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Dramatic Increase in the Relative Abundance of Large Male Dungeness Crabs *Cancer magister* following Closure of Commercial Fishing in Glacier Bay, Alaska

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Abstract.—The size structure of the population of the Dungeness crab *Cancer magister* was studied at six sites in or near Glacier Bay, Alaska, before and after the closure of commercial fishing. Seven years of preclosure and 4 years of postclosure data are presented. After the closure of Glacier Bay to commercial fishing, the number and size of legal-sized male Dungeness crabs increased dramatically at the experimental sites. Female and sublegal-sized male crabs, the portions of the population not directly targeted by commercial fishing, did not increase in size or abundance following the closure. There was not a large shift in the size-abundance distribution of male crabs at the control site that is still open to commercial fishing. Marine protected areas are being widely promoted as effective tools for managing fisheries while simultaneously meeting marine conservation goals and maintaining marine biodiversity. Our data demonstrate that the size of male Dungeness crabs can markedly increase in a marine reserve, which supports the concept that marine reserves could help maintain genetic diversity in Dungeness crabs and other crab species subjected to size-limit fisheries and possibly increase the fertility of females.

Introduction

Declining fish and invertebrate stocks around the world are creating concerns about the long-term sustainability of many fisheries (Jackson et al. 2001; Stergiou 2002; Myers and Worm 2003). Fisheries in Alaska are not immune to these declines, and crustacean fisheries, in particular, are prone to serial depletion and collapse (Orensanz et al. 1998). The Alaska fishery for Dungeness crabs *Cancer magister* began in the southeastern portion of the state in 1916 and subsequently expanded to Prince William Sound, Cook Inlet, and Kodiak (Orensanz et al. 1998). The fishery is open during specified seasons and is limited to male crabs with a carapace width greater than 165 mm (Koeneman

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1985). In southeastern Alaska, the Dungeness crab harvest has been characterized by large fluctuations on both annual and decadal scales. In other parts of the state, including Kodiak, Cook Inlet, and Prince William Sound, the fisheries declined during the 1980s and 1990s and have not shown significant rebounds (Orensanz et al. 1998).

Marine protected areas are being widely promoted as effective tools for managing fisheries while simultaneously meeting marine conservation goals and maintaining marine biodiversity (National Research Council 2001; Palumbi 2002). The positive effects of marine reserves on the size of individuals and increases in density, biomass, and diversity have been demonstrated in numerous studies of fish and invertebrate populations in both temperate and tropical ecosystems (for review, see Halpern 2003). Almost all of these studies, however, have focused on either coral reef or rocky-reef habitats. Data on the effectiveness of subarctic marine reserves or reserves in soft-bottom habitats are lacking.

Controlled experiments testing the impact of human exploitation on the population structure of marine species are rare (Underwood 1994, 1995) and even more unusual for crustaceans (Kelly et al. 2000). Closures of crustacean fisheries are usually prompted by major declines in the abundance of the harvested species, resulting in the collapse of those fisheries (Kruse 1993; Orensanz et al. 1998). Such closures normally remain in effect only until there is evidence that the fished stocks are rebounding; so there are limited opportunities to compare changes in the structure of crustacean populations in a closed area with comparable nearby populations still being exploited.

In 1991, the National Park Service proposed closing commercial fishing in Glacier Bay National Park, Alaska (U.S. Department of the Interior 1991). Intense negotiations among the stakeholders (National Park Service, environmental organizations, commercial fishing organizations, and the State of Alaska) ensued and were ended by Congressional action in 1998 (U.S. Congress 1998). The legislation created one of North America's largest marine reserves by closing commercial fishing in Glacier Bay. Although the closure included a phase-out period for some of the fisheries, the Dungeness crab fishery was closed immediately.

In anticipation of commercial fishery closures, we initiated a study in 1992 to document changes in the population structure of Dungeness crabs. Study sites were selected inside and outside the proposed closure areas. We collected 7 years of preclosure and 4 years of postclosure data. The many years of data provide powerful documentation of changes in population structure following the creation of the marine reserve.

Methods

Study Area

Our study area was located at the northern end of the southeastern Alaskan panhandle in and adjacent to Glacier Bay. The study area included six sites: North Beardslee Islands (58°33′N 135°54′W), South Beardslee Islands (58°33′N 135°53′W), Berg Bay (58°31′N 136°13′W), Bartlett Cove (58°27′N 135°53′W), Gustavus Flats (58°23′N 135°43′W), and Secret Bay (58°29′N 135°54′W; Figure 1). All study sites were located within Glacier Bay National Park and Preserve with the exception of Gustavus Flats, which was located adjacent to the park boundary in Icy Strait.

