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Benthic Invertebrates of the Eastern Bering Sea: A Synopsis of the Life History and Ecology of Snails of the Genus *Neptunea*

by
K. R. Smith, R. A. McConnaughey, and C. E. Armistead

U.S. DEPARTMENT OF COMMERCE
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by
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ABSTRACT

Snails of the genus *Neptunea* have a significant presence among the benthic fauna inhabiting the North American continental shelf in the eastern Bering Sea (EBS). This is reflected by the catch of annual bottom trawl-net surveys of the continental shelf conducted by the Resource Assessment and Conservation Engineering Division of the Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration. Together these surveys comprise a time-series assessing stocks of groundfish and benthic invertebrates in the EBS, from 1971 to the present. In the 1975 survey of shelf and upper slope, gastropods constituted 6.6% of the biomass of invertebrates caught. In some areas catch per unit effort (CPUE; i.e., catch per unit of area swept) exceeded 30 kg/ha.

Gastropods, mostly of the order Neogastropoda which includes *Neptunea*, in more recent EBS shelf surveys remain one of the top 50 EBS invertebrate taxa in both total abundance and frequency of occurrence at trawl stations. Among gastropods, by far the most abundant species in these surveys are those of the genus *Neptunea*, particularly the four species *N. pribiloffensis, N. heros, N. lyrata,* and *N. ventricosa.* Based on hauls at standard EBS shelf stations in surveys of selected years from 1983 to 2010, we include maps for each species showing the year-by-year distribution of abundance over the area as extrapolated from haul CPUE.

Because of its high abundance in the benthic fauna, the genus probably constitutes a significant element in the benthic ecology of the region. However, little direct study of local populations has occurred to date, leaving a dearth of information available on biology and ecological relationships. More extensive observations have been made of species of *Neptunea* in other marine regions of the Northern Hemisphere, and this paper presents information available from these studies along with that from local studies. The information forms a synopsis of the

probable characteristics of life history, trophic webs, and anthropogenic effects relating to the genus in the EBS.

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INTRODUCTION

Gastropods have a significant presence in the benthos of the eastern Bering Sea (EBS) continental shelf and upper slope, as shown in the results of annual bottom trawl surveys conducted by NOAA's National Marine Fisheries Service (NMFS) through the Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division (RACE). Together these surveys comprise an annual time-series, from 1971 to the present (Acuna and Lauth 2008), used to assess stocks of groundfish and benthic invertebrates in the EBS.

In the 1975 NMFS survey of the shelf and upper slope, gastropods constituted 6.6% of the biomass of invertebrates caught. In some areas trawl catch per area swept exceeded 30 kg/ha (MacIntosh 1980). Yeung and McConnaughey (2006) judged gastropods (mainly those of the order Neogastropoda) among the top 50 EBS invertebrate taxa in both abundance (by weight) and frequency of occurrence (percent of trawl stations where present), in each year from 1982 to 2002. Among large (length > 50 mm) species of gastropods occurring on the EBS continental shelf and upper slope, the most abundant, in both biomass and numbers, are *Neptunea* species. Of these, *N. pribiloffensis* is generally the most abundant, with *N. lyrata*, *N. heros*, and *N. ventricosa* also prominent[1] (MacIntosh 1980).

In addition to their ecological significance in the benthos, gastropods, mostly species of the genus *Neptunea*, have been harvested in the region as commercial seafood. Pot fishing was conducted by Japan in the 1970s (MacIntosh 1980), and by the United States as recently as 1997 (Bowers et al. 2008). Most of the catch (70%) retained by the Japanese fishery in 1973 was *N. pribiloffensis*, with an additional 23% composed of *Buccinum angulosum and B. scalariforme* (MacIntosh 1980).

[1] K.R. Smith, pers. obs.

Species of the genus *Neptunea* have shells of medium to shortened length (i.e., length of the shell from apex to end of anterior canal) relative to width. Shells are dextrally coiled, often with species-distinct patterns of spiral/axial sculpture. Sinistral coiling is rare (Nelson 1978, MacIntosh 1976a).

This synopsis outlines the geographic distribution of abundance of the four major *Neptunea* species in the EBS shelf area from 1983 to 2010 inclusively, as reflected by standard RACE bottom trawl surveys for selected years representing the period. It also summarizes from the available literature the findings by other investigators regarding the life history and ecology of species of *Neptunea* in the EBS shelf area. The total scope of such studies of local populations is as yet limited. Therefore, we summarize as well the somewhat more extensive findings of investigations of *Neptunea* species in other geographic regions within the range of the genus in the hope of presenting a more complete picture of general characteristics of life history and ecology applicable to the genus as a whole.

PHYLOGENY AND GEOGRAPHIC ORIGIN OF NEPTUNEA

Among gastropods, the genus *Neptunea* Röding, 1798, is of the subclass Prosobranchia, which includes the order Neogastropoda that in turn encompasses the Buccinidae (loosely termed whelks), the parent family of the genus. Species of the Neogastropoda have about twice as many chromosomes as other prosobranchs, suggesting a possible origin by polyploidy, and are considered the most derived prosobranchs (Ruppert et al. 2004).

Although the phylogenetic relationships among neogastropod species are often uncertain above the level of genus, a close relationship between the buccinid genera *Neptunea* and

Buccinum has been indicated by both morphological (Haasl 2000) and mitochondrial 16s rRNA gene (Hayashi 2005) comparisons. This is despite the obvious difference between the oval operculum of *Buccinum* with its centered nucleus, and the leaf-shaped one of *Neptunea* having a marginal nucleus, by which *Neptunea* resembles several other buccinid genera[1].

The genus is thought to have evolved in the western North Pacific (off northern Japan and Sakhalin Island) in the early Oligocene epoch (Nelson 1978). Its many species presently occur in continental shelf waters of the North Pacific (west and east), Arctic, and North Atlantic Oceans, as well as the North Sea and Mediterranean Sea (Nelson 1978). Although systematics within the genus are still being developed, several described species have been identified on the EBS shelf. In addition to the four major species mentioned above, these include *Neptunea borealis*, *N. amianta*, *N. neptunea*, and *N. insularis* (Clark 2006).

GEOGRAPHIC DISTRIBUTION OF *NEPTUNEA* IN THE EASTERN BERING SEA

Methods

The RACE EBS bottom trawl surveys index the abundance of each individual taxon in the catch by calculating the average number of organisms and/or average aggregate weight (biomass) caught per unit of bottom area swept by the net mouth (CPUE), for each haul. Area swept equals the average width of the net mouth times the distance trawled. Gastropod catch efficiency of the trawl gear is unknown. Certainly, bottom trawls are not efficient samplers for benthic infauna; however, they are deemed sufficient for monitoring relative abundance of certain epifaunal species. The derived abundance estimates may be thought of as a minimum for

potentially burrowing species such as gastropods (Yeung and McConnaughey 2006, MacIntosh 1980).

