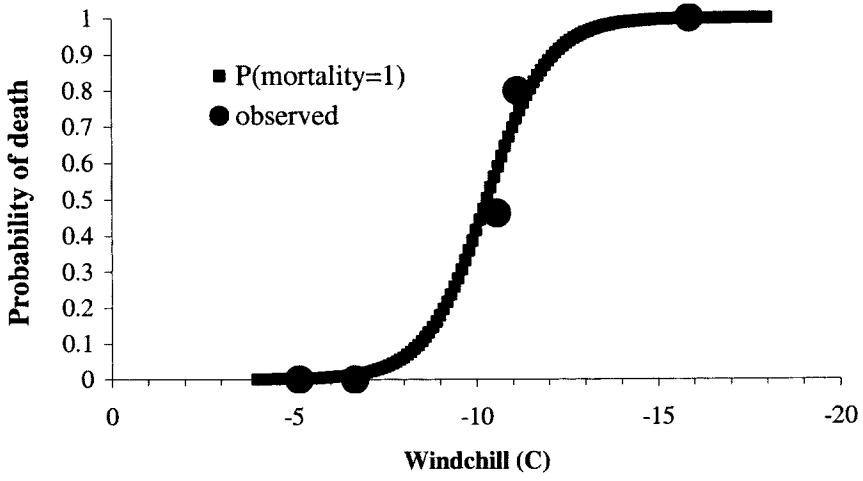

Figure 2. Probability of mortality of C. opilio after 5 minute windchill exposure.

case the transformation did not generate a normal underlying distribution. Instead, a nonparametric analysis of variance, the Kruskal-Wallis test, was used to test the hypothesis. The effect of the windchill treatments on autotomy was significant ($P = 0.002$). Dunnett's test was used to test significance of the treatments against the control. One crab from the control group autotomized one limb (average autotomy for control group = 0.01). The control group and the exposures of -2×8 m per second and -2×16 m per second were not significantly different from one another (Table 2). A significant difference existed among all other treatments. High variability was associated with autotomy within windchill treatments. For example, a range of 0-80% autotomy was observed at a windchill of –10.5ºC (Table 2).

The rear walking legs were dropped most frequently (Fig. 3). The third and fourth walking legs accounted for 75% of all autotomy. The chelipeds were rarely autotomized.

Righting Response

Each crab's righting response was measured before and after treatment so each crab served as its own control. The righting response times followed a modified Pareto distribution; that is, a skewed distribution of positive values with a long right-hand tail (Zar 1996). However, the righting response times were not measured past 300 seconds (assumption of no response past 5 minutes of no activity), which resulted in a bimodal Pareto distribution. The assumption of normality could not be met. Visual inspection of

Table 2. Autotomy by *C. opilio* following exposure to windchill treatments.

Treatment	Dunnett's Test (% autotomy)			Average autotomy (%)	Minimum autotomy (%)	Maximum autotomy (%)	N
	Mean difference[a]	Critical difference	Significant autotomy?				
Control	0	N/A	No	0.01	0	0.1	10
–2ºC × 8 m per second	–0.028	0.141	No	0	0	0	11
–2ºC × 16 m per second	0.032	0.144	No	0.4	0	5.0	12
–6ºC × 8 m per second	0.634	0.165	Yes	38.9	10	89	7
–5ºC × 16 m per second	0.740	0.237	Yes	66	50	82	2
–10ºC × 8 m per second	N/A	N/A	N/A	N/A	N/A	N/A	0
–5ºC × 16 m per second (2.5 minutes)	0.344	0.321	Yes	14.6	0	84	13
–10ºC × 8 m per second (2.5 minutes)	0.359	0.256	Yes	24.2	0	50	5

[a]Mean difference is the average difference between autotomy of crabs in the control treatment and the exposure treatment.

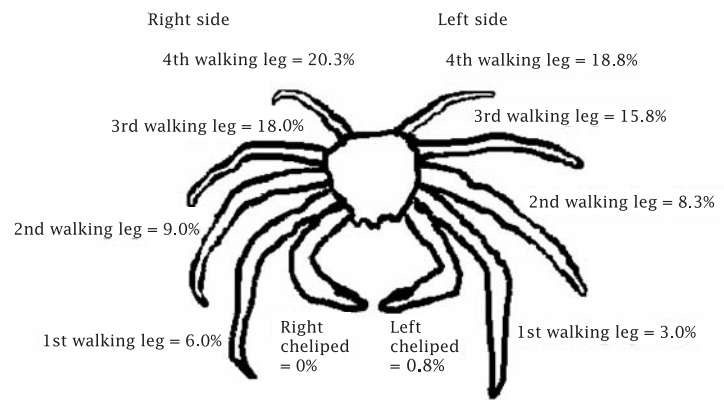

Figure 3. Frequency of types of limbs lost by C. opilio, all treatments combined. Results are pooled for all crabs (N = 120) with 133 limbs lost in total. Note that not all the crabs had a full complement of limbs prior to initiation of the experiment.

the distribution of residuals also disproved the assumption of homoscedasticity. The lack of homoscedasticity is mainly a function of the response times that are truncated at 5 minutes. Therefore, the severe treatments in which all the crabs did not right themselves after 5 minutes had lower variances than the control and the less severe treatments. Nonparametric analysis of the change in righting response was necessary. The Kruskal-Wallis test was used to test the effect of windchill treatment on the righting response time. The change in response times due to treatment was significantly different ($P = 0.002$). Dunnett's test (used for specifically comparing controls to other treatments) (Zar 1996) did not show a significant difference between the control and the least severe windchill treatment, but a significant difference did exist between the control and the other three treatments (Table 3). Response times were either significantly slower or nonexistent. Response times were also significantly slower after the 2.5 minute exposure treatments. However, there was no significant difference between the response times from the 2.5 minute exposure treatments and the 5 minute exposure treatments (Table 3).

Discussion

Mortality increased with increasing severity of treatment. The probability of mortality increased after a windchill exposure of –10.3ºC for 5 minutes; no mortality occurred at less severe exposures. Death occurred even when a snow crab was exposed for 2.5 minutes at a windchill of –10.3ºC. The rapid cooling associated with windchill may cause some failure at the cellular level. Ice crystals forming in the cytoplasm disrupt cell membranes and cell death occurs. As heat loss approaches lethal limits, neurons are the first cells to fail (Prosser 1991). Critical neuron failure is a probable cause of death. Body parts with high surface area to volume ratio are probably the most susceptible to freezing damage. The appendages, eye stalks, and mouth parts could become irreversibly damaged and would cause impairment to the crab. The filamentous gills are also susceptible; injury to the gills could initiate mortality.