Glacier Bay is a large (1,312 km^2), glacial fjord system with high sedimentation rates of clay-silt particles from streams and tidewater glaciers (Cowan et al. 1988). The maximum depth is approximately 450 m, and the tides are mixed semidiurnal with a maximum range of approximately 7.5 m. The primarily unconsolidated rocky coastline is highly convoluted, creating numerous small bays characterized by muddy bottoms that also commonly include sand, pebble, cobble, and shell substrates.

Selection of Study Sites

In 1991, the National Park Service proposed regulations to close commercial fishing in Glacier Bay National Park after a 7-year phase-out period (U.S. Department of the Interior 1991). At the time, the most likely scenario was that commercial fishing would initially close in the Park Wilderness waters (Wilderness Act of 1964, Public Law 88-577, 78 Stat. 890, 88th Congress, 3 September 1964), followed by closure of the rest of Glacier Bay. We initially selected five study sites; two sites were located in the Beardslee Islands wilderness area and two were located in non-wilderness waters. A fifth site was selected outside of the park to increase the odds that at least one of our study sites would remain open to commercial fishing.

By 1997, the Dungeness crab fishery had still not been closed, and, at that time, it appeared that portions of the wilderness waters would remain open to commercial fishing. To increase the probability that at

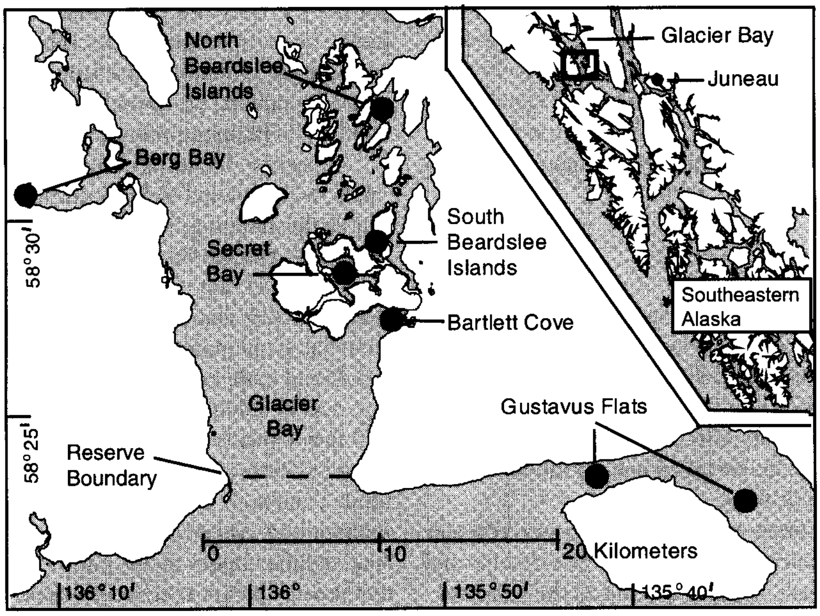

Figure 1.—Map of the study area showing the experimental sites (Bartlett Cove, Secret Bay, South Beardslee Islands, North Beardslee Islands, and Berg Bay) inside Glacier Bay and the control site (Gustavus Flats) outside the bay.

least two study sites would be located in areas that closed to commercial fishing, we added an additional site, Secret Bay, located in the southern portion of the Beardslee Islands wilderness area. When the closure decision was finalized in 1998 (U.S. Congress 1998), all of Glacier Bay immediately closed to commercial Dungeness crab fishing. The only study site that remained open to fishing was located outside of Glacier Bay (Gustavus Flats).

It is important to clarify that sport fishing and personal use fishing are allowed in Glacier Bay. Thus, it would be incorrect to classify Glacier Bay as a no-take marine reserve. However, only two of the study sites, Bartlett Cove and Gustavus Flats, are accessible via a boat ramp and a road from park headquarters and the town of Gustavus; the potential population of people participating in sport harvest is low (the population of Gustavus is about 400 people).

Sampling Procedures

Sampling was conducted from 1992 to 2002 during September when the commercial fishery is closed (the summer fishery is from 15 June to 15 August and the winter fishery is from 1 October to 30 November). Crabs were sampled with commercial crab pots (0.91 m in diameter, 0.36 m tall, with 5-cm-wire mesh). Escape rings were sealed with webbing on each pot to retain smaller crabs. Pots were baited with hanging bait (comprised of chum salmon *Oncorhynchus keta*, Pacific cod *Gadus macrocephalus*, or Pacific halibut *Hippoglossus stenolepis*) and bait jars (filled with herring and squid). Pots were soaked for 24 h. Within each study site, we set 25 pots in shallow water (0–9 m) and 25 in deeper water (10–25 m). Pot locations within the study area were placed in prime Dungeness crab habitat using knowledge from a local fisherman. The pots were set in strings parallel to shore at intervals of approximately 100 m. Each year, we attempted to place the pots in the same locations using a global positioning system (GPS; PLGR+96, Rockwell Collins, Cedar Rapids, Iowa). We estimate that the pots were set within 20 m from the original waypoints. Water depth (standardized to mean lower low water), set and retrieval time, and GPS location were recorded for each pot. Water temperature and salinity profiles were measured at each study site during each sampling period with a profiling conductivity-temperature-depth probe (SBE-19 SEA-CAT, Sea-Bird Electronics, Bellevue, Washington).