RACE Bottom Trawl Survey Design

Methods and gear used in these surveys are generally consistent from year to year. The present configuration of sampling stations and gear dimensions was first adopted in 1982 under the North Pacific Fishery Management Council's Bering Sea-Aleutian Islands Groundfish Fishery Management Plan (Acuna and Lauth 2008, Yeung and McConnaughey 2006). The annual surveys conducted since then have covered an area divided into a standard grid of 330 squares each 20 × 20 nautical miles (nmi) (37.04 × 37.04 km), thus encompassing approximately 341,880 km^2 overall. The standard trawl stations of the survey include 330 located at the respective centers of these squares, plus at the corners of select grid squares an additional 16 stations northeast of the Pribilof Islands and 10 stations southwest of St. Matthew Island as well. These extra stations are included to increase sampling density in areas historically having significant concentrations of *Paralithodes* species (king crab). An additional 20 squares with centered trawl stations were added at the northwest margin of the grid in 1988 to extend the standard survey area northwest and provide further information on the distribution of *Chionoecetes opilio* (snow crab) and *Theragra chalcogramma* (walleye pollock; Acuna and Lauth 2008). This established the current standard survey design of 376 stations in a grid of 350 squares covering approximately 362,600 km^2. This survey grid spans the EBS shelf from the Alaska Peninsula in the southeast to approximately 62º N near St. Matthew Island in the northwest, and cross-shelf from the 20 m isobath to the 200 m isobath.

Results: Distribution of Abundance

Like many benthic invertebrates, species of *Neptunea* are not uniformly abundant over the EBS. Along with other benthic species, these species generally occur as components of regional assemblages of taxa, likely the result of differing preferences for environmental elements such as temperature, depth, and prey.

Distribution Maps

Figures 1-4 depict the standard station layout and results from annual RACE EBS bottom trawl surveys, along with broad-scale bathymetry of the region. The maps show annual survey results for each of the four predominant *Neptunea* species *N. heros, N. ventricosa, N. pribiloffensis, and N. lyrata* in the EBS, displaying the year-by-year abundance distribution expressed as CPUE (kilograms per hectare). For a species, each grid square is color coded to represent one of five contiguous CPUE intervals that together cover the full range of densities observed during the surveys included. The color of each square is that of the coded interval encompassing the average CPUE of that year's trawl sample(s) taken within the square. This standardization of color codes allows comparison of densities between years.

The maps cover two periods: 1983 through 1988 and 2003 through 2010. These years were selected to represent any long-term changes in abundance or distribution, while adhering to the most consistent standards of taxonomic identification of any catch of the four individual species. Due to variations in emphasis by RACE personnel on taxonomic resolution in identification of various species as well as varying conditions and workloads in the field, historically such resolution has varied among and within years of the survey. In addition, there have been gradual improvements in taxonomic knowledge and training which have led to more informed classification of many fish and invertebrate taxa recently than on earlier surveys. Thus

there are prudent limits to confidence when considering the historic catch data for some taxa (Stevenson and Hoff 2009). However, a systematic search of the data revealed the years described above during which the amount by weight of catch classified as higher taxa conceivably including any species of *Neptunea* (i.e., "gastropod unidentified" or "*Neptunea* species") was subjectively judged insignificant. These years of relatively unambiguous data regarding the four species of interest were chosen using software programmed by the author to query the extensive RACE EBS bottom-trawl survey database for years wherein the data meet these criteria[2]. In each of these years, generally the entire catch amount reported for the two higher taxa was exceeded by each of the amounts for the four individual species by one or more degrees of magnitude.

None of the species show distinctive density trends of increase or decrease over the range of years 1983 through 2010. Rather, each generally shows a pattern of relatively consistent presence in a particular geographic portion of the shelf (Figs. 1-4). Thus although separated by 14 of the 28 years spanned by the data, the selected blocks of years 1983 through 1988 and 2003 through 2010 were deemed sufficient in representing abundance over the full range of years included.

Neptunea heros showed little change in abundance over the range of years examined. However, a vessel bias indicating some sort of misidentification is probable in 1987, 1988, and 2010. In these years in Bristol Bay parallel north-south lines of stations, each line having been trawled by only one of the two survey vessels alternately, repeatedly show *N. heros* reported in one line but not an adjacent one trawled by the other vessel (Fig. 1). This has been called the

[2]Addressing ambiguity due to variation in the resolution of taxonomic identification of a species among quantified fauna samples within large time-series-based databases, using query-based reclassification to lowest accountable inclusive taxon (LAIT). Unpublished data. K. R. Smith, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115.

column effect[3]. Nevertheless, even given the likely misidentification in these years, there is considerable consistency in the overall geographic range and density distribution of the species historically.

Neptunea ventricosa also showed little change over the range of years examined, except for stations in the extreme northwest of the survey area where presence of the species has seemed either patchy or fluctuating since the inclusion of these stations in 1988 (Fig. 2).

Neptunea pribiloffensis displayed the highest abundance overall. The species showed considerable shifts in distribution but no overall major trends. Lower than average numbers were found in 1986 and 2009. There was a noticeable pattern of occurrence along the shelf break from 61° N south to the Alaska Peninsula, but with a regular localized gap in presence just east of the Pribilof Islands. This gap seems unrelated to historical snail harvesting as the last recorded commercial catch in the area was in 1997 (Bowers et al. 2008). The species was reported at a block of stations southwest of Nunivak Island in 2010, but as this was an isolated report by a single vessel and did not occur in other years it likely represents taxonomic misidentification rather than a population shift of *N. pribiloffensis* (Fig. 3).

Neptunea lyrata is generally co-located with *N. pribiloffensis* (i.e., along the shelf break) but without the noticeable gap near the Pribilof Islands shown by the latter species. Some vessel-related misidentification as mentioned above for *N. heros* and *N. pribiloffensis* appears to occur. On the maps for the year 1983 and 2010, parallel station-columns alternately sampled by the two survey vessels show alternating consistent presence and consistent absence reported for the species, depending on the respective vessel sampling the column. This pattern occurs in areas on the mid-shelf and in Bristol Bay, north and northeast of the otherwise consistent distribution

[3] Chilton, E. A. 2011. NOAA, Alaska Fisheries Science Center, Kodiak Laboratory, Kodiak, Alaska. Pers. comm.

shown for other years along the outer shelf from west of St. Matthew Island thence southeast to the Alaska Peninsula (Fig. 4).