The mortality threshold between the –5ºC × 16 m per second and –6ºC × 8 m per second treatments may be due to the different wind speeds. High wind speed may increase the rate of water loss and evaporation from the gill chambers thereby increasing the potential for freezing damage to the gills. The threshold response could be affected by many factors. The time of water retention in the gill chambers could have varied depending upon the angle from which the crabs were removed from the water. Although size (measured as carapace width) and prior injuries were found to be insignificant in predicting mortality, a larger sample size controlled for these variables might have determined effects. However, the size range of crabs incidentally caught by the fishery is narrow so stratifying treatments by size may not be a useful endeavor.

Table 3. Change in righting response *of opilio* following exposure to windchill treatments.

Windchill (ºC)	Treatment	Righting response after 7 days (s) (Dunnett's test)		
		Mean difference[a]	Critical difference	Significant?
–5.14	–2ºC × 8 m per second	37.2	110.3	No
–6.67	–2ºC × 16 m per second	184.1	107.8	Yes
–10.5	–6ºC × 8 m per second	279.3	126.2	Yes
–11.2	–5ºC × 16 m per second	291.1	204.5	Yes
–15.8	–10ºC × 8 m per second	N/A, all crabs dead		
–16.1	–10ºC × 8 m per second (2.5 minutes)	263.4	122.3	Yes
–10.8	–5ºC × 16 m per second (2.5 minutes)	124.6	91.1	Yes

[a]Mean difference is the average difference in seconds between the righting response time of the crabs in the control treatment and the exposure treatment.

Mortality rates decreased when exposure time decreased. Physiological responses such as impaired oxygen delivery caused in part by freezing damage to the gills may cause death due to rapid cooling, but low demand for oxygen at cold temperatures by heterotherms and the quickness of the onset of mortality suggests neuronal cell damage.

Mortality of bycatch from the directed Bering Sea snow crab pot fishery was estimated at 24% (NPFMC 2000), but was based only on anecdotal information. Nevertheless, mortality estimates that integrated laboratory models of mortality, daily estimates of bycatch, and available weather data were close to what had been previously estimated (Warrenchuk and Shirley, in press).

Autotomy, a predator escape response, also results from a nonspecific stressor such as windchill. Autotomy of a limb initiates at the cleavage plane between the coxa and merus (Skinner 1985). A cuticular stress detector that responds to distortion of the cuticle may innervate the autotomy neuron (Wales et al. 1971). Windchill exposure that results in freezing of part or the whole of a limb may trigger the autotomy response.

Severe windchill treatments included death as a final response of the crabs to the treatments. Treatments that stressed a portion of the crabs to death complicated the results, as autotomy is a deliberate response that could be compromised by severe windchill. Severe windchill may damage the nerves associated with the autotomy response such that no further autotomy (or many other behaviors) is observed. Autotomy is probably

maximized when the windchill exposure is severe enough to trigger the synapse, but not so severe as to damage the nerves.

Autotomy resulting from windchill exposure differs from natural, predator-induced autotomy. Windchill-induced autotomy may be more severe as multiple limbs can be lost following exposure. Windchill exposure is a nonspecific stressor whereas predator-induced autotomy is directed toward one or a few limbs. The stress of windchill exposure is analogous to a predator that attacks every limb at the same time. Multiple limb loss in populations of the related Tanner crab is rare (Juanes and Smith 1995), but sampling bias is probable.

The extent that appendage loss might affect an individual varies with the number of damaged limbs. The loss of one walking leg would be expected to have a minimal effect on crab fitness. However, the additive effects of many lost limbs and the pattern by which they are lost will affect crab fitness. Autotomy does not necessarily preclude survival. A shore crab, *Hemigrapsus oregonensis*, can survive over a year with no limbs (S.D. Rice, National Marine Fisheries Service, Auke Bay Laboratory, Juneau, unpubl. data). However, there is probably some level of autotomy that may affect survival. Snow crabs have 10 limbs: four pairs of walking legs and a pair of chelipeds. The chelipeds are presumably the most important for survival and function in feeding, defense, and mating (grasping of females). Chelipeds were rarely lost as a result of windchill in our experiment. The rear (fourth) walking leg was the most readily autotomized limb, followed by any other walking leg. The rear walking legs may be important for some crab behaviors. When healthy crabs right themselves after being turned over, the most common technique involves a dorsal to ventral flip from anterior to posterior. Snow crabs with a full number of limbs use both rear (fourth) walking legs to first contact the substrate and initiate the flip. The smaller diameter limbs may be more susceptible to freezing damage and autotomy. Mathematical models have demonstrated that the limbs may cool faster and reach a lower temperature than the crab body (P. van Tamelen, Alaska Department of Fish and Game, pers. comm.).

Mating behaviors may be affected by autotomy. Tanner crab mating behavior such as standing over a female, standing "high-on-legs," kicking, and body lifting (of the female above the male) (Donaldson and Adams 1989) rely on leverage and balance and may be difficult without a full complement of limbs. These behaviors have also been observed during antagonistic interactions with other males (Donaldson and Adams 1989). Autotomy could affect both mating behavior and competitive ability of male snow crabs.

Snow crabs in the laboratory flare out their limbs when grasped. It is a behavior that may stem from predator avoidance. A predator that seizes the crab in the same fashion would be presented with a much larger effective prey size and would have difficulty fitting the crab into its mouth. A crab with fewer limbs would be easier to consume.

Injury rates of snow crabs aboard catcher-processors during the 1997-1998 Bering Sea snow crab fishery were assessed from 14,000 nonretained snow crabs from 394 sampled pots (Tracy and Byersdorfer 2000). Injury rates varied among vessels from 7% to 44% of crabs sampled with an average of 24%. Autotomized legs were the most prevalent injury and comprised 59% of the total injuries. Major damage (cracked carapace, bent or torn limbs, chela damage) composed 10.9% of the total injuries. Weather conditions were not noted during the injury assessment sampling.

Injury rates from observer data are the rates of instantaneous limb loss that occurs over the few minutes that the crabs are held. Instantaneous limb loss in the laboratory study occurred, but snow crabs also autotomized limbs over 7 days of observation. This suggests that estimates by observers of bycatch limb loss are conservative.

Annual pot surveys by observers on fishing vessels assess the crab condition (and hence previous injuries). If the rate of limb loss in discarded crabs is high, this should be evident in pot samples as the crabs are captured again the following year. However, if injury and limb loss reduce survival, then estimates of bycatch limb loss will be conservative.

