

## SERIAL DEPLETION OF MARINE INVERTEBRATES LEADS TO THE DECLINE OF A STRONGLY INTERACTING GRAZER

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**Abstract.** We investigated the relative roles of natural factors and shoreline harvest leading to recent declines of the black leather chiton (*Katharina tunicata*) on the outer Kenai Peninsula, Alaska (USA). This intertidal mollusk is a strongly interacting grazer and a culturally important subsistence fishery for Sugpiaq (Chugach Alutiiq) natives. We took multiple approaches to determine causes of decline. Field surveys examined the significant predictors of *Katharina* density and biomass across 11 sites varying in harvest pressure, and an integrated analysis of archaeological faunal remains, historical records, traditional ecological knowledge, and contemporary subsistence invertebrate landings examined changes in subsistence practices through time. Strong evidence suggests that current spatial variation in *Katharina* density and biomass is driven by both human exploitation and sea otter (*Enhydra lutris*) predation. Traditional knowledge, calibrated by subsistence harvest data, further revealed that several benthic marine invertebrates (sea urchin, crab, clams, and cockles) have declined serially beginning in the 1960s, with reduced densities and sizes of *Katharina* being the most recent. The timing of these declines was coincident with changes in human behavior (from semi-nomadic to increasingly permanent settlement patterns, improved extractive technologies, regional commercial crustacean exploitation, the erosion of culturally based season and size restrictions) and with the reestablishment of sea otters. We propose that a spatial concentration in shoreline collection pressure through time, increased harvest efficiency, and the serial depletion of alternative marine invertebrate prey have led to intensified per capita predator impacts on *Katharina* and thus its recent localized decline.

**Key words:** Akaike Information Criterion (AIC); black leather chiton; *Katharina tunicata*; model selection; prey switching; rocky intertidal; sea otter; serial decline; social-ecological system; subsistence fisheries; traditional ecological knowledge.

### INTRODUCTION

Competing hypotheses are often invoked to explain the decline of marine species. Because effective conservation plans and sustainable fisheries strategies necessitate that causal mechanisms driving declines be identified, a strong impetus exists to scrutinize the strength of evidence for alternative causes (NRC 1999, 2003). This presents an enormous challenge because ecosystems are affected simultaneously by multiple drivers of change, both top-down (consumer-driven) and bottom-up (resource-driven) (Fretwell 1977, Oksanen et al. 1981), anthropogenic and natural (Dayton et al. 1998), varying in magnitude and spatial extent (Levin 1992). Furthermore, present day perturbations operate within the context of historical alterations (Lewontin 1969) and lastly, drivers of change can interact, leading to complex and often synergistic effects (Hilborn and

Stearns 1982, Paine et al. 1998). Here we examine the multiple factors driving the recent decline of a nearshore benthic invertebrate, the black leather chiton (*Katharina tunicata*) on the rocky shores of the outer Kenai Peninsula, Alaska, USA.

In marine systems, species declines are often attributed to harvest pressure: direct and/or indirect, nonhuman predation pressure, environmental forces, or a combination of these causal agents. For example, the effects of fishing, natural predators, and large-scale forcing functions (e.g., Pacific Decadal Oscillation) have been implicated in the collapse of Steller sea lions in Alaska (NRC 2003), Peruvian anchoveta off South America (Clark 1981), and Atlantic cod in Canada (Hutchings and Myers 1994). In temperate rocky intertidal ecosystems, humans (Castilla and Durán 1985), sea otters (Estes and Palmisano 1974), sea stars (Paine 1966), and shorebirds (Wootton 1992) are all predators well known to alter rocky intertidal community dynamics (Menge and Branch 2001). In fact, in Alaska, humans and sea otters have been implicated in dramatic localized depletion of nearshore invertebrates leading to the alteration of coastal ecosystems (Simenstad et al. 1978, Duggins et al. 1989). Yet, at the same time, bottom-up

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processes such as nutrient availability and primary production have also been shown to govern nearshore dynamics elsewhere (Menge 2000, Nielsen and Navarrete 2004).

Distinguishing between drivers of change in marine systems is difficult because food webs are complex and typically not well understood (Larkin 1978), natural forcing functions are highly variable (Francis et al. 1998), fishing effort is spatially widespread, and true controls and replicates are often absent (Ludwig et al. 1993). Indeed, the syndrome of shifting baselines, in which the lack of information about the past can lead to underestimates of overall declines (Pauly 1995, Dayton et al. 1998, Jackson et al. 2001), may hinder the detection of change in the first place. Furthermore, emphasis on selected declines species-by-species or stock-by-stock can lead to a myopic perception of what is in fact a complex system and can thus mask more general phenomena, such as serial depletions.

The serial decline of marine resources is a symptom of ecosystem overfishing (Murawski 2000). Typically, fisheries first target the most lucrative stock and switch to the next most profitable stock when the marginal value of the former becomes too small to make its harvest worthwhile. This mechanism has been proposed for the sequential decline of crustaceans in the Gulf of Alaska (Orensanz et al. 1998) and abalone in California (Karpov et al. 2000). A progression of multispecies declines can also emerge when nonhuman predators switch among alternative prey, from most preferred and available to least preferred and rare. Certainly, switch points for human and nonhuman predators may differ, particularly when rare prey increase in commercial value. Under these circumstances, commercial harvest may continue unabated, often reducing prey to very low levels, whereas nonhuman predators and subsistence harvesters may switch to alternative prey earlier, when preferred prey become rare. The concept of prey switching by predators, a common phenomenon in natural systems (Holling 1959, Holt and Lawton 1994), has been proposed as one possible mechanism driving the consecutive decline of marine mammals in the north Pacific Ocean and Bering Sea (Springer et al. 2003). Yet, sequential declines are often difficult to identify because research tends to consider species singly over short periods of time. Furthermore, multiple causation, possible synergisms among drivers of change, and a paucity of historical data tend to obfuscate the causal mechanisms driving serial declines. Fortunately, retrospective analyses of archaeological data and traditional ecological knowledge (TEK) can provide historical context and insight on variability and patterns of change within ecosystems, extending farther back than contemporary scientific research (Simenstad et al. 1978, Cruikshank 2001, Jackson et al. 2001).

The value of TEK in contributing to ecological problem solving and conservation planning has become increasingly recognized (Berkes et al. 2000, Drew 2005).

Resource users can provide qualitative observations on the presence, absence, and/or relative abundances of various species at particular points in time and space when quantitative baseline information is scarce (Johannes 1998). Given their familiarity with an ecosystem and awareness of its peculiarities, subsistence users can also offer a synthesis of relative timing and rates of ecosystem change, identify important species interactions, raise entirely new scientific questions, or propose alternative testable hypotheses (Berkes 1999, Pierotti and Wildcat 2000, Moller et al. 2004, Drew 2005). In addition, subsistence users can simultaneously offer insight into the internal and external socioeconomic and ecological factors driving their own dynamic behavior as predators (Berkes et al. 2000, Turner and Berkes 2006). Ultimately, ecosystems are driven by social-ecological dynamics (Carpenter and Gunderson 2001, Gunderson and Holling 2002), and therefore a strong need exists to comprehend human behavior and the socioeconomic factors that motivate it (Ludwig et al. 1993). Consequently, TEK and social and ecological science have been increasingly combined to enlighten marine ecology research, inform management, and address conservation issues (Ellis and Swan 1981, Huntington 2000, Johannes 2002, Moller et al. 2004, Sala et al. 2004, Berkes et al. 2005). Here, we use TEK to reveal historical patterns of marine invertebrate abundance and subsistence harvest practices in south-central Alaska, USA.

On the rocky shores of the outer Kenai Peninsula, Alaska, the black leather chiton (*Katharina tunicata*) is an important traditional subsistence food item for Sugpiaq natives (also self-referred to as Chugach Alutiiq, see Plate 1; Stanek 1985).<sup>5</sup> This strongly interacting grazer is also well known to play an important functional role in structuring intertidal communities and reducing macroalgal production in the Pacific Northwest (Paine 1992, Markel and DeWreede 1998, Paine 2002). Known locally as “bidarkis,” these chitons were harvested by early inhabitants of this area, as suggested by shells found in nearby middens, some dating back 3000 years or more (de Laguna 1934). Furthermore, local Sugpiaq elders report that villagers have been harvesting this chiton for at least the past century. However, local declines of *Katharina* density and size were first observed 10–15 years ago, despite little human population growth in the area at that time (U.S. Census 2000, Brown et al. 2001). Elders further report that sea otters were absent locally in the early 1900s but began to reestablish by the early 1960s.

In collaboration with the Sugpiaq villages of Port Graham and Nanwalek, we examined the relative roles of top-down, bottom-up, and abiotic natural factors (sea otter predation, bird predation, macroalgal production, ocean temperature, and wave exposure), and anthropogenic perturbations (shoreline collection by humans) proposed by both village residents and ecologists as

<sup>5</sup> Sugpiaq (singular), Sugpiat (plural).