As the pots were retrieved, we counted and identified all organisms. We recorded the sex, carapace width, shell condition, reproductive condition, and appendage damage for all crabs. Carapace width was measured to the nearest mm immediately anterior to the 10th anterolateral spine with vernier calipers (Shirley and Shirley 1988; Shirley et al. 1996). All organisms were returned to the water where they were captured.

Data Analysis

We plotted average catch-per-pot as a time series, split by females, legal-sized males, and sublegal-sized males. We calculated product-moment correlation coefficients between year and average catch for the years before and the years after the fishery closure. Individual pots were the sampling unit for the correlation coefficient calculations.

For the experimental sites, we compared the size abundance distributions between preclosure and postclosure years. We also calculated the size-abundance distributions by study site and by year at both the experimental sites and the control site. Size distributions were grouped into 5-mm size-classes.

For each study site and year, we compared the relationship between average catch-per-pot and the average size for both males and females. Individual crabs were the sampling unit for size, and pot was the sampling unit for average catch. The number of pots sometimes deviated from 50 when a pot was lost or when the degradable cotton string securing the pot lid broke (range = 44–50 pots). We quantified the relationship before and after the fishery closure with a product-moment correlation coefficient. We examined the response of individual sites to closure of the fishery by plotting the data as a time series.

We used StatView (SAS Institute Inc., Cary, North Carolina) and Access (Microsoft Corp., Redmond, Washington) for all statistical tests and calculations.

Results

During the preclosure phase of the study (1992–1998), there was a significant decline in the average catch-per-pot for all size-classes and sex-classes (legal-sized males, sublegal-sized males, and females) in both the five experimental study sites and the one control study site (Figure 2). The experimental and control sites responded differently to the commercial fishery closure (Table 1). At the control site, the number of females caught per pot continued to decline but the average catch per pot increased for both sublegal males and legal males. In the experimental sites, sublegal males did not have a significant trend while females continued to decline; in contrast, the average catch per pot of legal-sized males increased dramatically (Figure 2A).

After the closure of commercial fishing, a dramatic shift occurred in the size-abundance distribution of the male population at the experimental sites (Figure 3). During the preclosure phase of the study, the number of male crabs over 165 mm (legal size) was relatively small compared to the number of sublegal-sized males. After the fishery closure, the number of male crabs over 165 mm began increasing, and by 2000, the number of crabs larger than 170 mm exceeded the highest abundance we had recorded during any of the 7 preclosure years. This trend continued and in each subsequent year the number and size of male crabs increased. In contrast, neither males at the control sites (Figure 4) nor females at the experimental sites (Figure 3) have shown a shift in size-abundance distribution toward larger-sized crabs.

Before the closure of the commercial fishery, there was a significant negative relationship ($R = -0.563$, $P = 0.0009$) between average size of male crabs per pot and average catch of male crabs per pot (Figure 5). After the fishery closure, this relationship reversed and became significantly positive ($R = 0.685$, $P = 0.0009$). The response at individual sites, however, was highly variable (Figure 6). The average catch per pot and the average size of crabs increased at the South Beardslee Island study site beyond the range of values we had observed before the closure (Figure 6A). The average catch per pot and the average size dramatically increased at the Secret Bay study site, although there were only 2 years of preclosure data for this comparison (Figure 6C). The average size of the Bartlett Cove crabs also increased beyond values we had previously observed, but the average catch was within the range of values we had measured during the preclosure study (Figure 6E). In contrast to the other experimental sites, North Beardslee Islands and Berg Bay did not exhibit a strong pattern after the fishery closure (Figures 6B, D). The postclosure sizes and abundances remained at the lower end of the range of values we had observed before the closure. At the control site, Gustavus Flats, the average catch of male crabs increased between 2001 and 2002, but all of the postclosure values were within the range we had observed prior to the closure (Figure 6F).