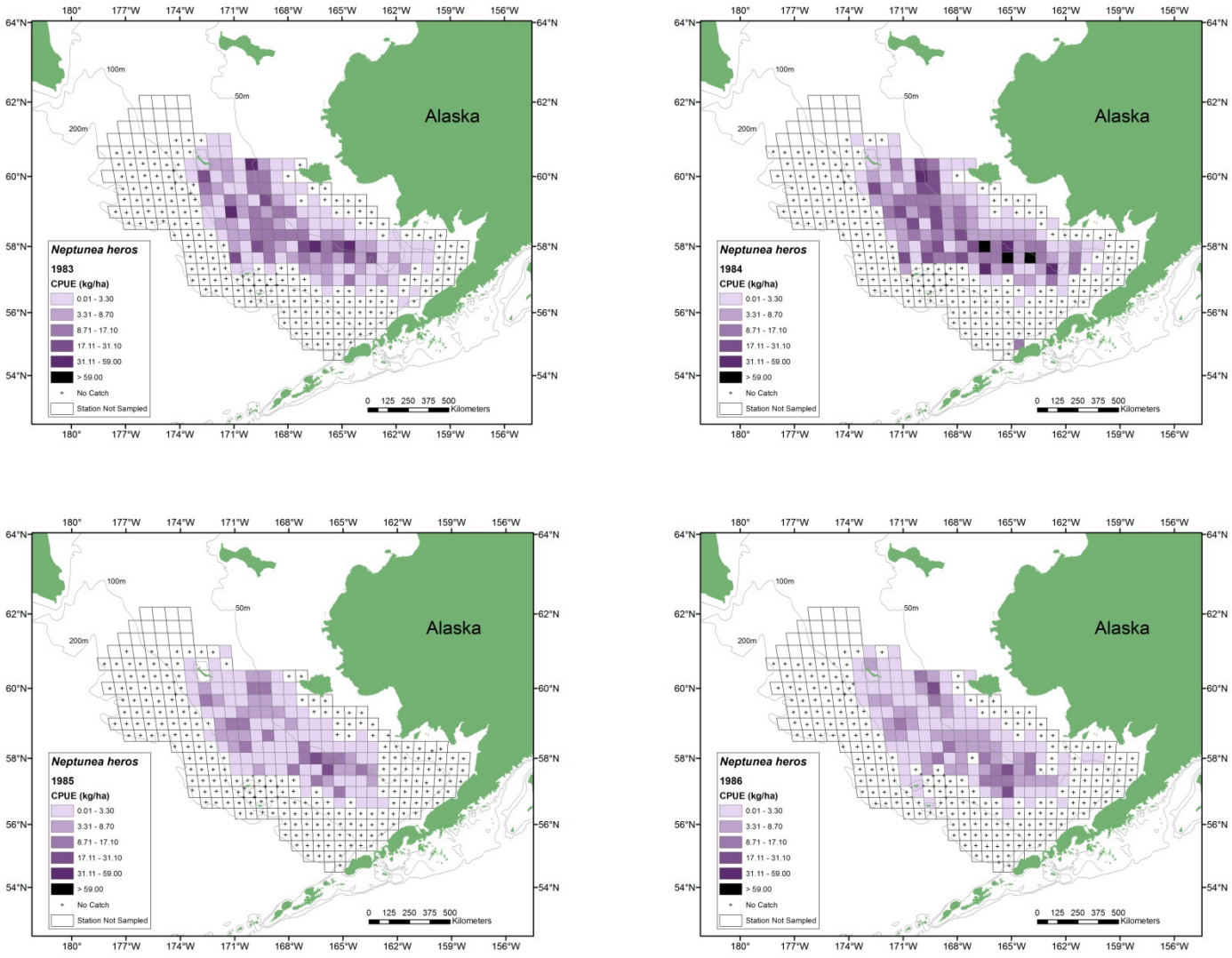
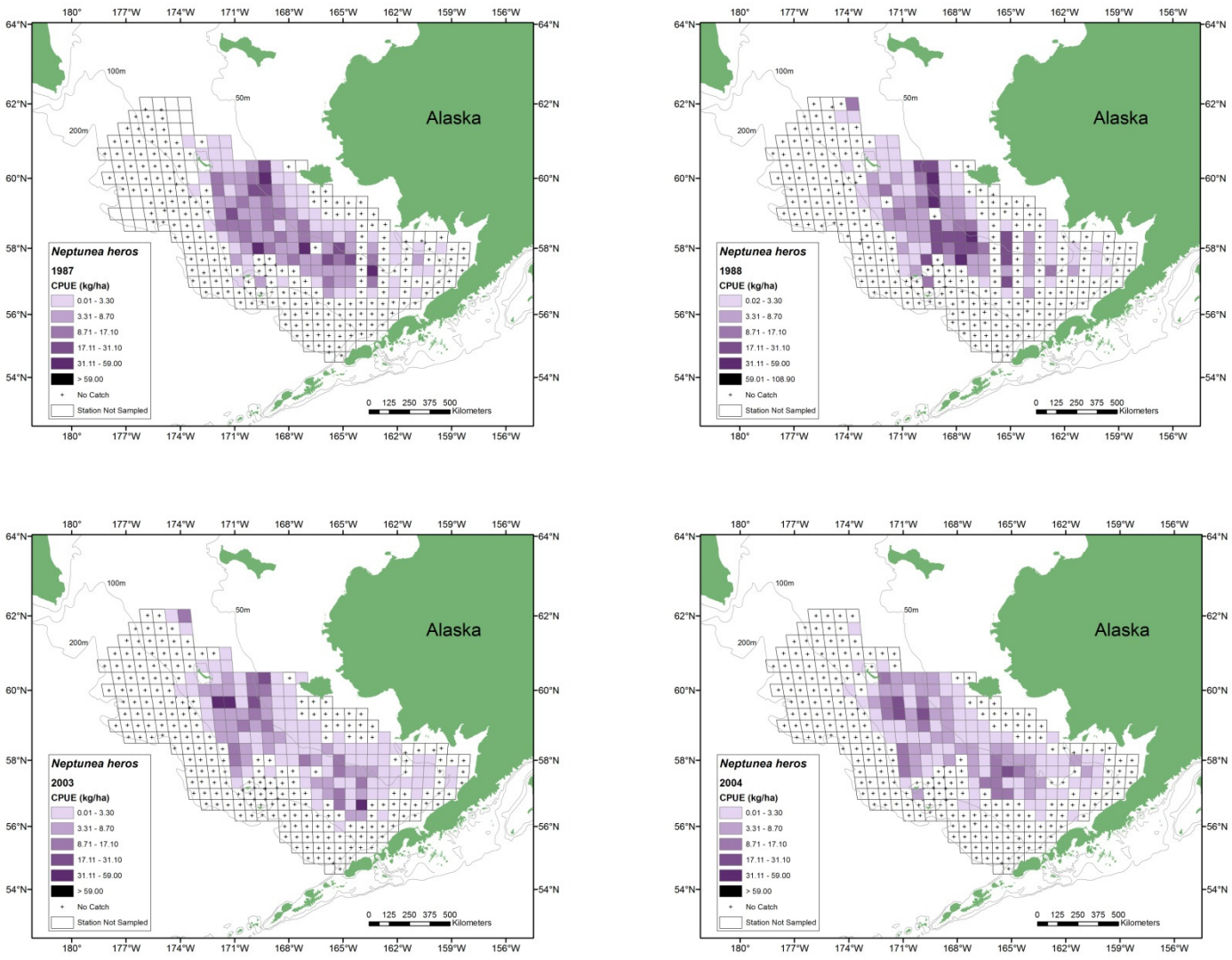


Figure 1. -- Abundance of *Neptunea heros* in the Eastern Bering Sea (EBS) shelf region as catch per unit effort (CPUE, kg/ha) by standard RACE annual bottom trawl sample surveys of groundfish and invertebrates for the select years 1983 through 1988 and 2003 through 2010. The grid of 20 nmi × 20 nmi contiguous squares represents the standard EBS shelf area covered by the surveys, with each square colored to represent the average CPUE of the species within that square.