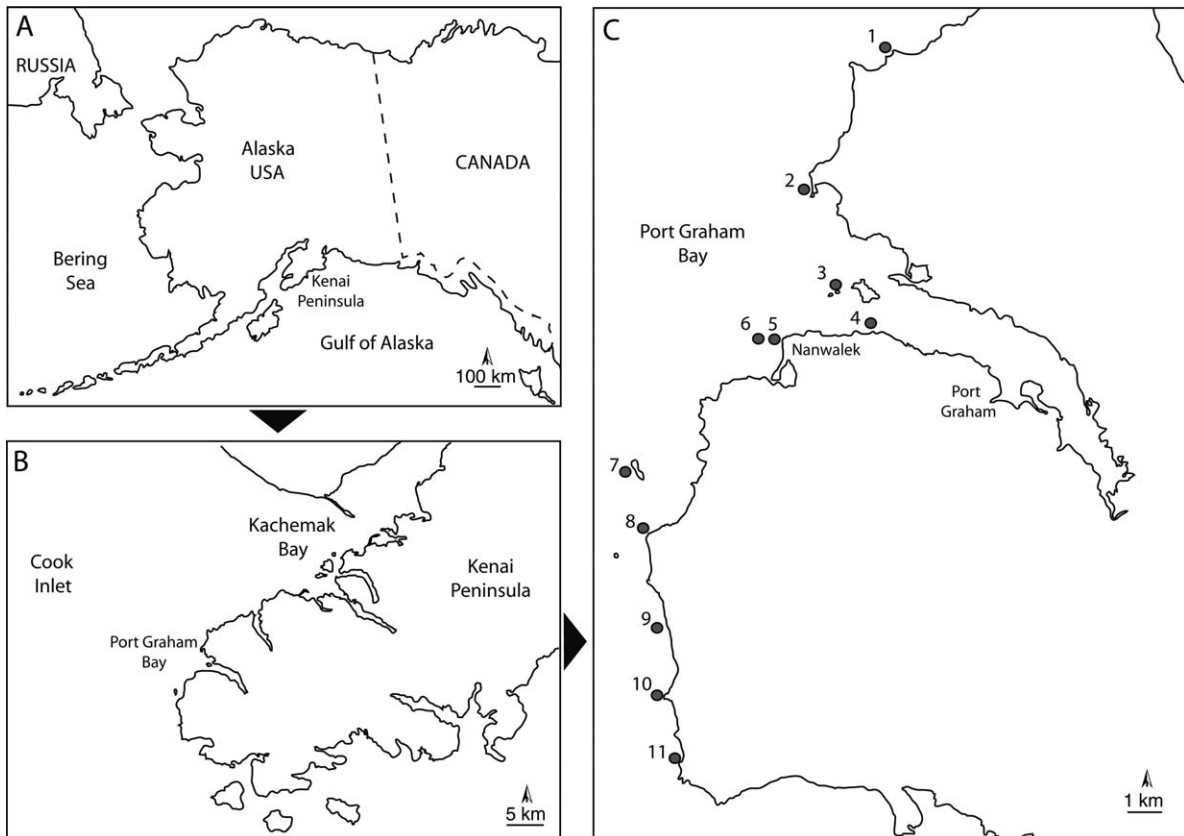


FIG. 1. (A) In south-central Alaska, USA, (B) on the outer tip of the Kenai Peninsula, we surveyed (C) 11 rocky intertidal sites surrounding the Sugpiaq native villages of Port Graham and Nanwalek. Sites differ in their accessibility to human harvesters and consequently encompass a gradient of shoreline collection effort. Sites are (1) Point Pogibshi, (2) Coal Mine, (3) Otter Rock, (4) Romanoff Point, (5) Inner Nanwalek, (6) Outer Nanwalek, (7) Flat Island, (8) Magnet Rock, (9) Golden Rocks, (10) Jagged Rocks, and (11) Point Adam.

potential causal factors driving *Katharina* decline. To examine the strength of evidence among alternative hypothesized causes of black leather chiton declines, we quantified the present-day spatial variation in *Katharina* and the factors listed above. We then used archaeological data, historical records, and semi-directed interviews with Sugpiaq elders to document temporal trends in subsistence harvest practices, relative nearshore benthic invertebrate abundances, and the ecological and socio-economic factors that likely triggered them.

#### METHODS

##### *Study area*

This research was conducted in south-central Alaska, USA, at 11 rocky intertidal sites on the outer tip of the Kenai Peninsula, in lower Cook Inlet, near two Sugpiaq native villages, Port Graham and Nanwalek (Fig. 1). Sites were identified by tribal elders to span a gradient in *Katharina* subsistence collection effort. Consequently, sites were located at varying distances away from the villages, from heavily exploited accessible sites located close to the villages, to less accessible, moderately exploited sites located farther from the villages (Fig. 1C).

Residents of Port Graham and Nanwalek rely heavily on wild resources as the basis of their mixed subsistence and cash economies. Although salmon and halibut comprise the bulk of their subsistence harvest, shoreline collection of marine invertebrates (Stanek 1985, 2006) and macroalgae (Kari 1991) remain important, as with other coastal native tribes in the northeastern Pacific (Ellis and Swan 1981, Turner 2003). While an exemption to the Marine Mammal Protection Act allows Alaska natives to take marine mammals for subsistence or craft purposes, marine mammals, primarily harbor seal and sea lion, comprised only 2.2% and 3.7% of the total subsistence biomass landed in 2003 in Nanwalek and Port Graham respectively (Stanek 2006). On average,  $5.3 \pm 1.7$  sea otters (mean  $\pm$  SE) were harvested annually from 1987 to 2003 in this region with the exception of 1993 and 1997, when 62 and 30 individuals were landed (Brown et al. 2001, Stanek 2006).

##### *Present-day factors governing variation in Katharina*

To determine the primary factors driving the spatial variation in *Katharina* density and size structure, we quantified the relative magnitude of the dominant

factors known to influence *Katharina* density and size across each site. Top-down factors included shoreline collection effort and predation pressure by other known *Katharina* consumers (sea otters, birds, and sea stars). Bottom-up factors included macroalgal production, while abiotic factors included wave exposure and water temperature.

**Harvest effort.**—We quantified the current spatial variation in shoreline collection effort of *Katharina* harvest by opportunistically surveying 39 village residents with a fixed questionnaire (a survey where all respondents are asked the same questions in the same order). Harvest surveys were conducted with a map of the area so that local residents could identify where they currently harvested and for how many days per year. This allowed us to estimate per capita harvest effort (number of days per person per year) at each site. We also documented locally observed spatiotemporal trends in *Katharina* density and size structure.

**Nonhuman predators.**—Site-specific sea otter and bird presence was estimated based on sightings made on the approach to each site and during each site visit within 100 m. Sightings were conducted in 2003 and 2004 for sea otters (*Enhydra lutris*) and in 2004 for known avian predators of *Katharina*: Glaucous-winged Gulls (*Larus glaucescens*), Black Oystercatchers (*Haematopus bachmani*), and Northwestern Crows (*Corvus caurinus*). To further describe the spatial distribution and abundance of sea otters in this region, we conducted three small boat surveys in June and July 2004. Beginning at our northeastern most site, Point Pogibshi (59°25.74' N, 151°51.35' W) and ending at our southwestern most site Point Adam (59°15.11' N, 151°58.68' W), we contoured the shoreline, within 50 m of the shore at a speed of 20 km/h or less, and recorded the number and GPS location of sea otters (adults and pups) observed by eye and with binoculars. These spatial data were displayed on maps using GIS (Appendix). At each site, we also quantified densities of benthic predators including predatory sea stars (*Leptasterias* spp., *Evassterias troschelii*, and *Pisaster ochraceus*) and predatory snails (*Nucella canaliculata*, *Lirabuccinum dirum*, and *Fusitriton oregonensis*) by recording individuals in 10 0.25-m<sup>2</sup> quadrats. Quadrats were randomly stratified along a 50-m transect line placed horizontal to the shore in *Katharina* habitat: the middle of the intertidal zone, an area dominated by the brown algae *Alaria marginata* and *Hedophyllum sessile*.

**Macroalgal production.**—We measured growth rates of the dominant benthic macroalga, *Alaria marginata*, the primary food source of *Katharina*. Thirty individuals per site were tagged with small zip ties and vinyl numbered tube tags secured around their stipe, below their sporophylls. Initial length and maximum width were measured. We estimated growth rates by punching two small holes, one on either side of the kelp blade's midrib, 1 cm above the meristem, and returning one tide series later to measure the distance between the punched

holes and the meristem (Pfister and Stevens 2002). This allowed us to quantify absolute growth rates (i.e., growth/time) and relative growth rates (absolute growth rate/length<sub>init</sub> × width<sub>init</sub>).

**Wave exposure.**—To quantify site-specific wave exposure, a factor well known to influence intertidal community assemblages, recruitment, and population size structure (Dayton 1971), we used three maximum-wave-force recorders (Bell and Denny 1994) deployed and revisited five times per site in June 2005. Swell and wind conditions during this sampling period represented typical spring conditions, similar to those observed during the June 2003 and 2004 sampling periods. On each visit, spring extensions were measured to the nearest 0.5 mm and reset. Spring extension data collected in the field were converted into maximum wave force (newtons), with calibration curves established earlier, in the lab. When drag forces were too small to cause observable spring extension, we assumed maximum wave force values equivalent to the minimum force required to overcome initial spring compression. We estimated differences in wave exposure among sites based on the mean maximum wave force recorded over the sampling period. We also ranked sites in terms of wave exposure based on the maximum wave force experienced at each site over the sampling period.

**Sea surface temperature.**—Because temperature is known to influence rocky intertidal species interactions on a local and regional scale (Sanford 1999) and can reflect upwelling events which are known to influence recruitment rates and species interactions (Menge et al. 2004), we measured site-specific sea surface temperature (SST) from June to September 2004 with temperature loggers placed at mean low water (MLW). To estimate daily SST, we averaged the temperatures recorded every 90 minutes during daily high tides when sea level was ≥3 m above MLW. Monthly mean values were calculated based on daily SST.

#### *Spatial variation in Katharina*

We quantified *Katharina* density and size structure in June 2003 and 2004 by measuring the maximum length of all individuals found in 10 0.25-m<sup>2</sup> quadrats randomly stratified along a 50-m transect line placed at two tidal elevations representing preferred habitat of *Katharina* (O'Clair and O'Clair 1998;  $n = 10$  low-zone and 10 high-zone quadrats per site). Intertidal elevation was based on biological assemblages; low quadrats were placed in the middle of the intertidal zone dominated by the brown algae *Alaria marginata* and *Hedophyllum sessile*, whereas high quadrats were placed in the middle of the intertidal zone dominated by the red alga *Endocladia muricata* and encrusting coralline species. This was done to ensure that *Katharina* habitat was adequately sampled given that *Katharina* size was observed to vary with tidal elevation. Individual *Katharina* biomass was estimated from a length–mass regression: biomass (in g) =  $6 \times 10^{-5}$  length<sup>2.98</sup> (in mm),

where  $n = 466$ ,  $R^2 = 0.942$ . Estimates of site-specific *Katharina* biomass per  $0.25 \text{ m}^2$  were derived by summing individual biomass estimates per quadrat and averaging across all quadrats surveyed in the low ( $n = 10$ ) and high ( $n = 10$ ) intertidal zones.

*Prehistoric and historic factors altering nearshore ecosystem dynamics*

*Archaeological and historical records.*—Based on the faunal remains collected from a previously excavated archaeological site (SEL-027) in Port Graham Bay, we compared the relative percentage of invertebrate species retrieved from deep strata representing a late prehistoric occupation (~1300–1500 AD) to those retrieved from shallow strata representing early historic occupation (20th century; W. Workman and K. Workman, *unpublished manuscript*). Temporal resolution was based on, and limited by, three radiocarbon dates and the Katmai volcanic ash layer of 1912. Relative species percentages were based on minimum number counts. We also reviewed archaeological literature and historical records of settlement patterns in lower Cook Inlet to provide further insight on the extent of prehistoric and historic human habitation and subsistence harvest in the area.