No significant relationship existed between average size of female crabs per pot and the average

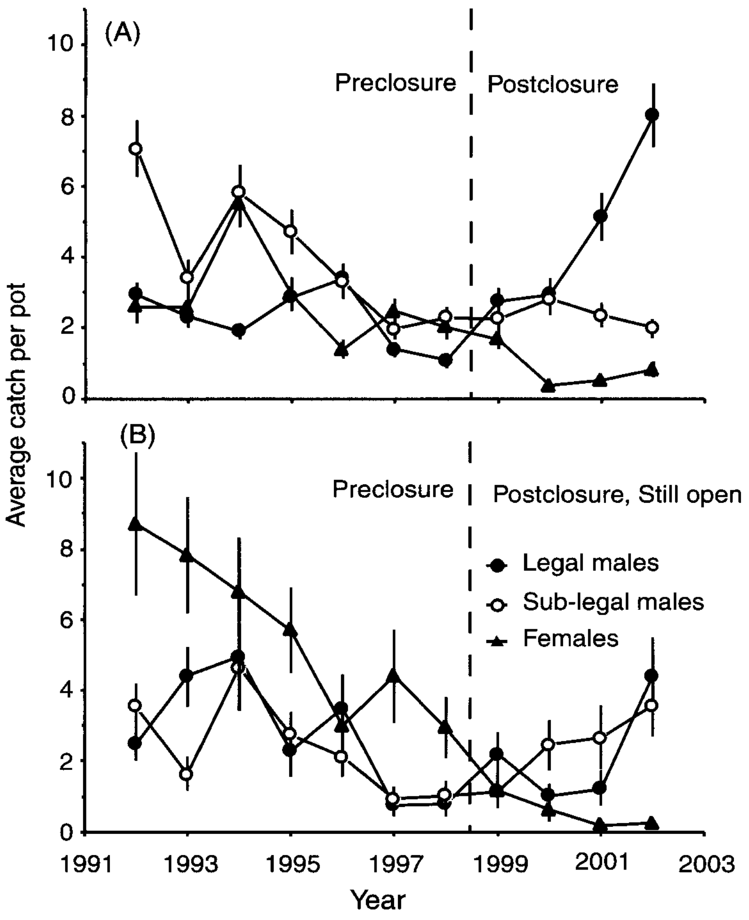

Figure 2.—The average catch per pot of legal-sized male crabs ($\geq$165 mm), sublegal-sized males, and females from 1992 through 2002 at (A) the five experimental sites and (B) the control site. Vertical bars are 95% confidence intervals. The dashed line indicates when the commercial fishery for Dungeness crabs closed.

catch per pot before ($R = -0.333$, $P = 0.07$) or after ($R = 0.316$, $P = 0.177$) the fishery closure (Figures 5C, D). Some variation occurred among sites (Figures 6G, H, I, J, K, L), however, none of the sites had increases in either catch or size after the closure.

Discussion

After the closure of Glacier Bay to commercial fishing, the number and size of legal-sized male Dungeness crabs increased dramatically at the experimental

Table 1.—Correlation coefficient between average catch and year (split before and after the closure of the commercial fishery) for legal-sized males (>= 165 mm), sublegal-sized males, and females.

	Experimental sites		Control site	
Category	Preclosure	Postclosure	Preclosure	Postclosure, still open
Legal males	–0.205 ($P < 0.0001$)	0.364 ($P < 0.0001$)	–0.304 ($P < 0.0001$)	0.272 ($P < 0.0001$)
Sublegal males	–0.328 ($P < 0.0001$)	–0.520 ($P = 0.1041$)	–0.300 ($P < 0.0001$)	0.297 ($P < 0.0001$)
Females	–0.123 ($P < 0.0001$)	–0.157 ($P < 0.0001$)	–0.367 ($P < 0.0001$)	–0.296 ($P < 0.0001$)