The snow crabs in this experiment were handled carefully after being exposed to the windchill treatments. Bycatch snow crabs are not handled as gently on a fishing vessel, and any rough handling would exacerbate limb loss.

The righting response was impaired in all but the least severe windchill treatments. A threshold exists above a severity of exposure of –2ºC and 16 m per second (~–6ºC windchill) where the righting response is impaired.

A functional righting response depends on the unanimity of the nervous system and the musculature. The nervous system is complex and even slight damage can result in a loss of function. Loss of coordination was evident by increased righting response times after red king crabs and Tanner crabs were exposed to wind and cold (Shirley 1998, 1999). Snow crabs exposed to windchill below –6ºC also had an impaired righting response. A snow crab with no righting response, in a state of chill coma, could be considered functionally dead.

Some red king crabs and Tanner crabs in a state of chill coma recovered seven days post exposure (Shirley 1999). In this study, several snow crabs with no righting response immediately after the less severe treatments recovered after seven days post exposure, suggesting the potential to recover from mild exposure. Snow crabs that survived severe to moderate windchill exposure were unlikely to recover.

Loss of mobility was evident after windchill exposure. Very little active movement was observed in crabs that survived windchill less than –10ºC. Only 4 of 8 surviving crabs from the –6ºC and 8 m per second treatment were observed actively moving. Sporadic motion of the limbs with no net movement described the remaining survivors. All crabs in the less severe windchill treatments actively moved, even when no righting

response was evident. Crabs that could move exhibited jerky, uncoordinated motion of the walking legs. High "standing-on-legs" travel was not noted. Crab movement could be described as lifting the walking legs, pushing and sliding the body across the substrate.

Impaired mobility could alter foraging efficiency, seasonal migration, and daily movement behaviors. However, little is known about movement patterns of snow crabs in the Bering Sea. A tagging and recapture experiment in the Gulf of St. Lawrence found that snow crabs moved up to 3 km in 48 hours (Brêthes et al. 1985).

Loss of mobility and coordination could make crabs more vulnerable to predation. Cod (*Gadus morhua*) prey seasonally on snow crab in the northwest Atlantic and can consume softshell males up to 110 mm CW (Robichaud et al. 1991). Heavy predation on Tanner and snow crabs occurs in the southeastern Bering Sea by Alaska and Bering skates, wattled eelpout, Pacific cod, and four sculpin species (Jewett 1982). Predation might be more severe if movement or escape responses of crabs were impaired.

It is ironic that the snow crab fishery itself, which catches the abundance of snow crab bycatch in the Bering Sea, is not constrained by any bycatch limits. The North Pacific Fishery Management Council could set limits on the bycatch of snow crab using management similar to the groundfish fisheries. The groundfish trawl fisheries are constrained by prohibited species catch (PSC) limits for snow crab. The snow crab PSC cap is set at 0.1133% of the Bering Sea stock abundance based on annual National Marine Fisheries Service trawl survey data, with a minimum PSC of 4.5 million crabs and a maximum of 13 million snow crabs (NPFMC 2000).

Another option is to incorporate the estimated bycatch mortality in guideline harvest levels. However, with bycatch mortality included in harvest limits, there would be no incentive for fishermen to release bycatch with any concern for survival.

Ultimately, the fate of harvested snow crabs lies with the fishermen. They can choose whether or not to fish during extreme cold and severe weather. Deckhands could prioritize returning discarded crabs to the water and do so as quickly as possible. Vessel owners can outfit their boats with slides or chutes to release bycatch as opposed to forcing crabs through the scuppers. In a fishery where the number of discarded crabs in one year can be higher than the allowable harvest the following year (i.e., in 1999-2000), ensuring the survival of discarded crabs makes good business sense.

Acknowledgments

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Testing Carapace Morphology Characteristics for Field Identification of *Chionoecetes* Hybrids

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Abstract

The ability of Tanner crabs, *Chionoecetes bairdi,* and snow crabs, *C. opilio*, to hybridize in the Bering Sea was first recorded in 1969 and biologists since then have struggled with the identification of the various forms of the hybrids. The hybrids are not uniformly intermediate between the parental types, but form a smooth cline of morphological types making the field identification of hybrids a difficult and subjective task. Over 1,000 genetically typed carapaces were examined in an effort to develop an accurate field identification technique for hybrids and their parental species. An ordinal scoring system was developed for six morphological characters with scores ranging from 1 for *C. bairdi* to 5 for *C. opilio*, with hybrids being intermediate. Photographs of character variation by crab type are presented. A classification tree and discriminant function analysis were applied to learning sets of carapace scores, and then to test sets, but neither technique could reliably identify carapaces when applied to data outside of the individual learning and test sets. The scoring system developed here can be used with good success for developing a classification scheme for a single scorer, but inconsistency of scorers, as demonstrated by components of variance analysis, proved an impediment to developing a broadly applicable scheme.

Introduction

Tanner crabs, *Chionoecetes bairdi,* and snow crabs, *C. opilio,* are both widely distributed in the North Pacific Ocean and Bering Sea, with the snow crab having a more northerly distribution that extends to the Arctic Ocean. Snow crabs also occur in the northwest Atlantic Ocean (Fig. 1). Hybrids of Tanner crabs and snow crabs were first recognized by their intermediate morphological characters in 1969 (Karinen and Hoopes 1971) in an area of distributional overlap in the eastern Bering Sea (Fig. 1). The hybridization was later confirmed through the use of protein electrophoresis by Johnson (1976) and expanded upon by Grant et al. (1978) and Merkouris et al. (1998). Hybrids in general do not present a single phenotype, but rather a wide range of types intermediate to the two parental species. In addition, the gradation is typically not uniform for all characters, but forms a mosaic of types (Barton and Hewitt 1985). The *Chionoecetes* hybrids follow this pattern. There is also evidence that these hybrids are fertile and will produce an F_2 generation or may backcross with the parental species (Merkouris et al. 1998). The F_2 and backcross hybrids have proven difficult to distinguish from the parental species using either genetic or morphological methods (Campton 1987).

The intermediacy of hybrid morphological characters and their gradation into those of the parent stocks pose problems in the field identification of *Chionoecetes* in the eastern Bering Sea. *Chionoecetes bairdi* and *C. opilio* have both supported valuable commercial fisheries in the eastern Bering Sea, and those identification problems have resulted in problems for fisheries management. During the 1990 commercial fishery for *C. opilio* in the Bering Sea, for example, concerns were raised due to sublegal *C. bairdi* being landed as "hybrids" (ADFG 1991). Those concerns were complicated by legal questions on identification of *C. bairdi*, *C. opilio*, and hybrid crabs during commercial fisheries and on the legality of retaining hybrids during the *C. bairdi* and *C. opilio* commercial fisheries. In 1991 the Alaska Board of Fisheries resolved those legal questions by adopting a regulatory definition of *C. bairdi* and *C. opilio* (5 AAC 35.521; ADFG 1992) that was intended to minimize commercial landings of *C. bairdi* as hybrids or *C. opilio*. Under that legal definition, *C. bairdi* are identified on the basis of eye color and epistome characteristics; all *C. bairdi*, *C. opilio,* and hybrids not conforming to those characteristics are legally considered *C. opilio*.