*Qualitative traditional knowledge.*—We conducted semi-directed interviews (Huntington 1998) with 10 tribal elders to document historical trends in nearshore ecosystem dynamics from the 1920s onward, including changes in subsistence shellfish resources and harvest practices, commercial fishing effort, social and economic drivers, and species interactions. The elders were selected by recommendation from village Tribal Councils and by chain-referral. In semi-directed interviews, researchers identify a set of topics to be addressed, but the respondent can pursue his or her lines of thought rather than being constrained by the format of a questionnaire. In this way, the respondent may indicate connections or additional information that the researchers did not or could not have anticipated. Furthermore, the course of the interview can follow the respondent's understanding of the topic, rather than the researchers' views.

We used the information from the interviews in two ways. First, we identified historical observations, both ecological and socioeconomic, and developed a timeline of events and trends. The timeline was presented to the elders and others in both communities to confirm the information. Second, based on the ideas proposed by the elders, we developed a set of formal hypotheses to explain the observed invertebrate declines. These hypotheses were also presented to the elders and others for confirmation, and were used in our analysis along with observations and hypotheses shared by local tribal members during the harvest effort surveys.

*Quantitative subsistence shellfish landings.*—We compared the traditional knowledge of marine invertebrate abundance trends with a time series of invertebrate subsistence landings data from 1987 and 2003 derived

from the Community Profile Database (CPDB) maintained by the Division of Subsistence of the Alaska Department of Fish and Game (Brown et al. 2001, Stanek 2006). The biomass of invertebrate landings from both villages, Nanwalek and Port Graham, were summed. Estimates of human population size for both villages were derived from the CPDB and U.S. Census Community Database (U.S. Census 2000, Brown et al. 2001). Only general qualitative comparisons were made between contemporary invertebrate subsistence landings data and archaeological invertebrate remains due to variable preservation of invertebrate species in middens (i.e., soft-bodied mollusks, like cephalopods, are not represented in archaeological remains and fragile species such as blue mussels are not quantifiable). Furthermore, relative species proportions based on abundance vs. biomass are not directly comparable.

*Statistical analysis*

To detect differences in the contemporary spatial variation in *Katharina*, sea otter, bird, sea star, and predatory snail density among sites and between years (2003 and 2004), we used generalized linear models (GLZs), each with a Poisson error distribution and a log-link function fit by maximum likelihood (SAS Proc Genmod V 9.1.3). Differences in *Katharina* biomass, shoreline collection effort, *Alaria* growth rates, and maximum wave exposure among sites were analyzed with GLZs on  $\log(x + 1)$ -transformed data, a normal error distribution and an identity link function, fit by maximum likelihood. We also compared *Katharina* population structure among sites and between years with size–frequency distributions. Differences in monthly sea surface temperatures among sites were analyzed with a repeated-measures GLZ. Post hoc comparisons were made based on Bonferroni adjusted  $P$  values. Linear regressions were used to quantify the relationship between shoreline harvest pressure and *Katharina* density and biomass.

To determine the strength of evidence among alternative hypothesized causal factors contributing to the contemporary variation in *Katharina* among sites, we took an information theoretic model selection approach (Burnham and Anderson 1998). We compared alternative candidate models of *Katharina* density and biomass as a function of four factors (harvest pressure, sea otter presence, bird presence, and wave exposure), because these factors varied significantly among sites and were expected to most affect *Katharina* distributions. These models, derived from integrating traditional knowledge and western science, represent a priori competing hypotheses regarding the primary factors governing the present spatial variation in *Katharina* density and biomass. This approach was taken over standard multiple-regression because the latter is sensitive to stepwise selection criterion, direction of fitting, and variable order. We used means in *Katharina* density

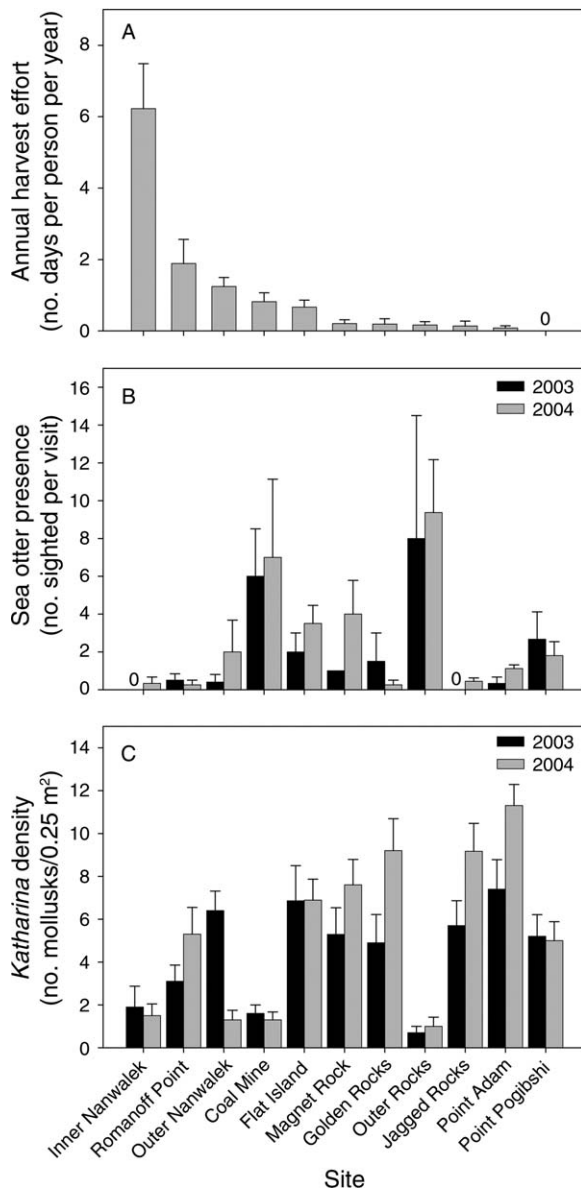


FIG. 2. Spatial variation in (A) annual per capita harvest effort, (B) sea otter presence, and (C) black leather chiton (*Katharina tunicata*) density (all data shown as mean + SE). Variation between years is shown in (B) and (C). Sites are ordered according to shoreline collection effort, from most heavily harvested to least heavily harvested.

and biomass and sea otter presence across years (2003 and 2004) when constructing each model.

We ranked candidate models based on small-sample bias-corrected Akaike's Information Criterion ( $AIC_c$ ) which we standardized to the best-fit model to produce  $\Delta AIC_c$  values. We normalized the likelihoods to a set of positive Akaike weights ( $w_i$ ) representing the strength of evidence in favor of a given model. We then examined the relative importance of each variable in contributing to the current spatial differences in *Katharina* by

calculating variable weights. This was done by summing the Akaike weights ( $w_i$ ) of all of the models in which a variable was found (Burnham and Anderson 1998). Given that four explanatory variables were used to construct all possible model combinations, a total of 16 models were compared for low- and mid-intertidal estimates of *Katharina* density. We report the top five models for each response variable.

RESULTS

Present-day factors governing spatial variation in *Katharina*

*Harvest effort.*—The spatial variation in current-day shoreline collection effort varied significantly among the 11 sites such that the most heavily harvested site, Inner Nanwalek, experienced 60 times more collection effort than Point Adam, the least harvested site (Fig. 2A, Table 1). However, in the low intertidal, harvest pressure alone explained only 22% of the spatial variation in *Katharina* density ( $R^2 = 0.22$ ,  $F = 2.56$ ,  $df = 10$ ,  $P = 0.14$ ) and only 18% of the spatial variation of *Katharina* biomass ( $R^2 = 0.18$ ,  $F = 1.97$ ,  $df = 10$ ,  $P = 0.19$ ) over 2003 and 2004.

TABLE 1. Differences in multiple factors among sites that may influence the spatial variation in current *Katharina* density and biomass in the low intertidal.

| Model                        | df | $\chi^2$ | P       |
|------------------------------|----|----------|---------|
| Shoreline collection effort† |    |          |         |
| Site                         | 9  | 665.12   | <0.0001 |
| Sea otter sightings          |    |          |         |
| Site                         | 10 | 265.04   | <0.0001 |
| Year                         | 1  | 3.93     | 0.047   |
| Bird sightings               |    |          |         |
| Site                         | 10 | 572.03   | <0.0001 |
| Sea stars‡                   |    |          |         |
| Site                         | 10 | 74.35    | <0.0001 |
| Year                         | 1  | 4.80     | 0.029   |
| Predatory snails‡            |    |          |         |
| Site                         | 10 | 240.26   | <0.0001 |
| Year                         | 1  | 0.08     | 0.773   |
| Macroalgal production§       |    |          |         |
| Site                         | 9  | 0.65     | 0.100   |
| Maximum wave exposure        |    |          |         |
| Site                         | 10 | 185.39   | <0.0001 |
| Sea surface temperature      |    |          |         |
| Site                         | 9  | 17.11    | 0.047   |
| Month                        | 2  | 19.96    | <0.0001 |
| Site × month                 | 18 | 13.15    | 0.783   |

† Point Pogibshi was excluded from this analysis because, when included, the algorithm failed to converge due to the lack of shoreline collection visits to this site.

‡ Although a Poisson error distribution was assumed, this model could not support an interaction term because of the high abundance of 0 counts.

§ Point Adam had no individuals of *Alaria marginata* large enough to tag at the appropriate tidal elevation.

|| Temperature data were not retrieved from Point Adam.