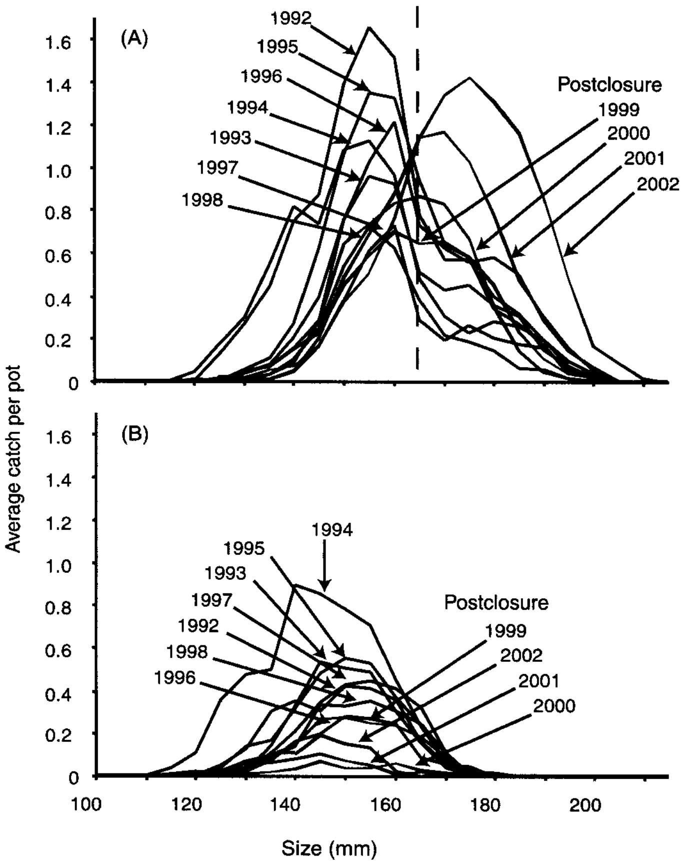

Figure 3.—Average size abundance distribution for (A) males and (B) females at all the experimental sites combined. Each line represents a year from 1992 to 2002. The dashed line represents the legal size limit (165 mm) for male Dungeness crabs.

sites (Figures 2, 3). The shift in the size-abundance distribution toward larger crabs has continued in the postclosure years.

The key question is whether the shift in the abundance distribution of male crabs was caused by a release from commercial fishing mortality; several lines of evidence support this hypothesis. First, there were large changes in abundance and considerable differences among study sites during the 7 preclosure years; however, we never observed high numbers of males larger than the legal size limit at any of the study sites before the closure. Second, female and sublegal male crabs, the portions of the population not directly targeted by commercial fishing, did not increase in size or abundance following the closure. Thus there is no evidence that a strong recruitment event occurred and caused the sudden increase in large males.

While commercial fishing was occurring there was a significant negative correlation between average size and average catch per pot (Figure 5). This relationship switched to a positive correlation after the closure, indicating that commercial fishing influenced the initial relationship. For females, no significant correlation existed between average size and average catch per pot before or after the commercial fishing closure. Since females are not harvested, they serve as a within-site control and provide further support that fishing mortality drove the preclosure male correlations. Finally, although the number of legal males did increase in the control site between 2001 and 2002, there was

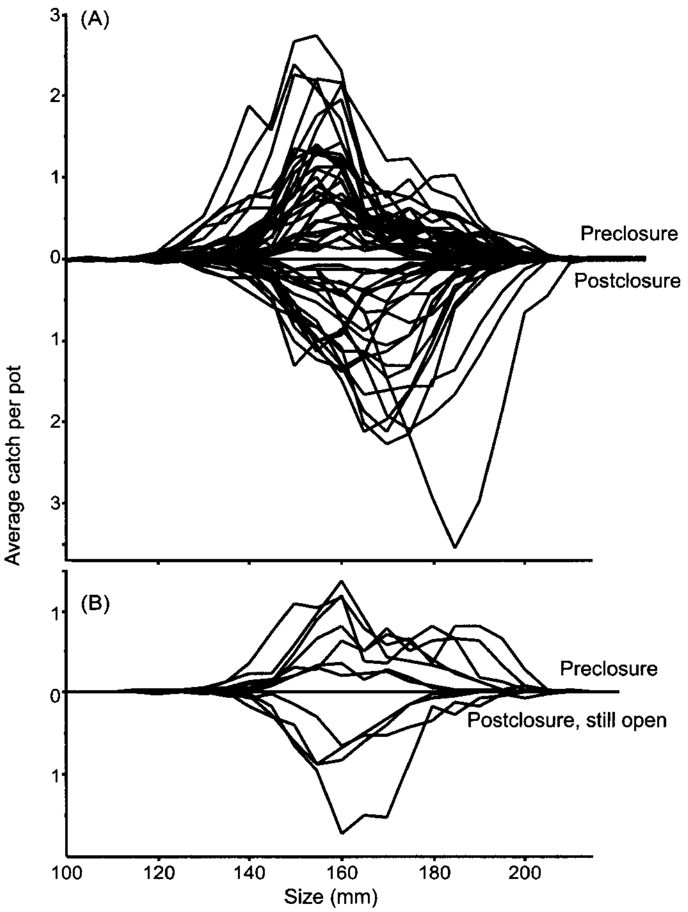

Figure 4.—Average size abundance distribution for male Dungeness crab at the (A) experimental sites and (B) control site. The distributions above the zero line represent data from each site in each year prior to the closure of the fishery. The distributions below the zero line show data from each site in each year after the fishery closure.

not a large shift in the size-abundance distribution of male crabs at this site (Figure 4).