Although the legal definition has apparently been effective in the purpose for which it was developed, it provides no means for distinguishing hybrids from *C. bairdi* or *C. opilio*, which is still an important need for fisheries management and assessing population trends. For example, accurate assessment of bycatch during commercial fisheries is hampered by the difficulty in reliably identifying the three crab types that can occur as bycatch. The potential errors can be great. Using the *C. opilio* fishery in 1997 as an example, it was estimated by the Alaska Department of Fish and Game (ADFG) that the bycatch of *C. bairdi* was 4.52 million, but the

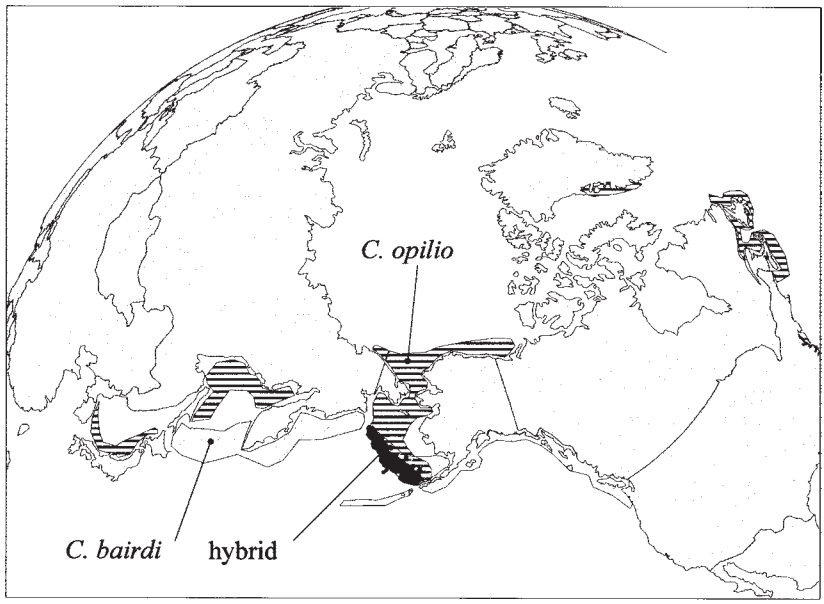

Figure 1. Worldwide range of Chionoecetes bairdi and C. opilio, with the location of hybrid observations.

hybrid bycatch was estimated to be nearly double that at 8.64 million (Moore et al. 1998). Misidentification of even a small percentage of the hybrids could drastically change the assessment of effects on *C. bairdi* caused by the *C. opilio* fishery. Electrophoretic techniques could provide a definitive means for detecting *Chionoecetes* hybrids, but they are costly, time-consuming, and require specialized laboratory equipment. A computer-image processing system has been developed that can identify the carapaces of *C. bairdi*, *C. opilio*, and hybrid crabs (Donaldson 1996), but it also is costly and requires specialized equipment.

Fishery observers, dockside samplers, and biologists on stock-assessment surveys must sort through thousands of crabs and cannot spend more than a few seconds identifying individual crabs. The goal of our study was to assess the use of previously identified morphological characters for the identification of hybrids by field biologists as a quick and reasonably accurate alternative to genetic and image-processing techniques.

Methods

A set of 1,114 crab carapaces (381 *C. bairdi*, 469 *C. opilio*, and 264 hybrids) that were genetically typed for previous studies (Merkouris et al. 1998,

Donaldson 1996) were available for this study. A literature review was conducted to identify morphological characters of the carapace that have been frequently noted to vary between the three crab types (Karinen and Hoopes 1971, ADFG 1993, Jadamec et al. 1999). Six characters were determined to be diagnostic and easy to recognize: carapace shape as indicated by visual impression of width:length ratio, shape of the ventral margin of the epistome, shape of the rostrum in dorsal view, shape of the rostrum in lateral view, development and spacing of pterygostomian spines, and degree of scalloping at the edge of the carapace (Fig. 2). The characters chosen for analysis exhibit a cline of forms varying from the *C. bairdi* to *C. opilio* types with hybrids being intermediate. Each character was divided into five classes, ranging from a score of 1 for the *C. bairdi* type to a score of 5 for the *C. opilio* type. Eye color, which was often mentioned as being a useful character, was not available for use with the dried carapace specimens. Eye color is not distinguishable by some colorblind individuals and its assessment can be affected by lighting conditions.

On December 15, 1999, a subset of 45 carapaces from 10 *C. bairdi*, 10 *C. opilio*, and 25 hybrids crabs was selected for scoring by 28 crab biologists from the Alaska Department of Fish and Game, the U.S. National Marine Fisheries Service, the University of Alaska, and the Canadian Department of Fisheries and Oceans and by 15 observer trainees from the University of Alaska Observer Training Center. The biologists had varying amounts of experience in identifying Bering Sea *Chionoecetes* and the observer trainees had no previous experience. The scorers were given a brief training session in identifying *C. bairdi*, *C. opilio*, and hybrid crab carapaces and were provided with an illustrated reference sheet depicting the 1-5 scale of scores for each character. The scorers were unaware of the genetic identity of the specimens or the number of carapaces from *C. bairdi*, *C. opilio*, or hybrid crabs in the sample. The results for the biologists and trainees from this session are not presented in our analysis because of the high frequency of unscored characters by a number of participants. However, the results of this session were used to develop an improved reference sheet for character scoring. The carapace specimen most frequently scored at a particular level for a particular character during this session was used to develop a photographic reference sheet of character scores.

The photographic reference sheet was used by a second set of six observer trainees on March 17, 2000 to score the same 45 carapaces that were scored in December 1999. Except for the use of the photographic reference sheet, the March 2000 scoring session was conducted under the same protocols used in the December 1999 session and the results were used in this analysis.