TABLE 2. Spatial variation in *Katharina* density and biomass in the low and high intertidal at 11 sites along a gradient of subsistence shoreline collection pressure.

| Model factor       | df | $\chi^2$ | P       |
|--------------------|----|----------|---------|
| Low intertidal     |    |          |         |
| Density            |    |          |         |
| Site               | 10 | 342.35   | <0.0001 |
| Year               | 1  | 0.60     | 0.440   |
| Site $\times$ year | 10 | 66.59    | <0.0001 |
| Biomass            |    |          |         |
| Site               | 10 | 101.66   | <0.0001 |
| Year               | 1  | 1.31     | 0.252   |
| Site $\times$ year | 10 | 20.89    | <0.022  |
| High intertidal    |    |          |         |
| Density            |    |          |         |
| Site               | 10 | 963.99   | <0.0001 |
| Year               | 1  | 36.98    | <0.0001 |
| Site $\times$ year | 10 | 103.47   | <0.0001 |
| Biomass            |    |          |         |
| Site               | 10 | 160.82   | <0.0001 |
| Year               | 1  | 5.02     | 0.025   |
| Site $\times$ year | 10 | 22.21    | 0.014   |

Out of 39 village residents surveyed, 100% currently collect and consume *Katharina*. Eighty-nine percent had observed a decline in *Katharina* size while 66% had observed a decline in the density of this chiton. Forty-six percent of village residents surveyed currently send *Katharina* to relatives residing outside of the village.

**Nonhuman predators.**—Sea otter presence varied significantly among sites and between years (Fig. 2B, Table 1). Coal Mine and Otter Rocks had the highest sea otter sightings among sites in both years. At these two sites, greater than seven sea otters on average were sighted per visit in 2004. In contrast, less than one sea otter was sighted per visit at Inner Nanwalek, Romanoff Point, Golden Rocks, and Jagged Rocks in 2004. These site-specific results are consistent with the three small boat surveys (Appendix) which consistently revealed low abundances of sea otters (0–1 individuals) in close proximity to village sites (Inner Nanwalek, Romanoff Point) and at the southwestern-most sites (Golden Rocks and Jagged Rocks), and high abundances (rafts of 10–42 individuals) at Coal Mine, Otter Rocks, Flat Island, and Point Pogibshi. Based on the three small boat surveys in 2004, on average we observed  $173 \pm 14$  adults and  $43 \pm 8$  pups (all data are mean  $\pm$  SE) along our shoreline transect from Point Pogibshi to Point Adam. Bird presence also varied significantly among sites (Table 1). Flat Island, the location of a Glaucous-winged Gull colony, had 286 times more bird sightings than Point Adam, the site with the fewest sightings. On Flat Island, *Katharina* shells were found scattered around gull nests located on nearby cliffs. The sea stars *Evasterias troschelii* and *Pisaster ochraceus* were exceedingly rare (1 *Evasterias* and 0 *Pisaster* were recorded in

209 0.25-m<sup>2</sup> quadrats). Densities of the dominant sea star (*Leptasterias* spp.) and predatory snails (*Nucella canaliculata*, *Lirabuccinum dirum*, and *Fusitriton oregonensis*) reached densities of  $1.9 \pm 0.3$  and  $1.7 \pm 0.5$  per 0.25 m<sup>2</sup>, respectively, and varied significantly among sites. *Leptasterias* densities also varied significantly among years (Table 1).

**Macroalgal production.**—The relative growth rate of the dominant low intertidal macroalga, *Alaria marginata*, did not vary significantly among sites (Table 1), although absolute growth rates ranged from  $1.10 \pm 0.05$  cm/day (Otter Rocks) to  $2.9 \pm 0.18$  cm/day (Jagged Rocks).

**Wave exposure.**—Wave exposure varied significantly among sites (Table 1) and ranged from 43.4 N (Golden) to <3.9 N (Romanoff Point, Otter Rocks, Inner Nanwalek).

**Sea surface temperature.**—Generally, sites experienced similar sea surface temperatures (SSTs) from June to August 2004, although in June, Point Pogibshi was significantly cooler than the other sites and experienced temperatures  $\leq 4.3^\circ\text{C}$  cooler than the warmest site, Flat Island. This temperature discrepancy disappeared by August. Water temperatures varied significantly among months; June ( $7.8^\circ \pm 0.1^\circ\text{C}$ ), July ( $9.6^\circ \pm 0.2^\circ\text{C}$ ), August ( $11.1^\circ \pm 0.2^\circ\text{C}$ ; Table 1).

**Spatial variation in *Katharina*.**—*Katharina* density in the low intertidal varied significantly among sites with no site difference between years but with a significant site-by-year interaction (Fig. 2C, Table 2). Densities ranged from as low as  $1.0 \pm 0.4$  chitons/0.25 m<sup>2</sup> to as high as  $11.3 \pm 1.0$  chitons/0.25 m<sup>2</sup>. Spatial variation in low intertidal *Katharina* biomass, integrating both density and size, also varied significantly among sites (Table 2). Compared with the most heavily harvested site, Inner Nanwalek, densities of chitons in 2004 were 6.1 and 7.5 times greater at two rarely harvested sites (Jagged Rocks and Point Adam; Fig. 2C), while biomass was 6.5 to 8.7 times greater. *Katharina* were more abundant in the high intertidal compared to the low intertidal, but the mean size was smaller (Fig. 3A, B). Both density and biomass of *Katharina* recorded in the high intertidal varied significantly among sites and years with a significant site-by-year interaction (Table 2). The population structure of *Katharina* varied among sites and between years (Fig. 3A, B). Large individuals ( $\geq 61$ mm) were less abundant at sites where either harvest effort or sea otter presence was high (Inner Nanwalek, Coal Mine, and Otter Rocks). Furthermore, the frequency of smaller (1–20 mm) and medium-sized (21–60 mm) individuals, primarily in the high intertidal, was greatest at sites where large individuals were abundant (Golden Rocks, Jagged Rocks, Point Adam). The proportion of smaller individuals was relatively higher in 2004 than in 2003 among those sites where human and sea otter predation pressure was low and adult *Katharina* densities were high.

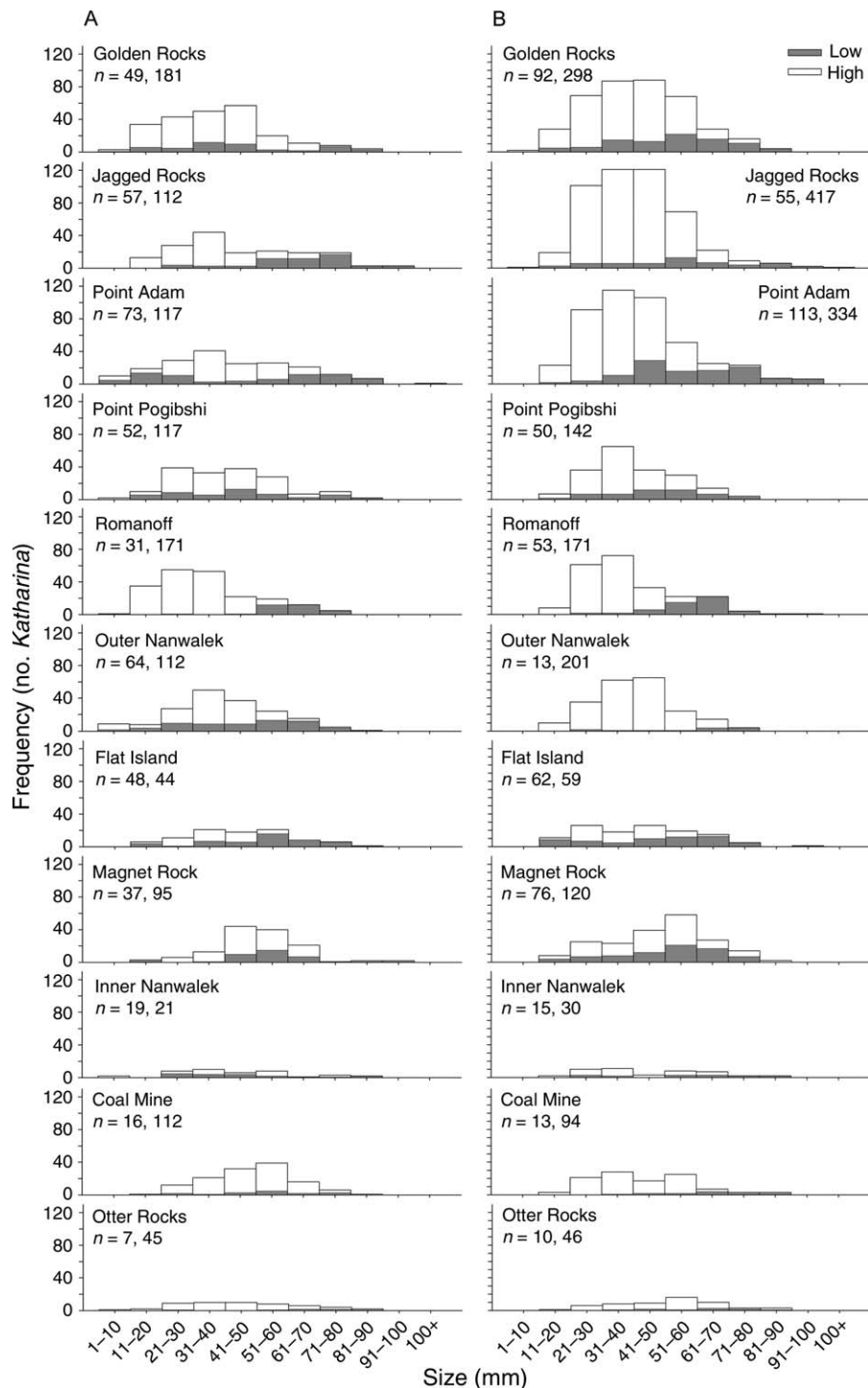


FIG. 3. Size-frequency distributions of *Katharina tunicata* in the low (shaded bars) and high (open bars) intertidal zone across all sites in (A) 2003 and (B) 2004. Sample sizes ( $n$ ) are given in sequence: low intertidal zone, high intertidal zone.