High variation occurred among the study sites inside the park (where commercial fishing was closed) before and after the closure, and the dramatic shift in the size-abundance distribution (Figures 3, 4) was driven by three of the five study sites: South Beardslee Island (Figure 6A), Secret Bay (Figure 6C), and Bartlett Cove (Figure 6E). The variation among sites demonstrates the importance of multiple study sites both inside and outside the reserve when testing reserve effectiveness (Underwood 1994). In addition to not having multiple control sites due to the evolving nature of the proposed closures, our single control was compromised for an additional reason. When Congress passed the legislation that closed fishing in the park, the commercial fishermen who held permits for Glacier Bay were bought out and their permits were retired. Most of the Dungeness crab fishermen who fished in the park also fished outside of the park at Gustavus Flats. Consequently, commercial fishing at Gustavus Flats was reduced until new fishermen recruited to the area.

In the presence of commercial fishing, we did not find areas that had both high crab abundance and large mean size. At Bartlett Cove, crabs were abundant but the average size of male crabs was small (Figure 6E); at Berg Bay, the average size of crabs was large but the average catch per pot was consistently low (Figure 6D). In the absence of commercial fishing, several sites exhibited high abundance and large mean size. In other studies, as the exploitation rate for

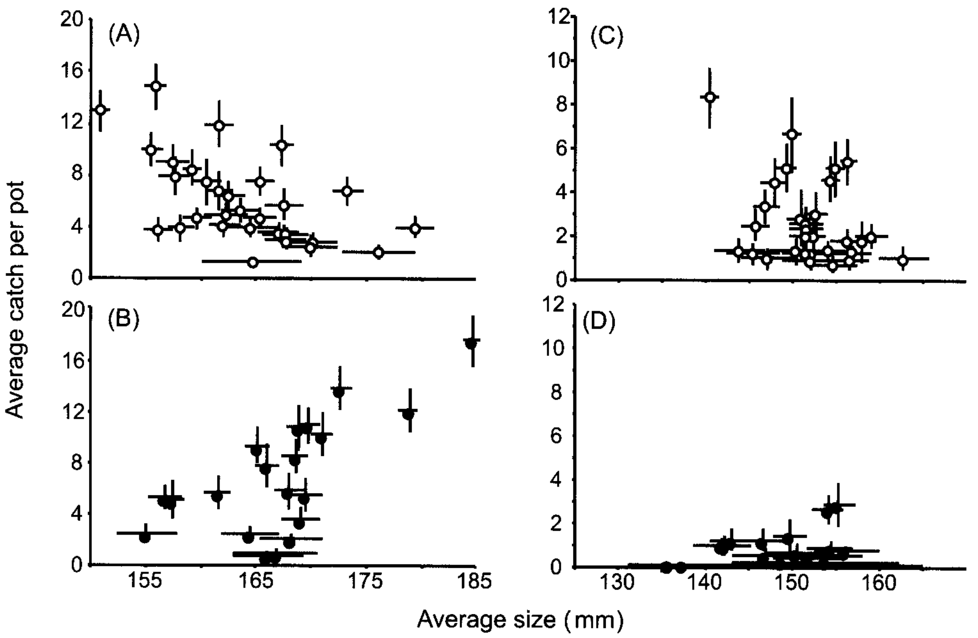

Figure 5.—Relationship between average catch per pot of males and average size of males for each site in each year (A) before the fishery closure and (B) after the fishery closure. Relationship between average catch per pot of females and average size of females for each site in each year (C) before the fishery closure and (D) after the fishery closure. Horizontal and vertical bars are 95% confidence intervals.

a size-limited fishery increased, the mean size of the individuals in the fished population decreased (Abbe and Stagg 1996). Based on this relationship, we hypothesize that the sites with higher catch per pot attracted intense commercial fishing effort, which resulted in the maximum size converging on the legal size limit, and this caused the observed lower mean sizes. Conversely, sites with large mean size and low average abundance, such as Berg Bay, did not change markedly after the closure. This low-abundance area may not have been attractive to commercial fishing; therefore, fishing effort was low. Thus, closing commercial fishing did not result in a large change.

In this paper, we have presented strong evidence that the size structure of male Dungeness crabs changed in the absence of commercial fishing. The increase in the number of large male crabs in the reserve is striking and could have other important population effects. One possible outcome of the population structure changes, for example, is an increase in female fertility. In the preclosure phase of the study, no female Dungeness crabs larger than 179 mm were ovigerous, and it is possible that this is due to the limited availability of large male crabs (Swiney et al. 2003). In Dungeness crabs, (Smith and Jamieson 1991) blue crabs *Callinectes sapidus* (Kendall et al. 2001, 2002), Tanner crabs *Chionoecetes bairdi* (Paul 1984), and snow crabs *Chionoecetes opilio* (Sainte-Marie et al. 2002), a population with more females than males or small-sized males can have lower quality or availability of sperm resources. A reduction in the abundance and size of males due to commercial harvesting may decrease fertility for females. Marine reserves may, therefore, increase the fertility of females where males are more abundant or larger than in commercially fished locations. Since Dungeness crabs have meroplanktonic larvae that are able to disperse during the pelagic phase (Epifanio 1988; McConnaughey et al. 1992), higher female fertility inside marine reserves could also result in an increase in larval export to areas outside of the reserve (Shanks et al. 2003).