The full set of 1,114 carapaces were scored by two "expert" scorers from ADFG. They were deemed experts due to their experience in identifying *Chionoecetes* and their study of carapace characters for discriminating among *C. bairdi*, *C. opilio,* and hybrid crabs. From the full typed carapace

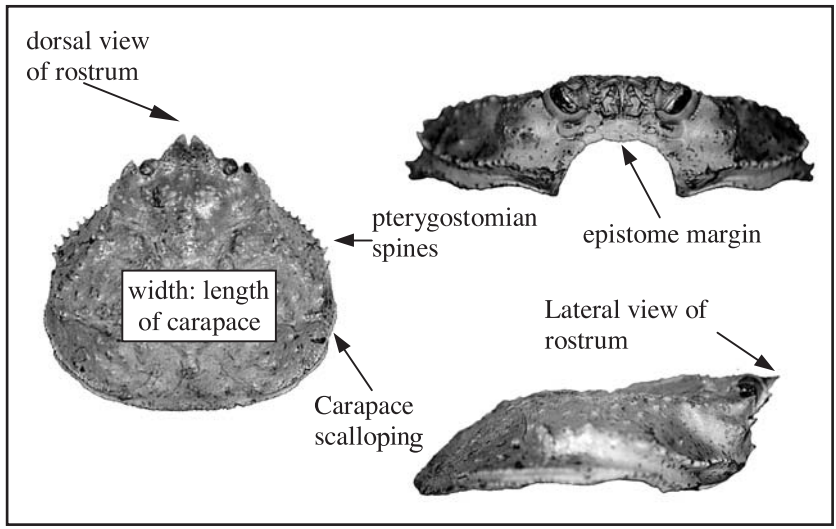

Figure 2. Characters used to distinguish Tanner crab, snow crab, and their hybrids.

set (not including the 45 that had been scored earlier by observer trainees), 250 carapaces of each type were randomly chosen for analysis. Each of the samples of 250 carapaces from the three genetic types was randomly subsampled to produce a "learning set" of 600 carapaces (200 from each genetic type) and a "test set" of 150 carapaces. The two experts also rescored five times each a randomly chosen subset of 100 carapaces composed of 28 *C. bairdi*, 34 *C. opilio*, and 28 hybrid crabs.

A number of statistical techniques were used to analyze the observer trainee and expert carapace scores. Discriminant function analysis (DFA), which has historically been used when a group of specimens from each category is known (Neff and Smith 1979), was used to determine the characters that were most important for discriminating between groups. While DFA may provide insights into the importance of the variables, the results can be difficult to interpret and utilize in a field situation. Classification tree algorithms (Breiman et al. 1984) were applied to the data sets as they were seen as being a useful tool in a field situation for distinguishing crab types. Classification trees have become a popular alternative to DFA and other multivariate procedures. Classification tree algorithms are applied to the data as a directed graphing technique where each split in a data set is used to decrease the "impurity" of the data with the final nodes reflecting the desired classification categories. Stopping criteria are key to the functioning of the classification tree procedure; without them each final

node would contain only a single case. The rules developed for splitting the data into a classification tree can then be used to identify unknown specimens.

The learning set scores of the two expert scorers were analyzed separately using the discriminant analysis routine and the classification tree module (CART) within the SYSTAT v.9.0 statistical program (SPSS 1999). SYSTAT allows for setting stopping criteria based on the maximum number of splits performed, the minimum proportion of reduction in error allowed for each split, the minimum proportion of values allowed at each split, and the minimum count of objects allowed at any node. The CART default settings for stopping criteria were used with minor modifications so that the tree for each expert would contain three split choices involving only two characters to reach the terminal nodes. Two characters were considered the limit of what could practicably be used in a field situation.

The analysis resulted in two classification tree algorithms, one tree derived from each of the two experts and a set of discriminant function coefficients for each character that provided a measure of the importance of the characters selected by the classification tree. The reliability of each of the classification algorithms was assessed by applying it to the learning and test set of each expert, the test set of the other expert, and the observer trainee scores from the March scoring session.

Components of variance analysis (Searle 1971) was used to provide descriptive measures of the magnitude and sources of variation in character scores within a genetic type. Data from the six observer trainees were evaluated for the components of variance due to individual character variation among carapaces within genetic types (Var_C), variation among scorers for the same carapace (Var_S), and residual error variation (Var_E) not attributable to either variation among carapaces or among scorers. Data from the rescoring of 100 carapaces by the two expert scorers were evaluated separately for the components of variance due to individual character variation within genetic types (Var_C) and variation in repeated scores for the same carapace (Var_R). The component Var_E for the observer trainee data set and the component Var_R for the two expert rescoring data sets both represent variation due to inconsistency in scoring.

Results

Character Scores

Photographs depicting the 1-to-5 scoring system for the six carapace characters are shown in Figs. 3 and 4. Characters grade from the *C. bairdi* type on the left, with a score of 1, to the *C. opilio* type on the right, with a score of 5.

The shape of the dorsal view of the carapace (Fig. 3) varies from being wider than long in *C. bairdi*, with a width:length ratio as high as 1.15, to being more rounded in *C. opilio*, with a width:length ratio as low as 0.95. It has been shown, however, that *C. bairdi* carapaces become proportionally

wider with greater length (D. Urban, unpubl. data), and this trend holds true for all three crab types in this study as reflected in the shape scores. It is especially obvious in the *C. opilio* carapaces in the collection. At any given size, however, *C. bairdi* are generally wider than *C. opilio* with hybrids being intermediate (Table 1). We did not include the carapace shape character in any of our subsequent analyses due to that character's dependency on size.

Figure 3 shows the deeply notched epistome margin of *C. bairdi*, which varies to the virtually straight margin of *C. opilio*. Not only the angle between the middle two plates of the epistome varies, but also the angle between the next two distal plates.

The lateral carapace margin varies from strongly scalloped in *C. bairdi* to the smooth margin found in many *C. opilio* (Fig. 3). Variation in the dorsal and lateral view of the rostrum is shown in Fig. 4. Viewed dorsally, *C. bairdi* rostrums are often sharp and angular with the medial margin forming a "V". Moving toward the *C. opilio* type, the rostrum points become more rounded and blunt. The medial margins gradually merge until nearly the entire margin can be in contact in *C. opilio*. The lateral view reveals a steeply inclined and recurved rostrum in *C. bairdi*. The dorsal margin of the *C. opilio* rostrum can be straight and slightly downward pointing.

Chionoecetes bairdi pterygostomian spines are strong and pronounced, closely spaced anteriorly and gradually becoming larger and more broadly spaced posteriorly (Fig. 4). Moving toward the *C. opilio* type, the spines gradually become less pronounced, more uniform in size, and more evenly spaced along the entire row of spines. At the *C. opilio* extreme, the spines are fine, small, and may be intermittent.