*Model selection: analysis of multiple present-day causes*

Strong evidence exists that harvest pressure and sea otter presence were the two most influential variables describing the spatial variation in *Katharina* density and biomass in the low intertidal and *Katharina* density in

the high intertidal. Harvest pressure in combination with sea otter presence comprised the best-fit models, indicated by their high Akaike weights ( $w_i$ ; Table 3). Individually, these two factors had the greatest variable weights in all three cases (Table 4). Furthermore, their



TABLE 3. Strength of evidence for alternative models explaining the spatial variation in *Katharina* density and biomass in the low and high intertidal zone among 11 sites.

| Response and model         | <i>N</i> | <i>K</i> | $\Delta AIC_c$ | $w_i$ | $R^2$ |
|----------------------------|----------|----------|----------------|-------|-------|
| Density, low intertidal    |          |          |                |       |       |
| Harvest + sea otter        | 11       | 4        | 0.00           | 0.84  | 0.80  |
| Harvest + sea otter + bird | 11       | 5        | 4.38           | 0.09  | 0.85  |
| Harvest + sea otter + wave | 11       | 5        | 7.28           | 0.02  | 0.81  |
| Sea otter                  | 11       | 3        | 8.09           | 0.01  | 0.34  |
| Harvest                    | 11       | 3        | 9.98           | 0.01  | 0.22  |
| Biomass, low intertidal    |          |          |                |       |       |
| Harvest + sea otter        | 11       | 4        | 0.00           | 0.59  | 0.68  |
| Sea otter                  | 11       | 3        | 3.29           | 0.11  | 0.30  |
| Harvest                    | 11       | 3        | 4.96           | 0.05  | 0.18  |
| Wave                       | 11       | 3        | 5.59           | 0.04  | 0.13  |
| Sea otter + wave           | 11       | 4        | 6.84           | 0.02  | 0.40  |
| Density, high intertidal   |          |          |                |       |       |
| Harvest + sea otter        | 11       | 4        | 0.00           | 0.35  | 0.67  |
| Wave                       | 11       | 3        | 1.99           | 0.13  | 0.37  |
| Harvest + sea otter + wave | 11       | 5        | 2.35           | 0.11  | 0.79  |
| Sea otter + wave           | 11       | 4        | 2.64           | 0.09  | 0.59  |
| Harvest + sea otter + bird | 11       | 5        | 2.86           | 0.08  | 0.78  |
| Biomass, high intertidal   |          |          |                |       |       |
| Wave                       | 11       | 3        | 0.00           | 0.54  | 0.57  |
| Harvest + wave             | 11       | 4        | 2.46           | 0.16  | 0.67  |
| Sea otter + wave           | 11       | 4        | 4.00           | 0.07  | 0.62  |
| Bird + wave                | 11       | 4        | 4.87           | 0.05  | 0.59  |
| Harvest + sea otter + wave | 11       | 5        | 4.90           | 0.05  | 0.79  |

Note: Models with varying numbers of parameters (*K*), were compared using small-sample bias-corrected Akaike Information Criterion ( $AIC_c$ ),  $AIC_c$  differences ( $\Delta AIC_c$ ), and normalized Akaike weights ( $w_i$ ).

relative importance was practically equal. However, the importance of wave exposure was considerable when predicting high intertidal *Katharina* biomass (Tables 3 and 4). The strength of evidence for the effect of bird presence on *Katharina* density and biomass was weak.

#### Prehistoric and historic factors altering nearshore ecosystem dynamics

*Archaeological and historical records.*—The faunal remains of archaeological site SEL-027 were primarily composed of macroinvertebrates, although sea otter, harbor seal, sea lion, porpoise, beluga, porcupine, sea ducks, albatross, salmon, cod, and halibut remains were

also present (W. Workman and K. Workman, *unpublished manuscript*). Out of all the invertebrate remains, the large predatory whelk *Neptunea* spp. was found in the greatest proportion, comprising 42% of the late prehistoric and 37% of the early historic invertebrates excavated (Fig. 4). Although the proportion of *Neptunea* in historic strata dropped by 5% compared to prehistoric strata, the proportion of smaller predatory whelks (*Nucella* spp. and *Volutharpa ampullacea*) increased by a factor of 1.5 and 2, respectively, collectively making up 29% of the historic invertebrate remains. The remaining bulk of invertebrates comprised lower trophic level bivalves including: softshell clams (*Mya truncata*), butter clams (*Saxidomus gigantea*), cockles (*Clinocardium nuttallii*), Pacific little neck clams (*Protothaca staminea*), and grazing periwinkle snails (*Littorina* spp.). Species each comprising <2% of the total invertebrates excavated included limpets (*Acmaea mitra*, *Lottia* spp., *Tectura* spp.), other clams (*Macoma* spp.), puppet margarite snails (*Margarites pupillus*), barnacles (*Balanus* spp.), surf clams (*Mactromeris polynyma*), other whelks (*Fusitriton oregonensis*, *Natica* spp.), jingle shells (*Pododesmus macroschisma*), and *Katharina*. While *Katharina* represented a minor component of the invertebrates excavated, its occurrence more than doubled from the late prehistoric occupation (0.4%) to the early historic occupation (1.1%). Blue mussels (*Mytilus trossulus*) and sea urchins (*Strongylocentrotus* spp.) were present but not quantifiable.

Historical records indicate that Nanwalek was established as a fur trading post in 1786. Port Graham was established as a permanent settlement between 1909 and 1912 as a transfer point for shipping and a cannery site, the latter playing a major role in the local economy for much of this century (Cook and Norris 1998). As Sugpiat became economically enmeshed with the fur trade followed by the fishing industry, formerly dispersed semi-nomadic populations settled in more permanent villages (de Laguna 1934, 1956, Stanek 2006).

*Qualitative traditional knowledge.*—Historical ecological and socioeconomic data collected from Sugpiaq elders and village residents highlighted temporal changes in the relative abundance of invertebrate resources,

TABLE 4. The relative importance of four variables (harvest pressure, sea otter presence, bird presence, and wave exposure) that contribute to the current spatial variation in *Katharina* density and biomass in both the high and low intertidal zones.

| Variable           | Response     |              |               |               |
|--------------------|--------------|--------------|---------------|---------------|
|                    | Density, low | Biomass, low | Density, high | Biomass, high |
| Harvest pressure   | 0.965 (–)    | 0.682 (–)    | 0.608 (–)     | 0.282 (–)     |
| Sea otter presence | 0.977 (–)    | 0.766 (–)    | 0.708 (–)     | 0.156 (–)     |
| Bird presence      | 0.100 (+)    | 0.051 (+)    | 0.133 (–)     | 0.082 (–)     |
| Wave exposure      | 0.029 (+)    | 0.368 (+)    | 0.082 (+)     | 0.875 (+)     |

Notes: Relative importance was based on variable weights, which were calculated by summing the Akaike weights ( $w_i$ ) over the subset of models for a specific response in which a variable was found. The sign of each variable coefficient in parentheses indicates the direction of the relationship between the response and each variable.

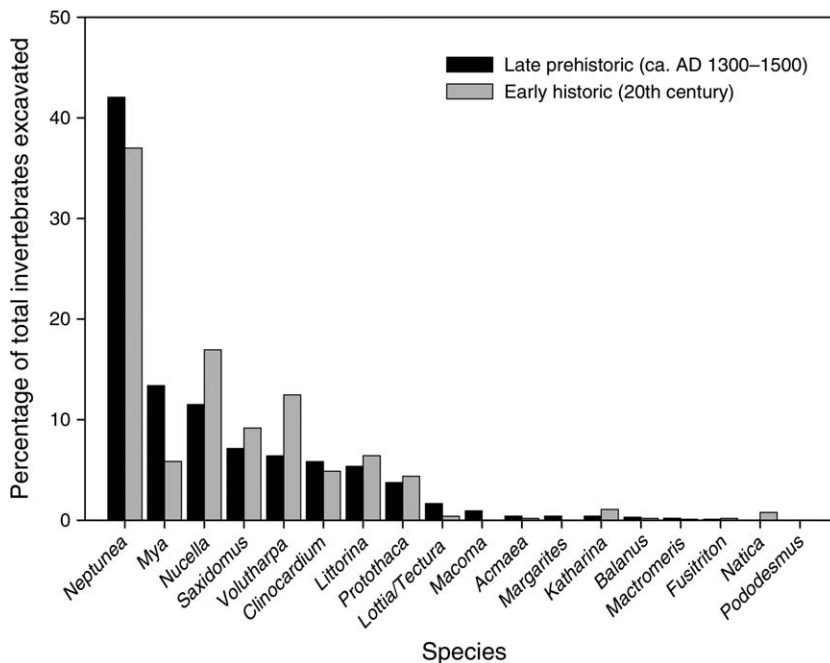


FIG. 4. Relative percentage of invertebrate species excavated from archaeological site SEL-027 in Port Graham Bay, Alaska, USA, representing both late prehistoric (ca. AD 1300–1500) and early historic (20th century) occupation. Note that blue mussels (*Mytilus trossulus*) and sea urchins (*Strongylocentrotus* spp.) were present but not quantifiable (W. Workman and K. Workman, unpublished manuscript).

changes in subsistence use, and sea otter presence from the 1920s to 2003 (Fig. 5A, Table 5). These data revealed a serial decline of marine invertebrates beginning in the early 1960s, co-occurring with the recovery of the local sea otter population and increased shoreline harvest efficiency (Table 5). According to local observations, sea urchin (*Strongylocentrotus* spp.) and sea cucumber (*Cucumaria* spp.) were the first invertebrates to decline in the 1960s, followed by Dungeness crab (*Cancer magister*) and shrimp (*Pandalus* spp.), which began declining in the late 1970s and were rarely harvested by the mid 1980s. *Saxidomus*, *Prototheca*, and *Clinocardium* were the next invertebrates to decline. Localized declines of *Katharina* were the most recent in a chain of declines (Fig. 5A). Traditional knowledge holders offered a variety of hypotheses regarding causes of historical marine invertebrate declines and contemporary *Katharina* declines (Table 6).

*Quantitative subsistence shellfish landings.*—From 1987 to 2003, *Katharina* was the primary invertebrate harvested in Port Graham and Nanwalek, comprising 40.4% ( $\pm 2.8\%$ ) of the mean annual subsistence invertebrate landings during this time period (Fig. 5B). *Saxidomus gigantea* and giant Pacific octopus (*Enteroctopus dofleini*) made up 27.1% ( $\pm 3.6\%$ ) and 15.7% ( $\pm 1.8\%$ ) of the mean annual catch, respectively, although their collection along with *Katharina* and most marine subsistence species dropped in 1989, following the *Exxon Valdez* oil spill. The remaining species, each comprising  $>2\%$  of the annual catch during this time

included *Protothaca staminea* ( $4.0\% \pm 1.2\%$ ), *Clinocardium nuttallii* ( $3.2\% \pm 0.9\%$ ), razor clams (*Siliqua patula*) ( $3.0\% \pm 0.5\%$ ), and *Nucella* spp. ( $2.5\% \pm 0.3\%$ ). In 1992, landings of *Protothaca staminea* began to decline followed by a steep decline in *Saxidomus giganteus*. Species making up  $<2\%$  of the annual catch from 1987 to 2003 included mussels (*Mytilus* spp.;  $1.9\% \pm 0.5\%$ ), gumboot chitons (*Cryptochiton stelleri*;  $1.7\% \pm 0.7\%$ ), *Cancer magister* ( $0.4\% \pm 0.1\%$ ), Tanner crab (*Chionoecetes bairdi*;  $0.2\% \pm 0.1\%$ ), *Pandalus* spp. ( $0.2\% \pm 0.1\%$ ), whelks (*Fusitriton oregonensis* and *Neptunea* spp.;  $0.09\% \pm 0.03\%$ ), *Strongylocentrotus* spp. ( $0.05\% \pm 0.02\%$ ), and *Cucumaria* spp. ( $0.01\% \pm 0.01\%$ ).