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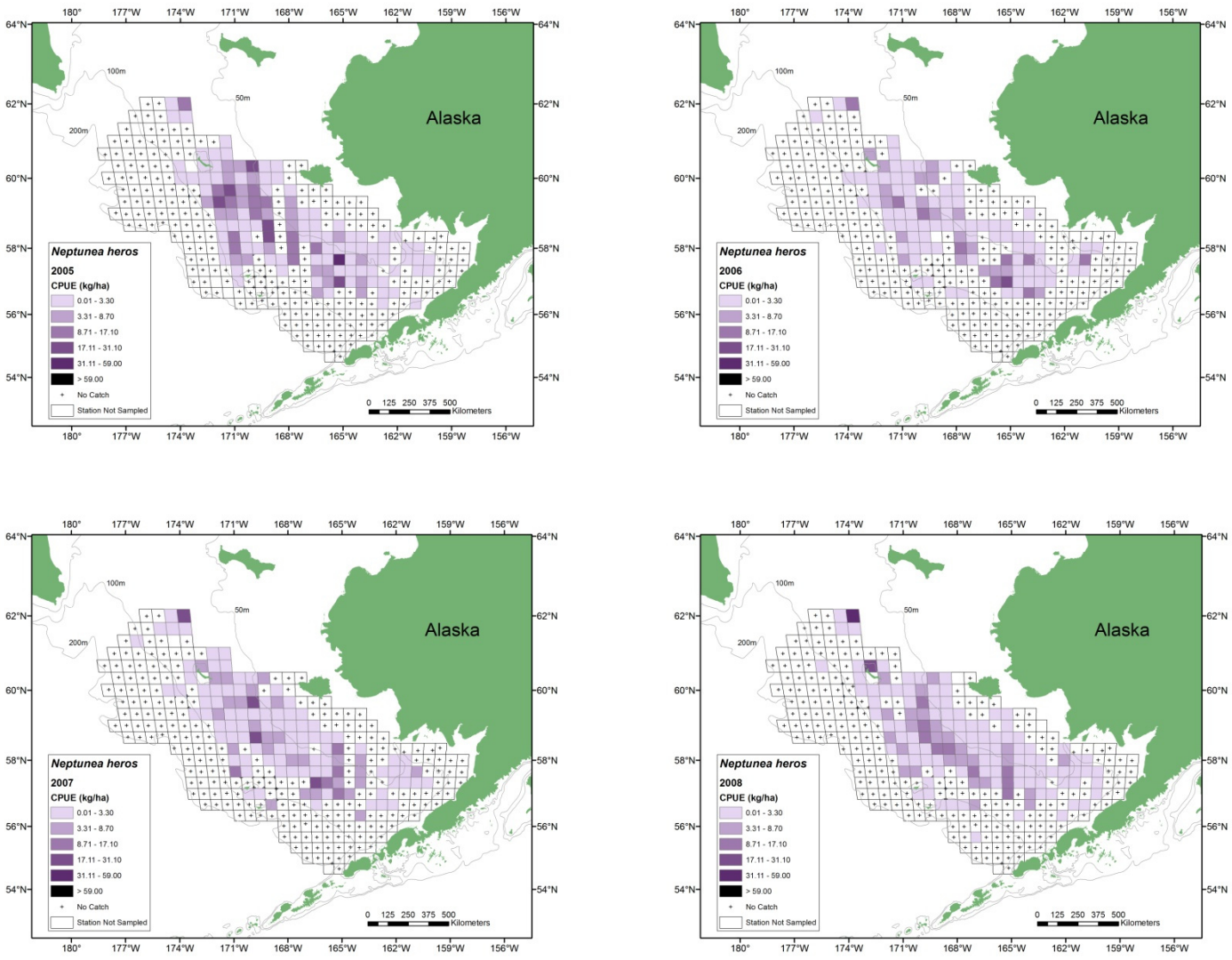

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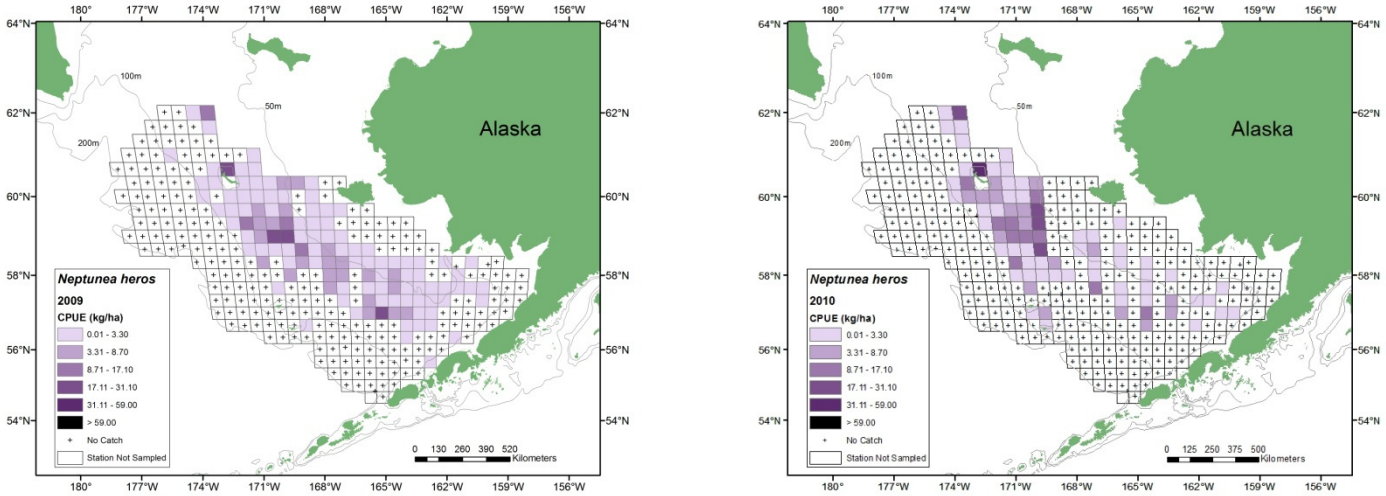