The bar graphs below each character photograph in Figs. 3 and 4 show the proportion of genetic types for each character score recorded by the experts on the set of 1,114 carapaces. The scores for each character were consistent with the genetic type of the carapace, with hybrid crabs generally receiving scores intermediate to the parental types. The distribution of the average score for all characters of each carapace also showed this pattern.

Discriminant Function Analysis

Nearly all (>99%) the variation among types was accounted for by the first discriminant function with overlap between *C. opilio* and hybrids on this axis greater than that between *C. bairdi* and hybrids (Fig. 5). When the coefficients of the first discriminant function were standardized within variances (SPSS 1999), the epistome character coefficient was largest for both experts, indicating it was the most important in discriminating crab types, with the pterygostomian spines second (Table 2). For Expert 2, the scalloping character was nearly identical to the pterygostomian spines in importance.

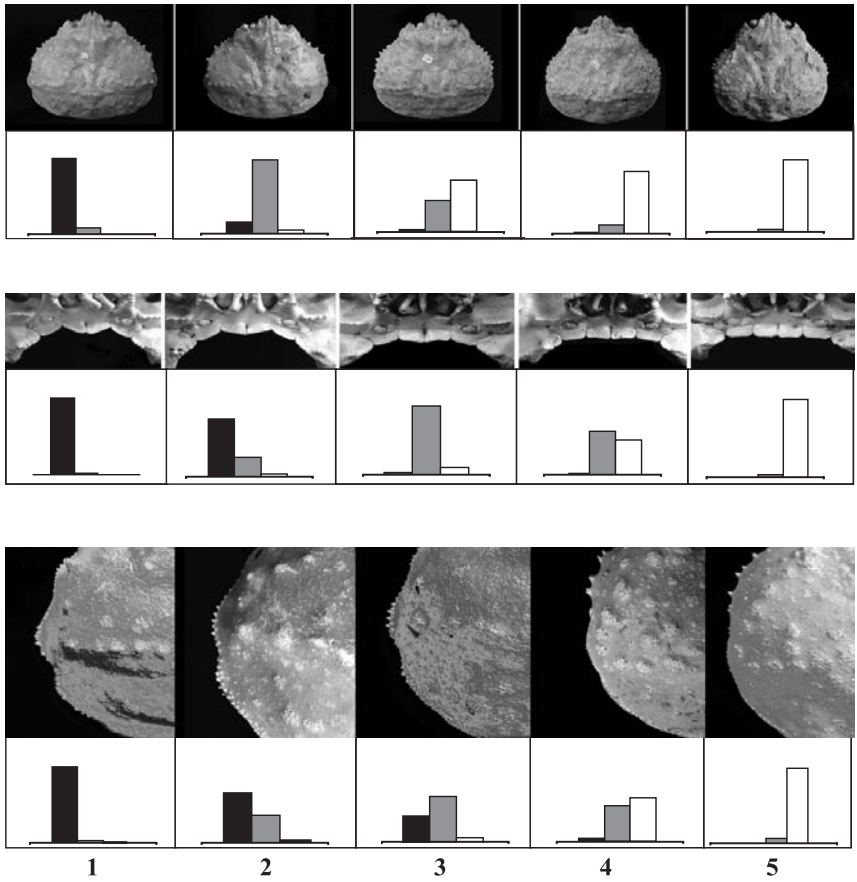

Figure 3. Photographs of the typical carapace shape, epistome margin, and carapace scalloping with the relative proportion of genetically typed C. bairdi (black bars), hybrids (gray bars), and C. opilio (white bars) scored for each type.

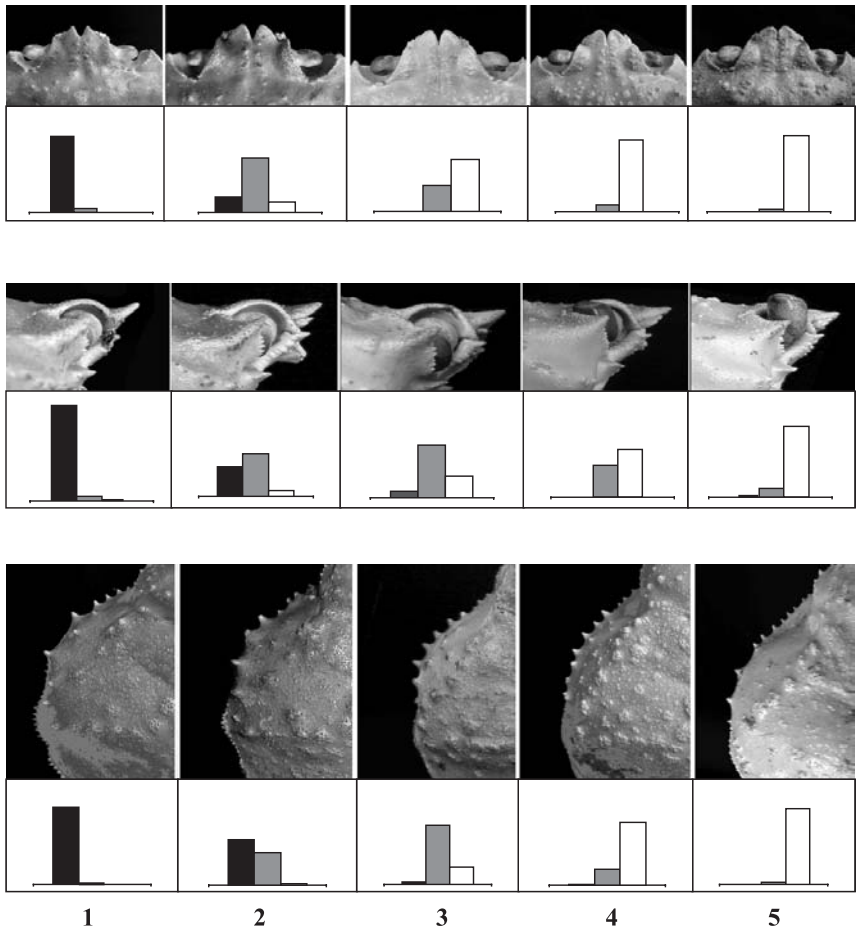

Figure 4. Photographs of the typical dorsal and lateral view of the rostrum, and pterygostomian spines with the relative proportion of genetically typed C. bairdi (black bars), hybrids (gray bars), and C. opilio (white bars) scored for each type.

Table 1. Average carapace shape score for *Chionoecetes bairdi*, *C. opilio* and hybrid crab of increasing size as scored by Expert 1.