#### DISCUSSION

Recent localized declines of the black leather chiton, *Katharina tunicata*, on the outer tip of the Kenai Peninsula, Alaska, USA can be attributed to changes in socioeconomic and ecological dynamics. Strong evidence from field surveys suggests that present-day spatial variation in *Katharina* density and biomass is driven by a combination of human harvest and sea otter predation, with the relative magnitude of these top-down factors varying among sites (Figs. 2 and 3, Tables 3 and 4, Appendix). However, the likely long-term causal mechanism driving *Katharina* declines was revealed through an investigation into the historical, ecological, social, and economic dynamics of the local and regional marine ecosystem. This temporal depth was provided by archaeological data, historical records, and

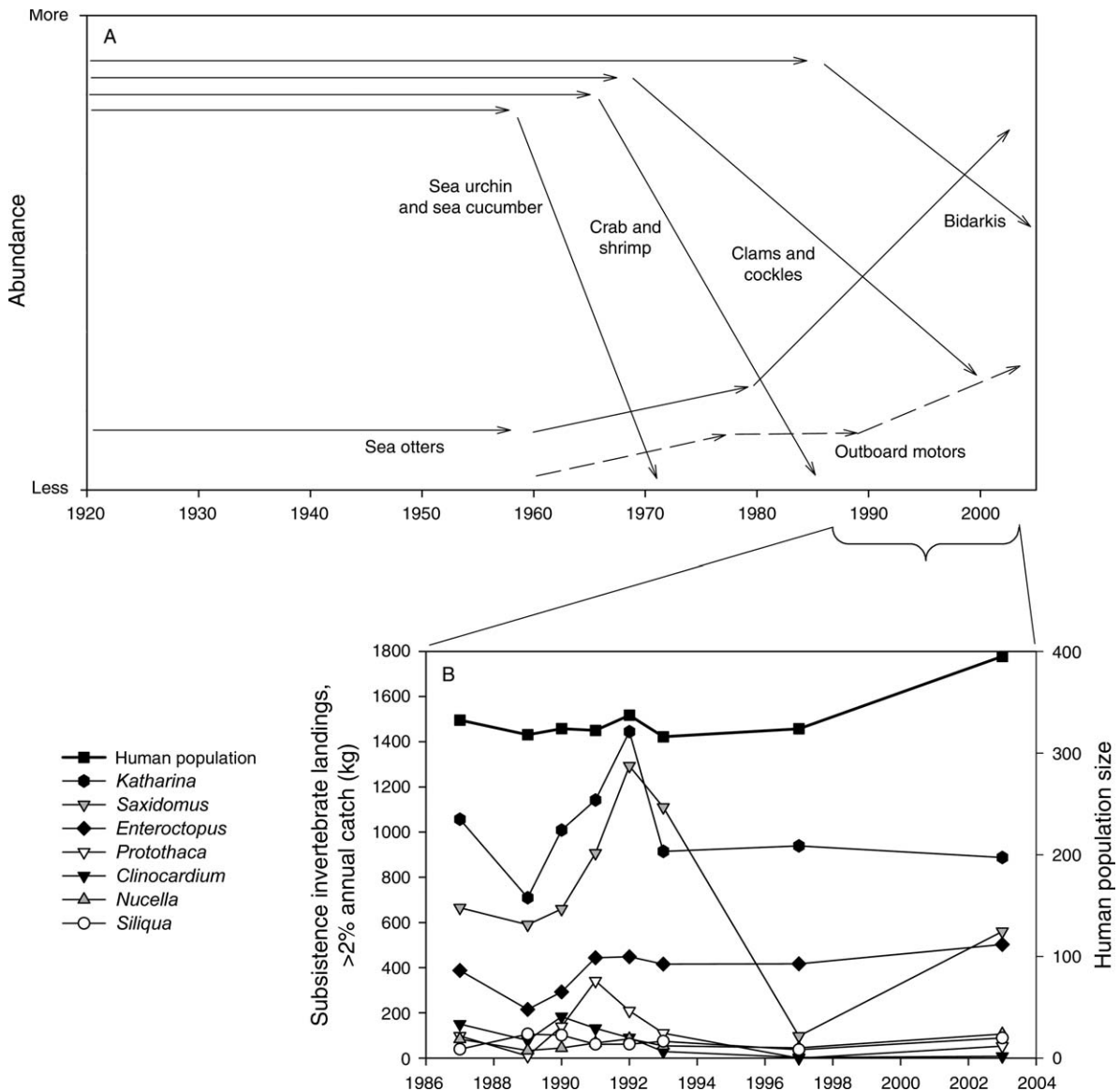


FIG. 5. (A) Serial depletion of marine invertebrates from 1920 to 2003 revealed through qualitative traditional knowledge. The dashed line represents the increase in outboard motor use. Key to species: sea urchin, *Strongylocentrotus* spp.; sea cucumber, *Cucumaria* spp.; crab, *Cancer magister*; shrimp, *Pandalus* spp.; clams and cockles, *Saxidomus giganteus*, *Prototheca staminea*, and *Clinocardium nuttallii*; bidarkis, *Katharina tunicata*; sea otters, *Enhydra lutris*. (B) Subsistence invertebrate landings of species comprising >2% of the annual invertebrate catch from Nanwalek and Port Graham, Alaska, USA, from 1987 to 2003 (*Katharina tunicata*, *Saxidomus giganteus*, *Enteroctopus dofleini*, *Prototheca staminea*, *Clinocardium nuttallii*, *Nucella* spp., and *Siliqua patula*), and local human population size (U.S. Census 2000, Brown et al. 2001).

traditional ecological knowledge (Figs. 4 and 5, Tables 5 and 6).

#### Historical factors altering nearshore ecosystem dynamics

We propose that five salient historical events likely triggered the serial decline of marine invertebrates leading to localized reductions of *Katharina*: (1) spatial restriction of human impacts, (2) extirpation and subsequent recovery of sea otters, (3) new technologies leading to increased fishing efficiency and effort, (4) regional commercial exploitation of crustacean stocks,

and (5) indirect socioeconomic effects of the 1989 *Exxon Valdez* oil spill. We begin by describing prehistoric baseline conditions.

Archaeological evidence from sites in lower Cook Inlet dating back 4500 years suggests that prior to the Russian occupation in the 1780s, Suqpiq natives were semi-nomadic, traveling from small settlements to numerous seasonal camps for specific harvest activities (Cook and Norris 1998, Steffian 2001, Stanek 2006). Faunal remains excavated from middens in this region indicate that Suqpiq hunters and gatherers relied

TABLE 5. Time series of historic ecological and socioeconomic observations based on representative quotes from Sugpiaq elders and tribal residents from Port Graham and Nanwalek, Alaska; *Katharina* are known locally as “bidarkis.”

| Time        | Event   | Traditional ecological knowledge—observation   |
|-------------|---|--|
| 1800s–1960s | sea otter extirpation                                     | “When the Russians came they cleaned the sea otters out. When I was 18 yrs old [1953] there were no sea otters around Port Graham.”  |
| 1930s–1950s | high invertebrate densities and low kelp biomass          | “We used to be able to get all the Dungeness we wanted. We used to collect clams and cockles, nobody ever missed a tide. I didn’t have concept of poor or rich in a western world sense. We were so rich because there was so much out there.”<br>“The sea back then was a dinner table set at low tides.”<br>“There was not much kelp in front of Nanwalek when I was young.” |
| 1960s       | sea otter recovery  | “They came back in the early 60s. The population exploded in the late 70’s early 80’s.”<br>“Boy, those things multiply!”   |
| 1960s       | invertebrate decline begins                               | “We used to see sea urchins all over Nanwalek Reef in the early 1940s. By the late 60s sea urchins were mostly gone.”  |
| 1964        | Great Alaska earthquake                                   | “After the earthquake, there was sunk land and no minus tides for about four years. After that it came back to normal.”<br>“The earthquake damaged the clam beds. This quake did not take the bidarkis, snails, and other invertebrates. If it did, they came back.”   |
| 1970s       | increased harvest effort with increased storage abilities | “In the past we picked just enough to eat and snack on. But when electricity and then freezers came to the village, people began to pick more because they could store them.”  |
| 1980s       | commercial crustacean crash                               | “[Dungeness] were wiped out because of commercial crab fisheries and dragging. They came right into this bay. Now they haven’t been able to come back because of the sea otters.”  |
| 1989        | <i>Exxon Valdez</i> oil spill                             | “The oil spill impacted nature’s cycles, the seasonal clock work of our culture, our life ways . . . It had lingering effects, not only in our water but in our lives.”<br>“Clams and cockles and Dungeness crab were declining before the oil spill. The oil spill may have made it worse but they were already declining before the spill.”                                  |
| 1989        | increased harvest efficiency                              | “People locally were hired to help clean up the spill. Then there was more money that came to the village. More money let more people own more boats and bigger boats with better outboards. Many people could now go to places that they couldn’t go to in the past.”   |
| 1990s       | change in bidarki numbers and size                        | “I started noticing bidarki declines 10–15 years ago.”<br>“It’s harder to find the big ones now.”  |
| 1990s–2000s | compensatory growth                                       | “There are more little ones but they are not big enough to pick. I used to not see so many little ones.”   |
| 1990s–2000s | serial decline  | “The urchins were the first to go, then crab, then the clams. Bidarkis, they’re the most recent change.”   |

heavily on intertidal macroinvertebrates, marine mammals, sea birds, and fish (de Laguna 1934, Klein 1996, Steffian 2001). In Port Graham Bay, harvest of the large predatory whelk *Neptunea*, the main invertebrate excavated from a 700-year-old midden (Fig. 4), likely had important ecological ramifications for low intertidal and subtidal benthic community dynamics. Evidence from this and other archaeological sites suggests that the nearshore ecosystems of the Kenai Peninsula have been modified by this maritime culture for at least the past 4500 years.