In addition to reductions in fertility, fisheries that remove most of the large individuals from a population can select against genotypes that promote fast growth (Reznick et al. 1990; Conover and Munch 2002), and slower growth can reduce productivity of fisheries (Conover and Munch 2002). If reserves protect adult animals, they have also protected the oppor-

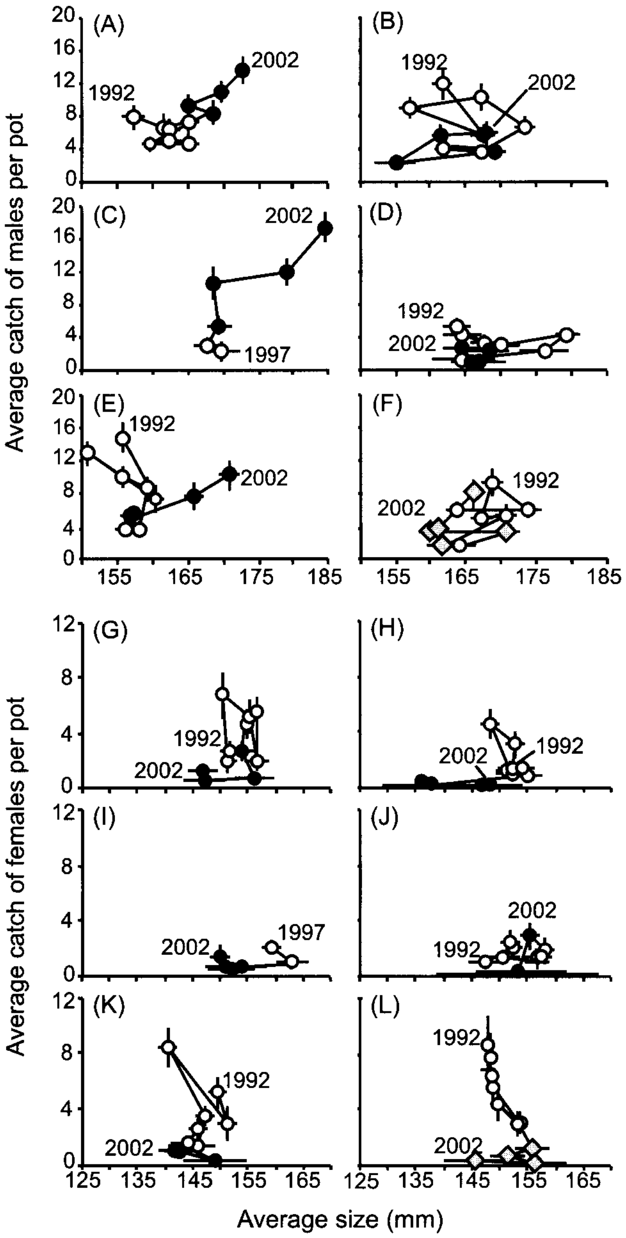

Figure 6.—Relationship between average catch per pot of males and average size of males for each year in (A) South Beardslee Islands, (B) North Beardslee Islands, (C) Secret Bay, (D) Berg Bay, (E) Bartlett Cove, and (F) Gustavus Flats. Relationship between average catch per pot of females and average size of females for each year in (G) South Beardslee Islands, (H) North Beardslee Islands, (I) Secret Bay, (J) Berg Bay, (K) Bartlett Cove, and (L) Gustavus Flats. Open circles are samples collected before the fishery closure, black circles are samples collected after the fishery closure, and gray diamonds are samples from the control site after the fishery closure. Horizontal and vertical bars are 95% confidence intervals. The first and last samples are labeled and the lines between the data points indicate the chronology.

tunity for adults to grow to a larger size. Large males have higher reproductive success than do small males, so the genetic consequences of commercial fishing could potentially be mitigated by strategically located marine reserves (Trexler and Travis 2000; National Research Council 2001). Data that we have presented demonstrate that the size of male Dungeness crabs can markedly increase in a marine reserve, which supports the concept that marine reserves could help maintain genetic diversity in Dungeness crabs and other crab species subjected to size-limit fisheries.