	Genetic type		
Carapace width	*C. bairdi*	Hybrid crab	*C. opilio*
70-90 mm	n/a	n/a	4.68 (22)
91-110 mm	2.20 (5)	2.36 (64)	3.83 (265)
111-130 mm	1.71 (15)	2.30 (160)	3.28 (174)
131-150 mm	1.12 (219)	1.92 (36)	n/a

Scoring ranged from 1 for the widest crabs to 5 for crab appearing more round. Sample size is given in parentheses; n/a indicates a sample size less than 5.

Table 2. Loadings of the first canonical discriminant function for the two expert learning set scores standardized within variances.

Carapace character	Expert 1	Expert 2
Epistome	0.480	0.500
Rostrum - dorsal view	0.241	0.103
Rostrum - lateral view	0.372	0.142
Pterygostomian spines	0.444	0.333
Scalloping	0.240	0.332

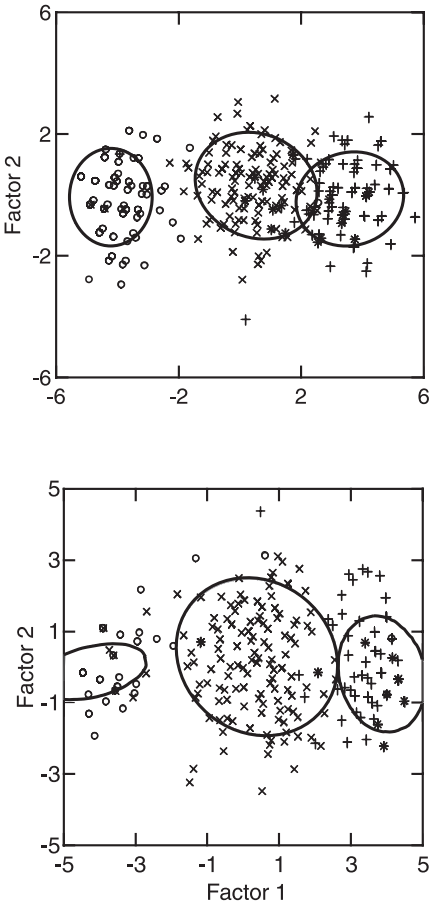

Figure 5. Canonical scores plots from Expert 1 (upper plot) and Expert 2 (lower plot) showing relation of the C. bairdi (o), C. opilio (+) and hybrid crab (×) values with the 95% confidence ellipses for each crab type shown. Over 99.5% of the variation among the types was accounted for by the first discriminant function.

Classification Tree

The classification tree developed for each expert is shown in Fig. 6. Both classification algorithms rely upon the epistome character to separate the *C. bairdi* from *C. opilio* and hybrids and *C. opilio* from hybrids, with the addition of either carapace scalloping or pterygostomian spines to further separate the hybrid crabs from *C. opilio*. These are the same features identified by the DFA as being important for discriminating crab types. Both of these classification algorithms had a >90% success in identifying the parental species when applied to the scores for the learning set from which they were derived and over 80% when applied to the hybrids (Table 3). When the classification tree derived from the expert's scores for the learning set was applied to the test set, success in identification remained similar. However, when the classification tree for Expert 1 was applied to Expert 2's test set, the percentage of hybrids correctly identified fell to 62%. When the classification tree for Expert 2 was applied to the scores for Expert 1, the percentage of the *C. bairdi* correctly identified fell to 66%.

Success in classification was also poor when either of the classification trees was applied to the scores recorded by six observer trainees for the 45 carapaces that they examined (Table 3). Neither classification tree improved the overall success rate in identification relative to the trainees' own identification success. The classification tree based on Expert 1's scores only identified 54.7% of the hybrids correctly and Expert 2's tree identified only 68.3% of the *C. opilio*.

Sources of Variation within Genetic Types of Carapace Scores

The largest component of variance in the scores of characters within genetic type by the six observer trainees was generally due to residual error that could not be attributed to individual variation among carapaces or among scorers (Var_E). The only exceptions were in the scores for the two rostrum characters in the *C. opilio* sample for which the estimated component of variance attributable to individual variation among carapaces (Var_C) was unusually large (Fig. 7). In a character-by-character comparison, Var_E was usually larger in the hybrid scores than in the *C. bairdi* or *C. opilio* scores. Variation due to consistent differences among scorers (Var_S) was the smallest component of variance in the scores of the hybrids and *C. opilio*. Estimates of Var_C for each character tended to be lowest in the *C. bairdi* scores and highest in the *C. opilio* scores. A notable result was the consistency with which the six observer trainees scored the epistome character for the 10 *C. bairdi* carapaces as 1; only the score by one trainee for one *C. bairdi* carapace was not 1.

Analysis of variance indicated that Var_C was usually a larger component of variance within genetic type in the experts' scores than was the component attributable to repeated scoring of the same specimen (Var_R).

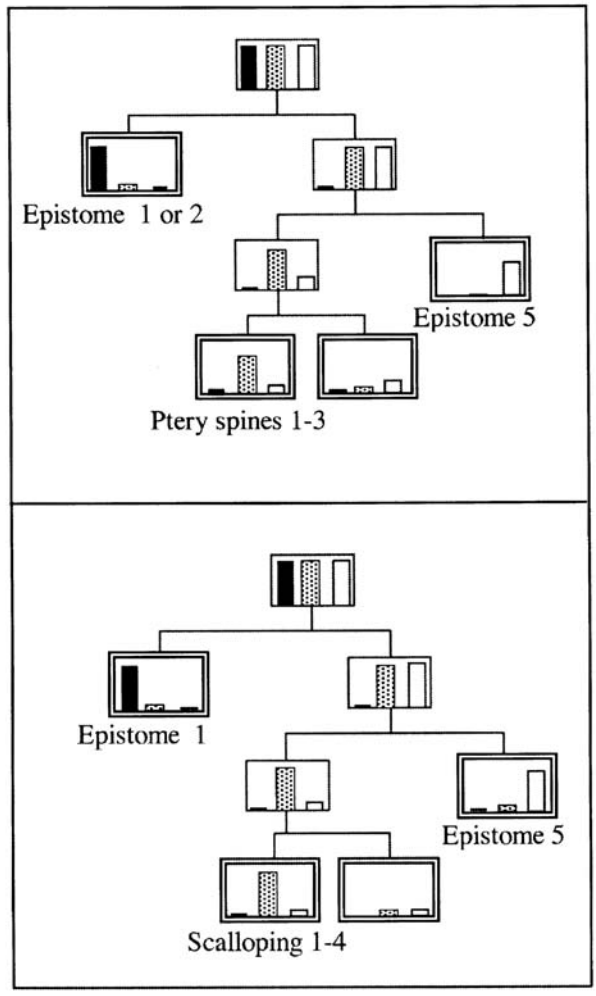

Figure 6. Classification trees developed for a randomly chosen sample of 600 C. bairdi, hybrid crab, and C. opilio. The three bars inside each node represent the proportion (from left to right) of C. bairdi, hybrid crab, and C. opilio. Terminal nodes are designated by a double line border.