After the arrival of the Russian fur traders in the 1780s, both commercial fur trading companies and the Russian Orthodox Church sought to centralize services in larger villages. Thus, regional consolidation eventually led to the demise of smaller settlements and the creation of larger, more permanently established villages (de Laguna 1956, Cook and Norris 1998, Stanek 2006).

By the late 1880s, commercial fishing and canneries gradually replaced fur trading as the major source of local jobs and income, again promoting more stationary settlement patterns. Consequently, subsistence hunting and shoreline collection effort likely became increasingly concentrated in space, leading to an increase in localized harvest impacts (Table 6).

Due to the lucrative fur trade, sea otters became locally extirpated from Alaska’s coastline by the early 1900s with only several pockets of animals remaining (Estes and Palmisano 1974). From the early 1900s to the 1950s, sea otters were never observed in Port Graham Bay or its surrounding rocky shores by today’s elders (Table 5). However, sea otter invertebrate prey, including sea urchins, crab, clams, cockles, mussels, octopus, and chitons, were abundant and kelp beds were sparse (Table 5). With the extirpation of sea otters from Alaska south to California, benthic macroinvertebrate prey

TABLE 6. Competing hypotheses, formulated from traditional and local knowledge, regarding the factors causing the decline of benthic marine invertebrates and *Katharina* (bidarkis) specifically.

| Formal hypothesis  | Traditional ecological knowledge—cause of decline   |
|--|---|
| Historical shift in collection behavior                    | "[Before the Russian occupation] when resources became low, people moved on. They took all of their camp out. Then they would go back when resources returned. Villages didn't exist, there were seasonal camps. They always traveled, from fall to spring. That's what is happening here, we're not moving."   |
| Sliding baselines  | "Maybe people's range of acceptable harvest sizes has increased."   |
| Effective population size, local population size           | "We ship bidarkis to friends and family. Most go to Anchorage in zip-lock bags."  |
| Overfishing  | "There are limits, limits of what you can harvest. Some people go beyond it."   |
| Growth overfishing   | "It's harder to find the bigger ones so I'm getting the smaller ones."  |
| Recruitment overfishing                                    | "They are getting wiped out and are having trouble reproducing."  |
| Lack of seasonal restrictions                              | "March was the month our elders stopped us from hunting. The animals had little ones inside. If you want to see them in the future, leave them alone. New generation, it's not that way. They go out and get whatever they want whenever they want."  |
| Breakdown in information transfer from elders to community | "Now, the new generation doesn't have an understanding or meaning. Poor kids don't know no better. We elders haven't told the younger ones what the nature does."<br>"We are blaming the younger generation but we are to blame. We are not teaching them."   |
| Sea otter predation  | "Sea otters are part of the problem...they eat every thing we eat."   |
| Bird predation   | "The bidarki remains you find on the beach mostly in the spring when the spring birds are around when the sea birds come, nesting birds will eat them. That is when the bidarkis are most vulnerable."  |
| Increased harvest efficiency                               | "Now everyone has a skiff and we can see the immediate impact on the resource."   |
| Multiple causation and sequential perturbations            | "It's not just overharvesting. Declines are due to a chain reaction. There is still to this day, no one reason for all of these declines."  |
| Change in human and sea otter prey species breadth         | "Years ago, people didn't only go for bidarkis, everything was available. Why would they want to just hit the bidarkis? They had crab, mussels, and urchins. The sea otter will change their diet, like any other animal, like us. What are they going to turn to? They turn to bidarkis. Because that's our only diet from here now."<br>"People always used to have native food. People eat less native food now, but people still eat bidarkis." |

populations likely flourished throughout the early 1900s (Tegner and Dayton 2000).

With the protection of sea otters in 1911, this keystone predator began to recover along Alaskan coastlines. Sea otters returned to the nearshore of Port Graham and Nanwalek by the early 1960s (Table 5). Sea urchins, most likely *Strongylocentrotus droebachiensis*, and sea cucumbers, which were once plentiful on Nanwalek Reef in the 1940s, were mostly gone by the late 1960s.

With the introduction of the cash economy in the early 1900s, fishing boats that were once wooden dories were gradually replaced by motorboats for fishing and travel, thereby increasing harvest efficiency. By the early 1980s, 10 years after the introduction of electricity to the villages, freezers began to be used by subsistence harvesters to store food. This storage ability allowed people to increase their harvest effort (Table 5).

In Cook Inlet, commercial crab and shrimp fisheries, landings of which peaked in the early 1960s with inshore harvests in bays like Port Graham Bay (Cook and Norris 1998; Table 5), required increased effort and movement offshore to maintain harvest levels. By the early 1980s, crustacean stocks began to collapse sequentially in the Gulf of Alaska (Orensanz et al. 1998). Coincident with the serial collapse of crustaceans

was a conspicuous shift in benthic species composition from shrimp in the 1970s to ground fish in the 1980s (Anderson and Piatt 1999) and variations in the distribution and abundance of marine mammals and sea birds (Springer et al. 1999), in part attributed to the Pacific Decadal Oscillation and the resulting climatic regime shift of 1977 (Mantua et al. 1997). Whatever the cause, by the 1980s, native subsistence users found Dungeness crab (*C. magister*) increasingly hard to collect while their main competitor, the sea otter, populations of which were thriving, were observed consuming juvenile Dungeness crab, among other invertebrates (Table 5).

The 1989 *Exxon Valdez* oil spill in neighboring Prince William Sound had severe cultural, social, and ecological effects in Port Graham, Nanwalek, and the surrounding area, even though relatively little oil came into Port Graham Bay (Table 5; Peterson et al. 2003, Stanek 2006). Local people hired to help clean up the spill earned unusually high incomes over a short period of time. Many people bought new and better boats and outboard motors. Although initially people avoided subsistence foods for fear of oil contamination, subsistence harvest largely resumed within a few years (Fig. 3B). With better boats, people could visit more shoreline

per tide and access beaches in previously prohibitive conditions (Table 5). Consequently, and ironically, a delayed indirect effect of the spill was an increase in shoreline harvest efficiency likely leading to an increase in invertebrate mortality due to fishing. Although the spill may have had some direct effects on local marine invertebrates, elders observed that shellfish declines began prior to the spill (Table 5).

In sum, historical subsistence harvest differed in several ways from today's practices. In prehistoric times, prior to European contact, subsistence harvest effort was less spatially concentrated because communities shifted among seasonal camps. With migration of regional clans to trading posts throughout the 1800s, intentional consolidation of native villages by the Orthodox religion in the mid to late 1800s, and the creation of canneries in the late 1880s, central-place subsistence foraging gradually replaced dispersed optimal foraging. The introduction of modern technologies (freezers and better boats) facilitated increased harvest effort and efficiency, contributing to increased fishing mortality. Yet, even with the increased ability to travel with better boats, central-place foraging among subsistence shoreline collectors remains common, particularly in the winter when stored salmon supplies caught the previous spring become low and dangerous weather prohibits travel. Lastly, according to traditional knowledge, subsistence prey items from the 1920s to 1950s included a wider range of invertebrates, such as whelks, sea urchins, sea cucumbers, crab, mussels, clams, and cockles, because all of these invertebrates were present in abundance (Fig. 5A). Over the last decades of the 20th century, these resources became scarce sequentially, likely due to intensified consumption by an increasing sea otter population, rising subsistence and regional commercial harvest effort, and prey switching by sea otters and human harvesters.

#### *Synergistic serial depletion*

We propose that the recent localized depletion of *Katharina* is a consequence of the serial decline of alternative prey leading to increased per capita predator impacts by both humans and sea otters on *Katharina*. Sea otters are well known to reduce a diversity of herbivorous epibenthic macroinvertebrates (sea urchins, chitons, and limpets) and filter feeding bivalves (clams, cockles, and mussels) (Estes and Palmisano 1974, Simenstad et al. 1978, Kvitek et al. 1992). In the early 1900s, the breadth of Sugpiaq subsistence diets was broader than it is today, due to the availability of a wide range of nearshore benthic invertebrates. Consequently, human and sea otter predation pressure was formerly distributed over several species with preferred and most accessible prey items targeted first. As preferred species became less abundant, we postulate that predation pressure intensified on those species that remained, resulting in a gradual decline in the number of species consumed. Sequential prey switching provides a mech-

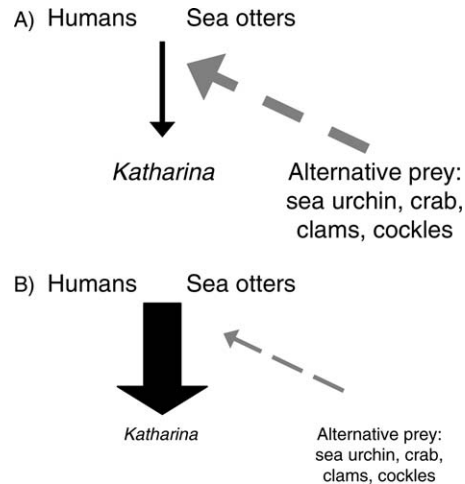


FIG. 6. (A) Interaction modification (dashed gray arrow) by alternative prey reduces the per capita predator impacts (solid black arrow) by humans and sea otters on *Katharina* biomass. (B) When alternative prey items are scarce, per capita predator impacts on *Katharina* are magnified.

anism for serial declines. Consequently, the recent localized depletion of *Katharina* may in fact reflect the serial depletion of nearshore benthic invertebrates by both humans and sea otters resulting in increased per capita *Katharina* mortality due to a scarcity of alternative prey.

Empirical and theoretical evidence suggests that the presence of alternative prey can modify the direct interaction between predator and prey by reducing per capita predator impact through predator satiation or increased handling time (Wootton 2002). In the past, the availability of sea urchin, sea cucumber, crab, clams, cockles, and other alternative benthic invertebrate prey may have reduced the per capita impact of humans and sea otters on *Katharina* (Fig. 6A). Consequently, present-day per capita predation rates on this strongly interacting grazer are likely higher because alternative prey items are now scarce (Fig. 6B, Table 2).