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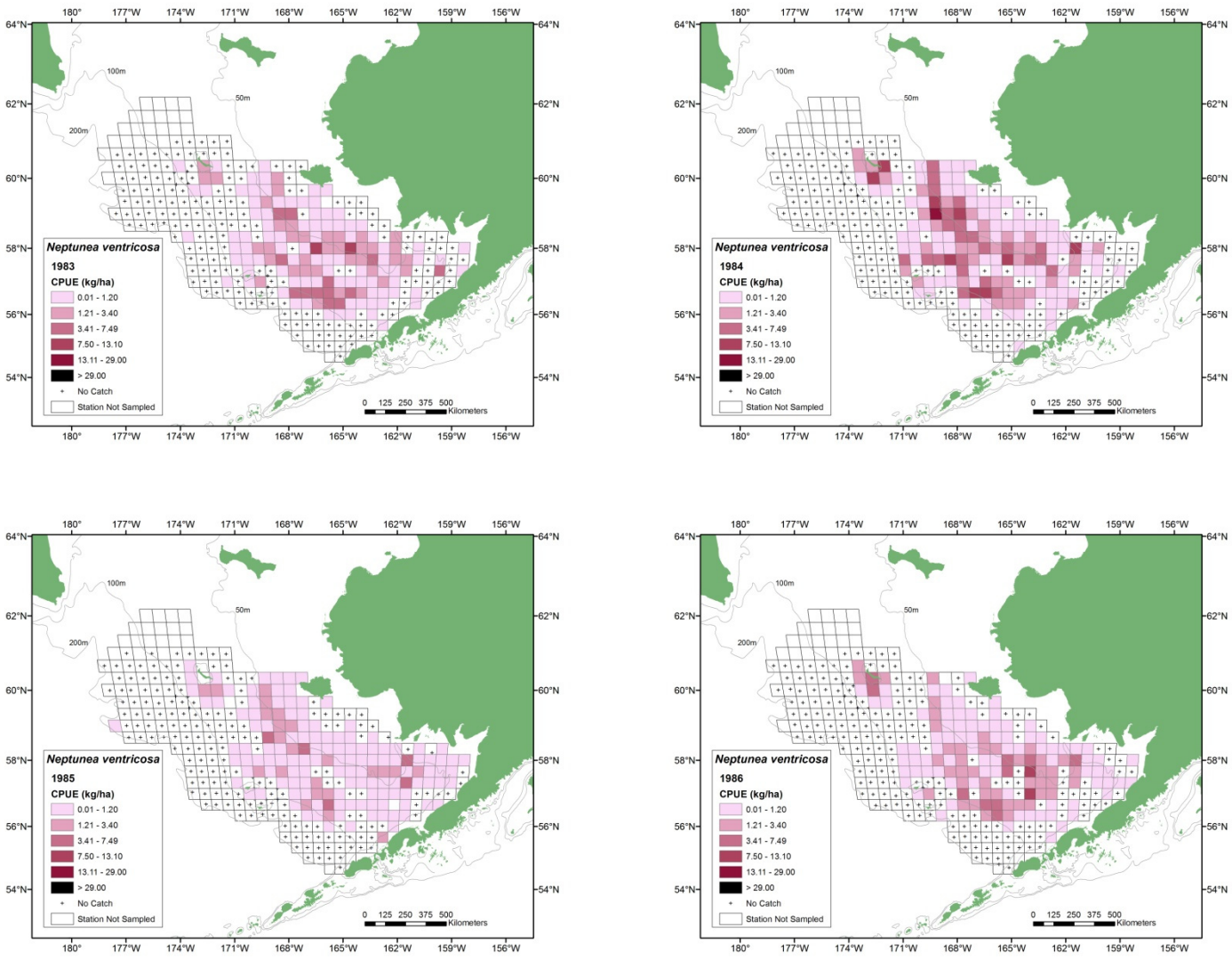
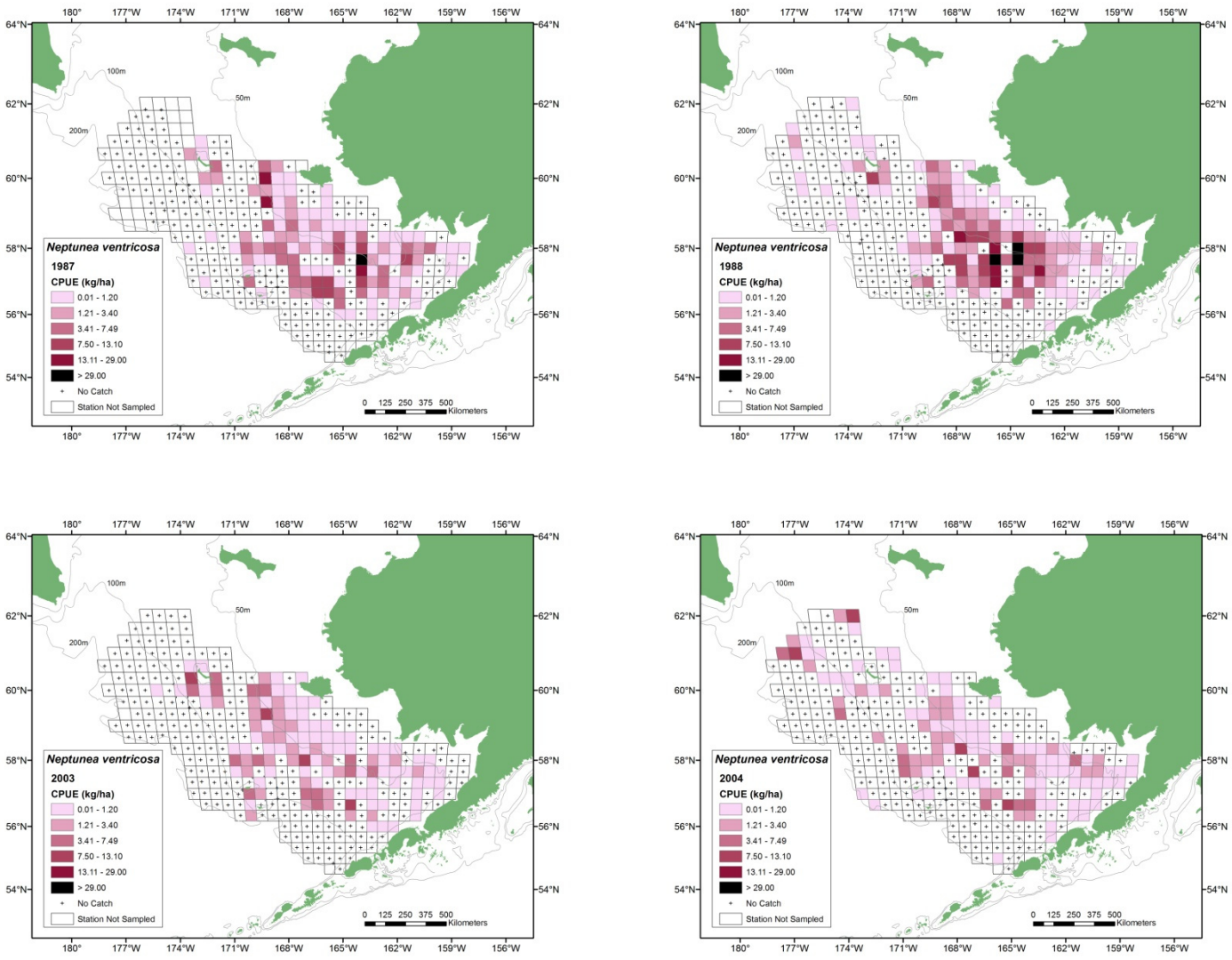


Figure 2. -- Abundance of *Neptunea ventricosa* in the Eastern Bering Sea (EBS) shelf region as catch per unit effort (CPUE, kg/ha) by standard RACE annual bottom trawl sample surveys of groundfish and invertebrates for the select years 1983 through 1988 and 2003 through 2010. The grid of 20 nmi × 20 nmi contiguous squares represents the standard EBS shelf area covered by the surveys, with each square colored to represent the average CPUE of the species within that square.