Table 3. Percentage of *C. bairdi*, hybrid, and *C. opilio* carapaces correctly identified using two classification tree algorithms.

Tree	Scorer (sample)	Percentage correctly identified: *C. bairdi* (*N*)	Hybrid crab (*N*)	*C. opilio* (*N*)
CT1[a]	Expert 1 (l-set)	98.0 (200)	81.0 (200)	92.0 (200)
	Expert 1 (t-set)	100.0 (50)	82.0 (50)	94.0 (50)
	Expert 2 (t-set)	98.0 (50)	62.0 (50)	100.0 (50)
	Observers	98.3 (10)	54.7 (25)	78.3 (10)
CT2[b]	Expert 2 (l-set)	96.0 (200)	87.0 (200)	97.5 (200)
	Expert 2 (t-set)	98.0 (50)	84.0 (50)	96.0 (50)
	Expert 1 (t-set)	66.0 (50)	94.0 (50)	86.0 (50)
	Observers	91.7 (10)	78.7 (25)	68.3 (10)

[a]Classification tree developed from scores by Expert 1 for learning set of 600 carapaces.

[b]Classification tree developed from scores by Expert 2 for learning set of 600 carapaces.

Algorithms were applied to character scores by two expert scorers for a learning set (l-set) and a test set (t-set) of carapaces and average percentage correctly identified by the algorithms applied to character scores by six observer trainees.

When the estimate of Var_R was not smaller than Var_C, both estimated values were small (<0.100). The estimates of Var_C and Var_R in the scores for all characters in the *C. bairdi* sample scored by Expert 2 were notably low (0.00-0.02) in comparison to the estimates for Expert 1. Although we did not estimate the variance component due to differences between scorers, the two experts tended to score differently for at least some characters. In particular, the experts' mean scores differed by 1.0 for rostrum shape in dorsal view in the *C. opilio* sample and for carapace scalloping in the *C. bairdi* sample. Additionally, Expert 2 rarely scored any character of a *C. bairdi* carapace as >1, resulting in average scores for *C. bairdi* carapaces that ranged only from 1.00 to 1.03. In contrast, average character scores by Expert 1 for *C. bairdi* carapaces were higher and ranged from 1.11 to 1.96.

Discussion

We hoped a simple classification tree could be developed that would reliably identify crab types on the basis of carapace scores recorded by field biologists. We were not entirely successful in reaching that objective. Although the scoring system developed here was successful when used for developing a classification scheme for a single scorer, lack of consistency in scoring proved the greatest impediment to a broadly applicable scheme.

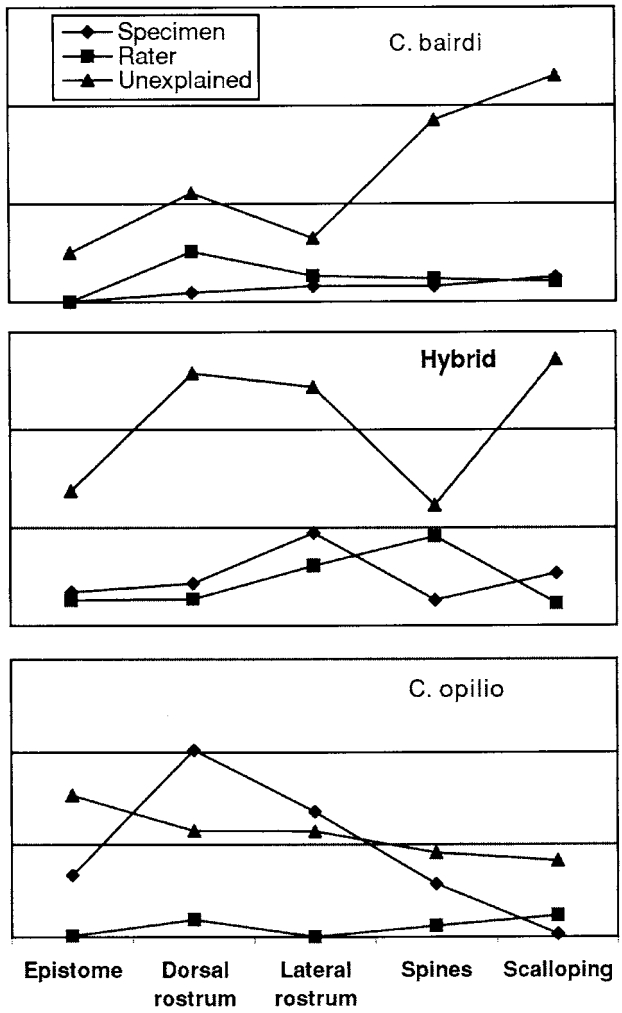

Figure 7. Components of variance of the carapace scoring by the observer trainees. Unexplained variance (Var_E) can be attributed to inconsistency in scoring.

Several examples illustrate that point. Expert 2 gave nearly all the epistomes of *C. bairdi* carapaces a score of 1, which is reflected in that expert's classification tree. However, when Expert 2's classification tree was applied to Expert 1's more variable *C. bairdi* epistome scoring, it performed poorly. Similarly, Expert 1's tree had very poor success in identifying hybrid crabs when applied to the observer trainees' scores. That poor success can be explained by the high Var_E (0.816) in the scores of the trainee observers for the pterygostomian spines character, the character that Expert 1's tree relied on to identify the hybrid crabs.

The greatest component of variance in character scores by trainee observers was due to inconsistent scoring of carapaces (i.e., poor repeatability). Character variation within types and consistent scoring differences among novices were lesser components of variance. That suggests more training is needed if character scoring by novice field biologists is to be used in identifying types through a classification algorithm.

The results of the expert scorers indicated that they were consistent in repeated scores for the same carapace. A greater problem is that the experts may not be consistent with each other in interpreting a character scoring. Each expert seems to have developed their own concept of the crab types and they rely on it more heavily than a reference score sheet, first generally recognizing the carapaces by gestalt. This gestalt subliminally seems to influence their scoring of characters. Again, this suggests the need for greater objectivity if character scoring is to be used in identifying types through a classification algorithm. The photographic scoring guide developed for this project will, we hope, assist in reaching this goal.

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