This hypothesis of synergistic serial depletion is substantiated by the multispecies trends in benthic invertebrate subsistence landings in Port Graham and Nanwalek from 1987 to 2003 (Fig. 5B). Landings of alternative prey (whelks, sea urchin, sea cucumber, mussels, Dungeness crab, Tanner crab, and shrimp) were low between 1987 and 2003, remaining well below 2% of the mean annual catch during this period. These quantitative landings data are consistent with the qualitative traditional knowledge that these invertebrate abundances were in short supply due to previous declines (Fig. 5A). Relative to sea urchin and crab, a greater biomass of clams and cockles was landed during the late 1980s, in accordance with the traditional knowledge that these bivalves declined after sea urchin and crab. Landings of bivalves began to decline by the early 1990s, yet *Katharina* landings were greater in 1991



PLATE 6. On her way to jig for halibut in Port Graham Bay, Alaska, Vera Meganack, a Sugpiaq Elder, rows her skiff as they did in the past before outboard engines, standing at the stern, facing forward to watch for oncoming seas. Vera is among many subsistence resource users in the area who have observed changes in the abundance and behavior of species at particular points in time and space, and can offer insight into the ecological and socio-economic factors driving ecosystem dynamics now and in the past. Photo credit: Lisa Williams, June 2005.

and 1992, compared with 1987, and have remained high, despite the dip in quantity in 1989 due the scare from the *Exxon Valdez* oil spill.

Looking deeper into the past, dramatic shifts in the species composition, trophic level, and general size of subsistence shellfish species landed have occurred over the past 700 years in Port Graham Bay, Alaska (Figs. 4 and 5B). While the large, upper-trophic-level predatory whelk *Neptunea* comprised the greatest proportion of invertebrate midden remains during the late prehistoric and early historic occupation, it and other whelks, such as *Volutharpa*, are all but absent from today's subsistence shellfish landings (Fig. 5B). Rather, *Katharina*, a considerably smaller, lower trophic level grazer, is now the primary invertebrate harvested in Port Graham and Nanwalek, comprising  $40\% \pm 3\%$  (mean  $\pm$  SE) of the mean annual invertebrate catch. Certainly, both sea otters and humans are size-selective predators, generally targeting and removing larger prey species and larger individuals within a species. This is evident from the variation in *Katharina* size-frequency distributions across sites (Fig. 3) and from the archaeological data, which suggests that *Neptunea*, reaching maximum

lengths of 18 cm (O'Clair and O'Clair 1998), were targeted over *Nucella*, *Volutharpa*, which reach lengths no greater than 5 cm. Yet, with the 5% reduction in *Neptunea* landings from late prehistoric to early historic occupations came 1.5–2 fold increase in the landings of the smaller whelks *Nucella* and *Volutharpa* (Fig. 4). This transition in invertebrate landings from large high trophic level predators to smaller, mid-trophic level predators and finally to lower trophic level herbivores suggests that fishing down marine food webs (Pauly et al. 1998) may have begun as early as AD 1300.

In many ecological studies, diet breadth and prey preferences of predators are typically assumed to remain constant. However, increasing evidence suggests that behavioral flexibility by predators may be a common phenomenon (Estes et al. 2004). Evolutionary theory implies that consumers have evolved flexible responses to varying environmental conditions, such as the ability to substantially alter foraging strategies and food sources. Like sea otters, fishermen tend to switch "targets" as relative abundance and market values change. This reinforces the importance of understanding human and nonhuman predator behavior when devel-

oping sustainable fisheries strategies and effective marine conservation plans.

*Compounding social complexities contributing to invertebrate decline*

Certainly, present-day causal mechanisms other than overharvest and sea otter predation have contributed to black leather chiton declines (Table 6). Elders point to the deterioration in information transfer to the younger generation of harvesters as a critical problem leading to overall resource declines. *Katharina* sizes deemed acceptable by younger harvesters are smaller than those used by today's elders in their own youth (i.e., shifting baselines). Furthermore, traditional subsistence management practices such as seasonal restrictions are no longer being adhered to. Lastly, the effective human predator population size in these villages is greater than the local human population size. Teenagers, young adults, and the ill often leave the villages for schooling or health care provided by local city centers (Stanek 2006), yet are still sent subsistence food items, as are relatives who have moved away (Table 6). This again illustrates the importance of understanding the social dynamics motivating human behavior.

*Current ecological complexities contributing to Katharina decline*

Additional ecological complexities may be contributing indirectly to *Katharina* declines. We observed that *Katharina* recruitment is typically high where adult density is high (Fig. 3). This could be due to the maintenance of GABA (gamma-aminobutyric acid) producing coralline crusts by adult *Katharina* actively grazing on turfing and foliose macroalgae. GABA is a recognized chemical settling cue for many molluscan species, including *Katharina* (Strathmann 1987); consequently, coralline crusts form important settlement habitat for invertebrate larvae, facilitating recruitment and, in turn, future grazing. Conversely, where adult *Katharina* densities have been reduced by harvest and/or sea otter predation, *Katharina* recruitment tends to be low (Fig. 3). Reduced densities of adult *Katharina* may indirectly impede *Katharina* recruitment by releasing macroalgae from grazing pressure and allowing species like *Endocladia muricatum* in the high intertidal and *Alaria* spp. in the mid to low intertidal to flourish. These macroalgal species can overgrow and shade out encrusting corallines thereby reducing valuable settlement habitat and the production of the settling cue GABA. Furthermore, macroalgae can mechanically sweep away larvae competent to settle. In sum, food web alterations caused by the exploitation of a dominant consumer may in fact hinder recruitment of that very consumer.

Alternatively, when adult densities are low, local recruitment may be reduced simply due to limited larval supply. *Katharina* reach reproductive maturity at ~35 mm, their reproductive output increases cubically with length, and larvae are pelagic for ~6 days (Strathmann

1987, Salomon et al. 2006). *Katharina* subpopulations may be heavily reliant on local sources of larvae, particularly where local currents, eddies, and boundary layer effects impede widespread dispersal and facilitate local recruitment. Certainly, local retention is more common than previously thought (Jones et al. 1999, Swearer et al. 1999), and the risk of recruitment overfishing is becoming increasingly recognized (Walters and Kitchell 2001; Table 6). In the context of fisheries management, there is now broad empirical evidence suggesting that low parental stock sizes can result in lower mean recruitment (Myers et al. 1999).

*Integrating multiple data sources*

By drawing on multiple data sources, we have pieced together a conceptual model of the local and regional ecosystem that sheds insight into the likely causes of recent *Katharina* declines. Contemporary field surveys provided evidence that predation by humans and sea otters influenced *Katharina* abundance, density, and biomass. Interviews with elders offered evidence of serial declines of nearshore invertebrates over time, together with changes in human subsistence activity. A time series of subsistence invertebrate landings afforded a quantitative calibration and validation of traditional knowledge from 1987 to 2003. Finally, archaeological data and historical records revealed coarse changes in the invertebrate catch and the spatial distribution of subsistence harvest pressure, allowing us to scale our contemporary research with a deeper time perspective. The hypothesis of synergistic serial depletion emerged from multiple lines of evidence, quantitative and qualitative, current and historical, considered simultaneously.

*Value of traditional knowledge and historical perspectives*

Although often neglected in ecological studies, historical data are vital for revealing the "ghosts" of ecosystem past, the true magnitude of change of ecosystems present, and the dynamics that link the two (Pauly 1995, Dayton et al. 1998). Here, an analysis of present-day ecological data alone could not have explained the ultimate causal mechanisms governing recent localized *Katharina* declines. Rather, knowing the historical change in alternative invertebrate prey, human settlement patterns, subsistence harvest practices, and predatory population dynamics of sea otters was critical to our current understanding of the factors leading to recent declines of the *Katharina*, linking the results of our fieldwork with longer term social-ecological dynamics. We argue that the explanation of decline was revealed only through the examination of specific historical events and an understanding of how these events may have led to the presence or absence of key consumers in the community.

Here, the value of western science was in developing the quantitative relationship between predation pressure and resource density. The value of traditional knowl-



edge was in providing qualitative assessments of shifts in predator and prey abundance and subsistence behavior prior to ecological study. In this case, the two methods agree on the major direct drivers of environmental change, yet traditional knowledge provided important historical ecological, socioeconomic, and cultural considerations that were otherwise not available.

Indeed, debate exists over the relationship between traditional knowledge and science (Berkes 1999) and even over the degree to which a simple dichotomy between the two withstands scrutiny (Agrawal 1995). Certainly, both knowledge systems are not without their limitations, and skepticism regarding the use of traditional ecological knowledge (TEK) exists for multiple reasons (Huntington 2000, Moller et al. 2004). In addition, drawing on TEK requires attention to cultural context to avoid misinterpretation or misrepresentation (Smith 1999, Huntington et al. 2006). Despite the limitations, we bridge these two alternative yet complementary knowledge systems and profit from their strengths to inform the causal mechanisms driving *Katharina* declines. Through the documentation of TEK via interviews and collaborative fieldwork, we draw on TEK as one of several sources of information needed to reconstruct ecological history. Perhaps most importantly, exchanging and combining scientific and traditional knowledge, while using a participatory research approach, built community partnerships, raised awareness, and provided quantitative and qualitative data to inform future conservation strategies.

#### CONCLUSION

Ultimately, assessing the relative magnitudes and relationships among human impacts, interspecific interactions, and physical factors will reduce our uncertainty in detecting drivers of change and increase our likelihood of designing effective conservation strategies for nearshore ecosystems (Salomon et al. 2001, Salomon et al. 2002). However, management will fail if it focuses on the most recent symptoms of decline rather than on its deep historical causes (Jackson et al. 2001). This research showcases the insight ecologists can glean from delving into both ecological and social history. By considering pivotal socioeconomic drivers across multiple scales in time and space and integrating western science and traditional knowledge, we obtained an enhanced understanding of the causes driving *Katharina* declines and consequently are now better equipped to collaboratively develop an effective conservation plan for the nearshore. This was and continues to be a complex system subject to the vagaries of natural predators, the physical environment, and socioeconomic factors which motivate human behavior.

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#### APPENDIX

Maps of the spatial distribution and abundance of sea otters (*Enhydra lutris*) observed during three small boat surveys conducted in the summer of 2004 in and around Port Graham Bay, Alaska, USA (*Ecological Archives* A017-073-A1).