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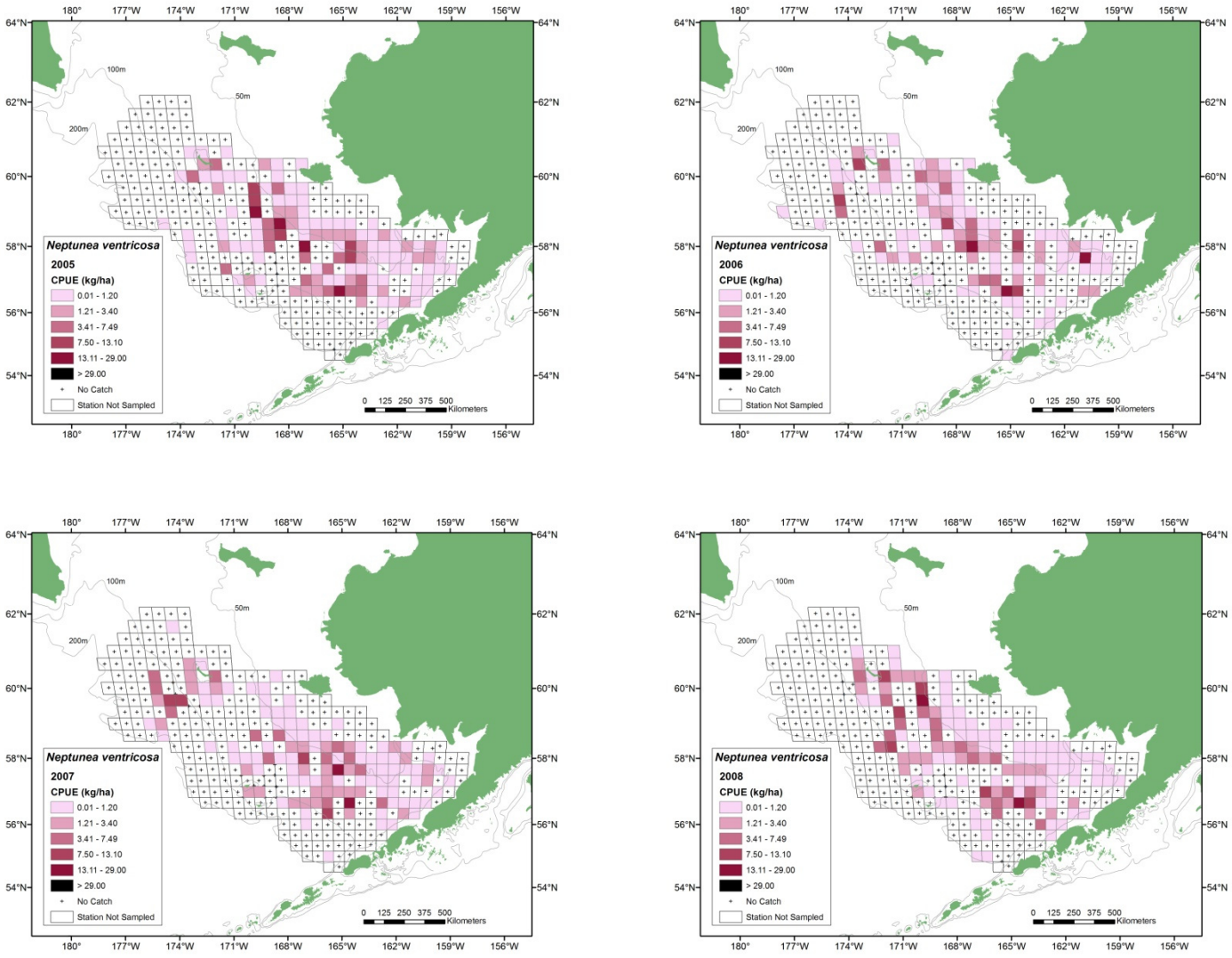

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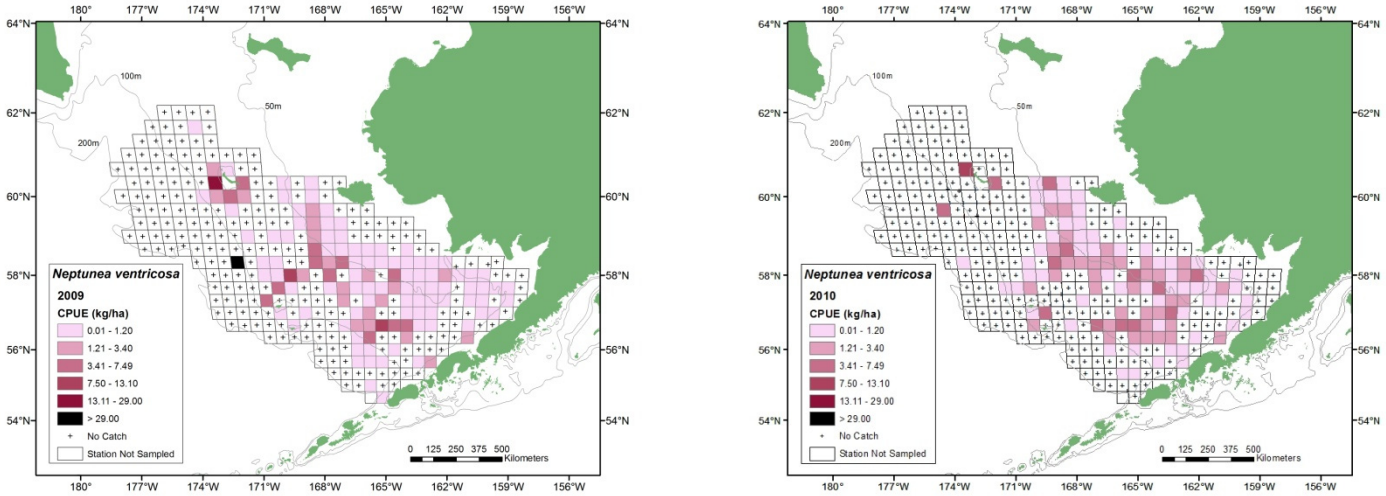