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References

Abbe, G. R., and C. Stagg. 1996. Trends in blue crab (*Callinectes sapidus* Rathbun) catches near Calvert Cliffs, Maryland, from 1968 to 1995 and their relationship to the Maryland commercial fishery. Journal of Shellfish Research 15:751–758.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94–96.

Cowan, E. A., R. D. Powell, and N. D. Smith. 1988. Rainstorm-induced event sedimentation at the tidewater front of a temperate glacier. Geology 16:409–412.

Epifanio, C. E. 1988. Transport of invertebrate larvae between estuaries and the continental shelf. Pages 104–114 *in* M. P. Weinstein, editor. Larval fish and shellfish transport through inlets. American Fisheries Society, Symposium 3, Bethesda, Maryland.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications 13:S117–S137.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Kelly, S., D. Scott, A. B. MacDiarmid, and R. C. Babcock. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. Biological Conservation 92(3):359–369.

Kendall, M. S., D. L. Wolcott, T. G. Wolcott, and A. H. Hines. 2001. Reproductive potential of individual male blue crabs, *Callinectes sapidus*, in a fished population: depletion and recovery of sperm number and seminal fluid. Canadian Journal of Fisheries and Aquatic Sciences 58:1168–1177.

Kendall, M. S., D. L. Wolcott, T. G. Wolcott, and A. H. Hines. 2002. Influence of male size and mating history on sperm content of ejaculates of the blue crab *Callinectes sapidus*. Marine Ecology Progress Series 230:235–240.

Koeneman, T. M. 1985. A brief review of the commercial fisheries for *Cancer magister* in southeast Alaska and Yakutat waters, with emphasis on recent seasons. University of Alaska Sea Grant Report 85-3:61–76.

Kruse, G. H. 1993. Biological perspectives on crab management in Alaska. Alaska Sea Grant College Program Report 93-02: 355–384.

McConnaughey, R. A., D. A. Armstrong, B. M. Hickey, and D. R. Gunderson. 1992. Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. Canadian Journal of Fisheries and Aquatic Sciences 49(10):2028–2044.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature (London) 423:280–283.

National Research Council. 2001. Marine protected areas: tools for sustaining ocean ecosystems. National Academy Press, Washington D.C.

Orensanz, J. M., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion—the multifaceted decline of crab and shrimp fisheries in the greater Gulf of Alaska. Reviews in Fish Biology and Fisheries 8:117–176.

Palumbi, S. R. 2002. Marine reserves: a tool for ecosystem management and conservation. Pew Oceans Commission, Arlington, Virginia.

Paul, A. J. 1984. Mating frequency and viability of stored sperm in the Tanner crab *Chionoecetes bairdi* (Decapoda, Majidae). Journal of Crustacean Biology 4:375–381.

Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature (London) 346:357–359.

Sainte-Marie, B., J.-M. Sevigny, and M. Carpentier. 2002. Interannual variability of sperm reserves and fecundity of primiparous females of the snow crab (*Chionoecetes opilio*) in relation to sex ratio. Canadian Journal of Fisheries and Aquatic Sciences 59:1932–1940.

Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13:S159–S169.

Shirley, S. M., and T. C. Shirley. 1988. Appendage injury in Dungeness crabs, *Cancer magister*, in southeastern Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 86:156–160.

Shirley, T. C., G. Bishop, C. E. O'Clair, S. J. Taggart, and J. L. Bodkin. 1996. Sea otter predation on Dungeness crabs in Glacier Bay, Alaska. Alaska Sea Grant College Program Report 96-02:563–576.

Smith, B. D., and G. S. Jamieson. 1991. Possible consequences of intensive fishing for males on the mating opportunities of Dungeness crabs. Transactions of the American Fisheries Society 120:650–653.

Stergiou, K. I. 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. Fisheries Research 55:1–9.

Swiney, K. M., T. C. Shirley, S. J. Taggart, and C. E. O'Clair. 2003. Dungeness crab, *Cancer magister*, do not extrude eggs annually in southeastern Alaska: an in situ study. Journal of Crustacean Biology 23:280–288.

Trexler, J. C., and J. Travis. 2000. Can marine protected areas restore and conserve stock attributes of reef fishes? Bulletin of Marine Science 66:853–873.

U.S. Congress. 1998. Omnibus consolidated and emergency supplemental Appropriations Act for FY 1999. Federal Register 63:Section 123(signed 21 October 1998):268–270.

U.S. Department of the Interior. 1991. Glacier Bay National Park, Alaska: fishing regulations. Federal Register 56:Section 13(5 August 1991):37262–37265.

Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications 4:3–15.

Underwood, A. J. 1995. Ecological research and (and research into) environmental management. Ecological Applications 5:232–247.