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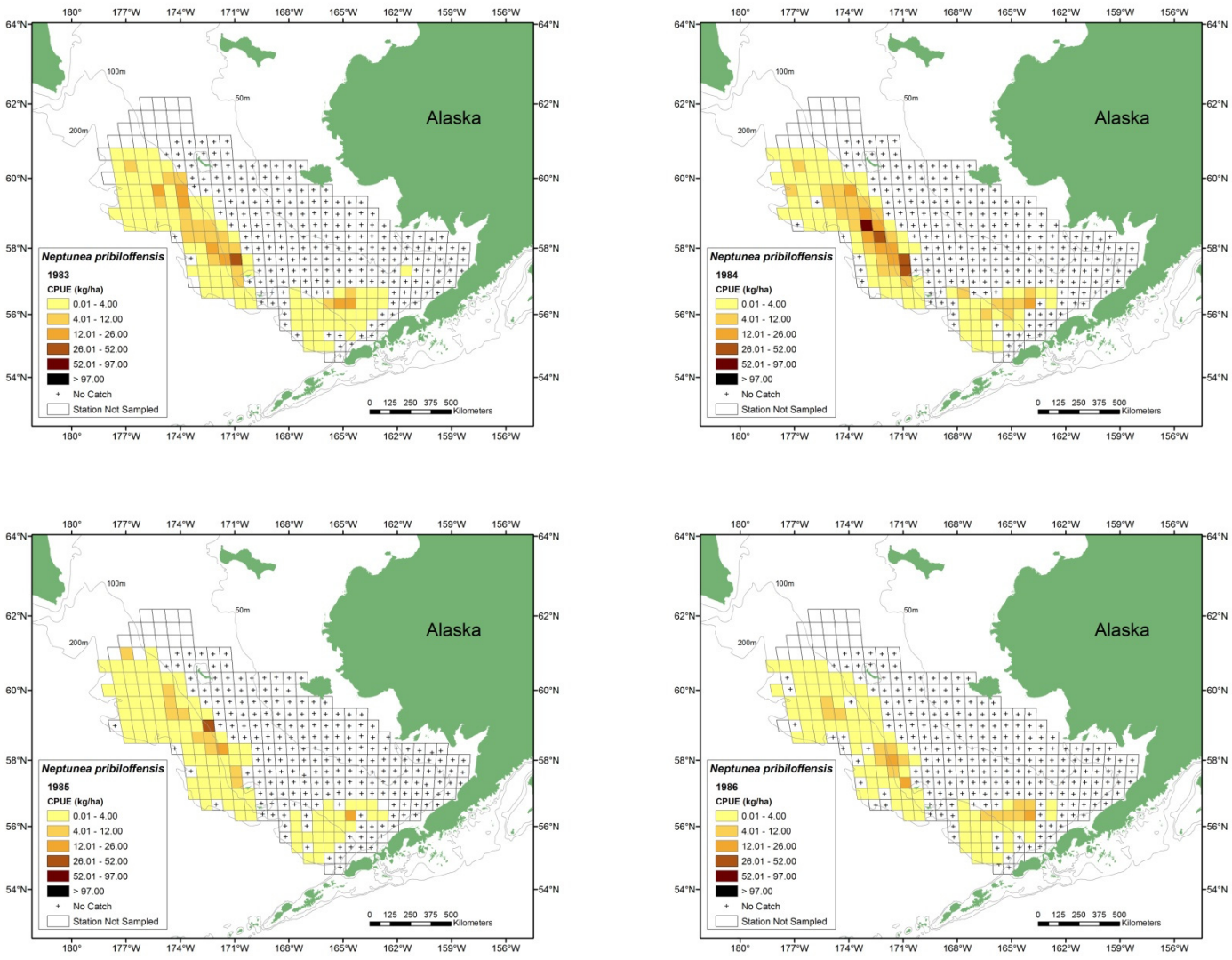
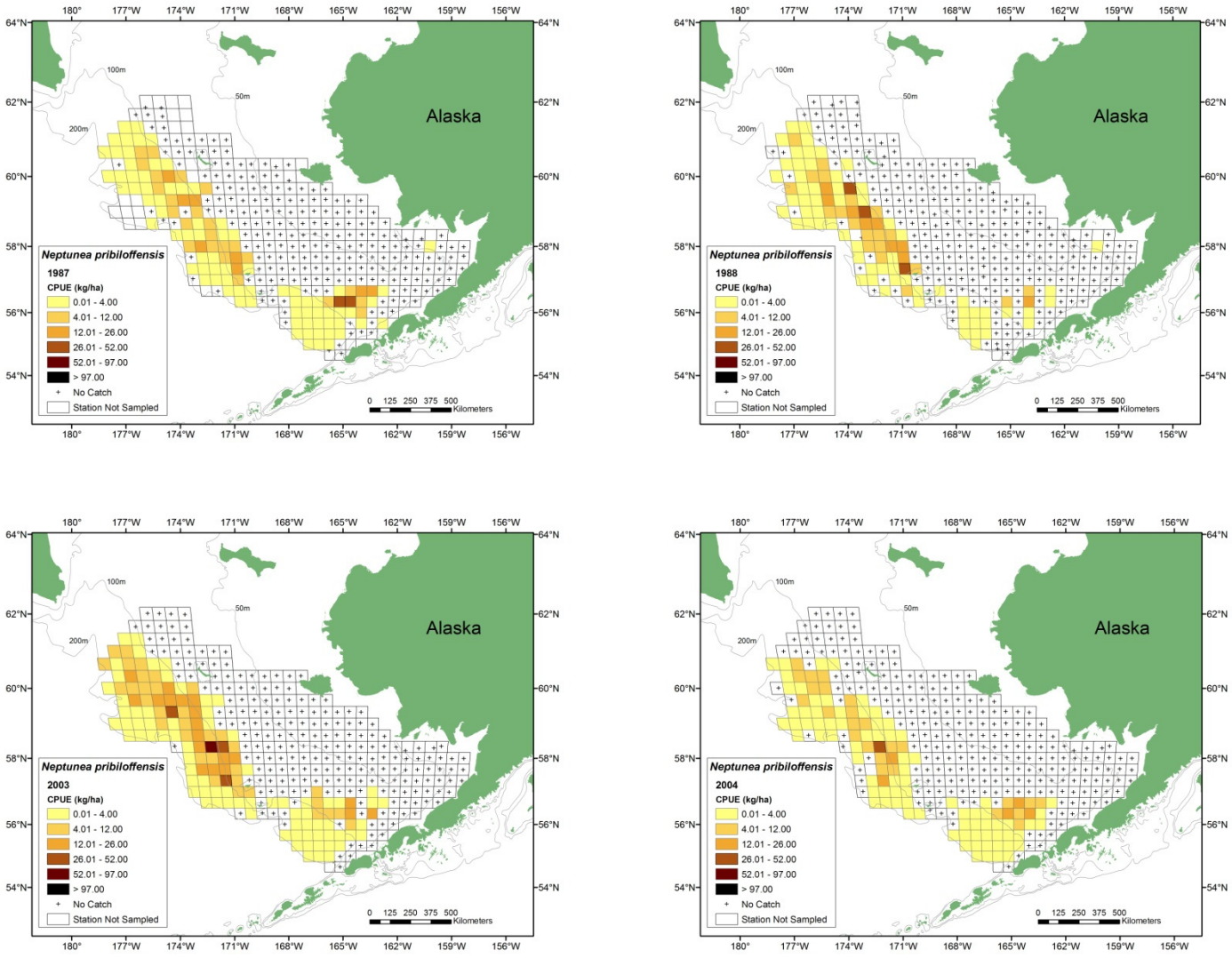


Figure 3. -- Abundance of *Neptunea pribiloffensis* in the Eastern Bering Sea (EBS) shelf region as catch per unit effort (CPUE, kg/ha) by standard RACE annual bottom trawl sample surveys of groundfish and invertebrates for the select years 1983 through 1988 and 2003 through 2010. The grid of 20 nmi × 20 nmi contiguous squares represents the standard EBS shelf area covered by the surveys, with each square colored to represent the average CPUE of the species within that square.



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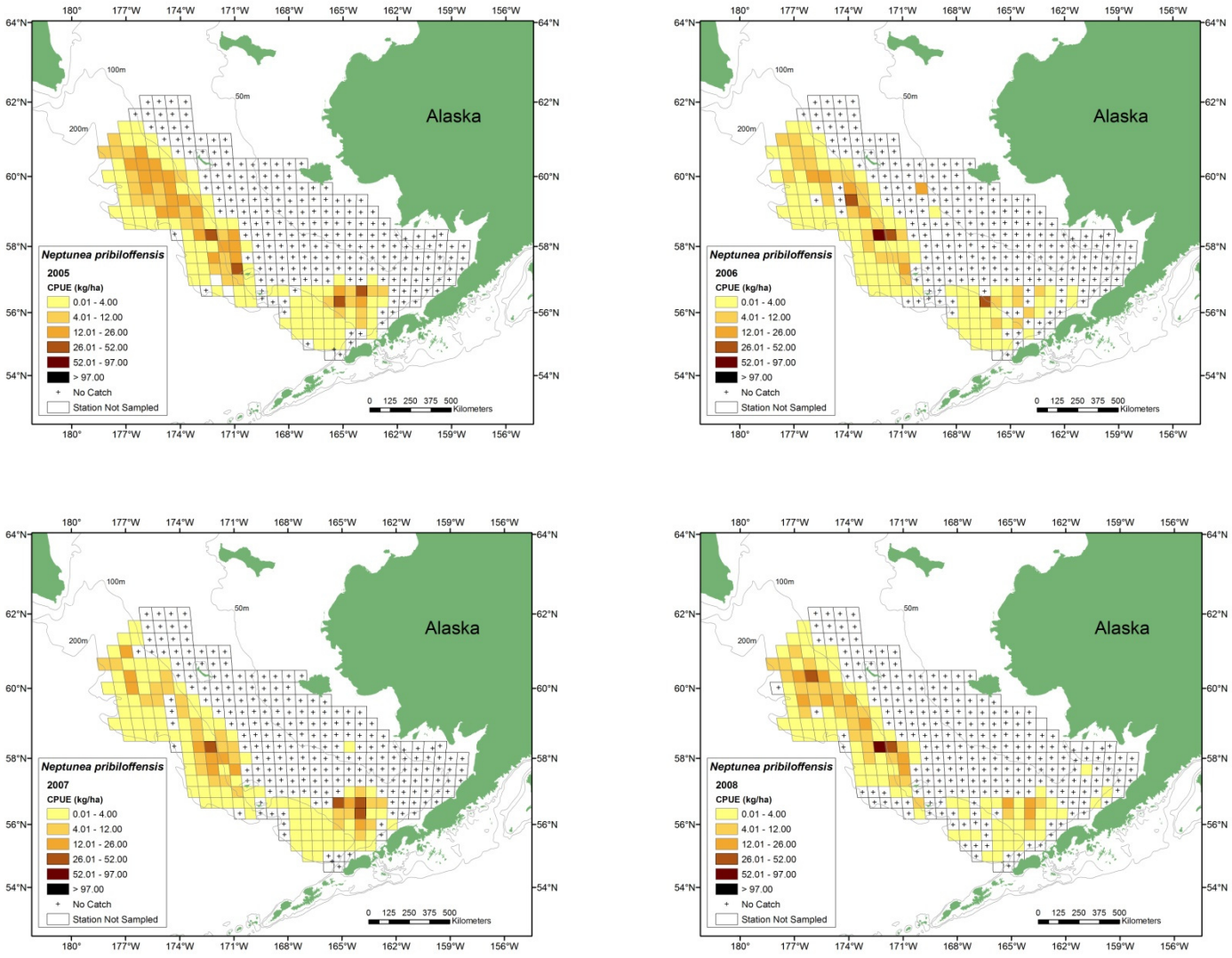

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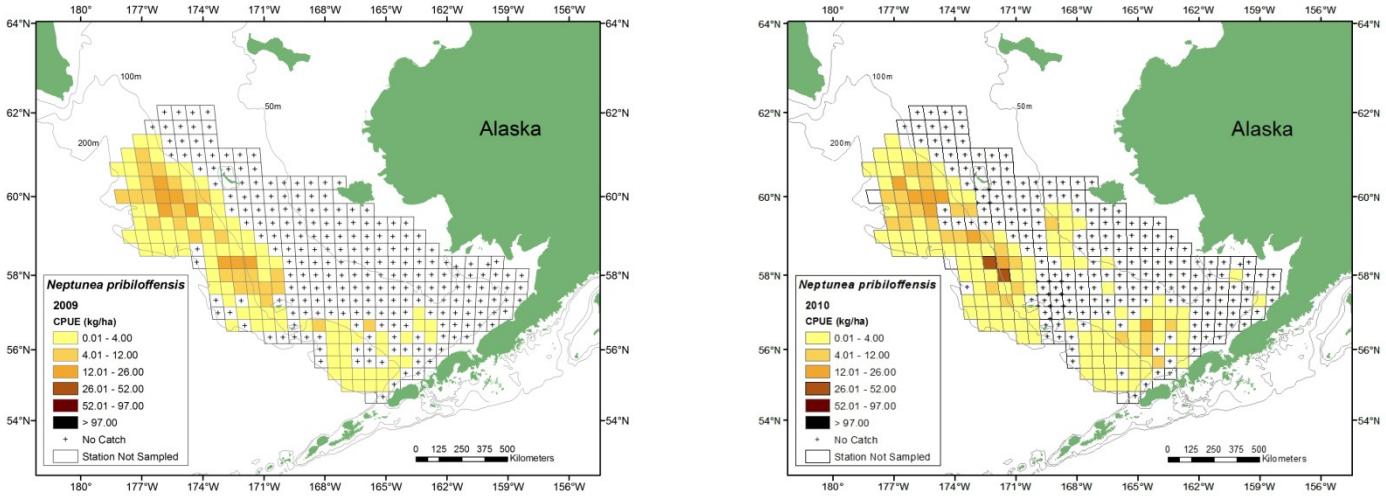

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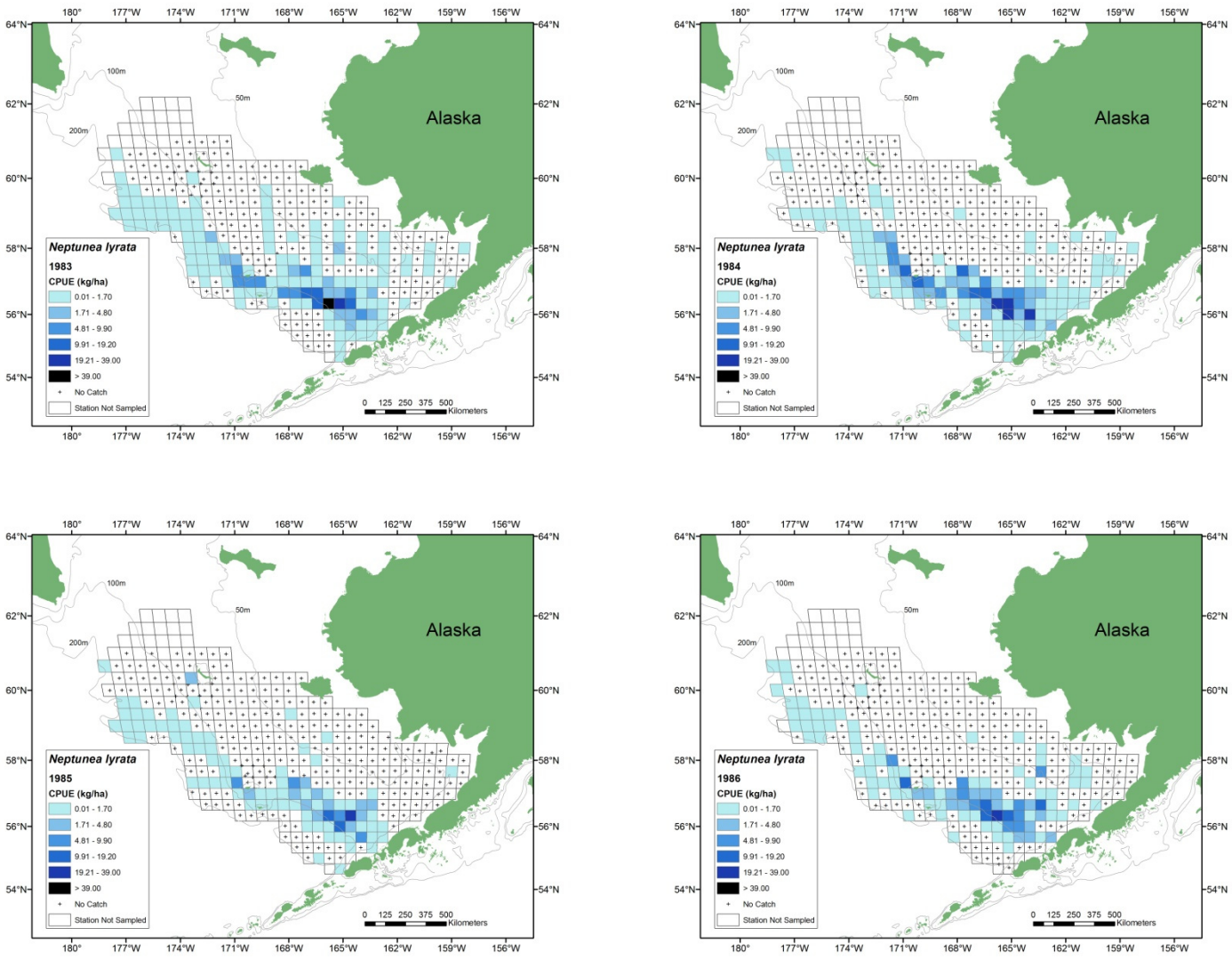
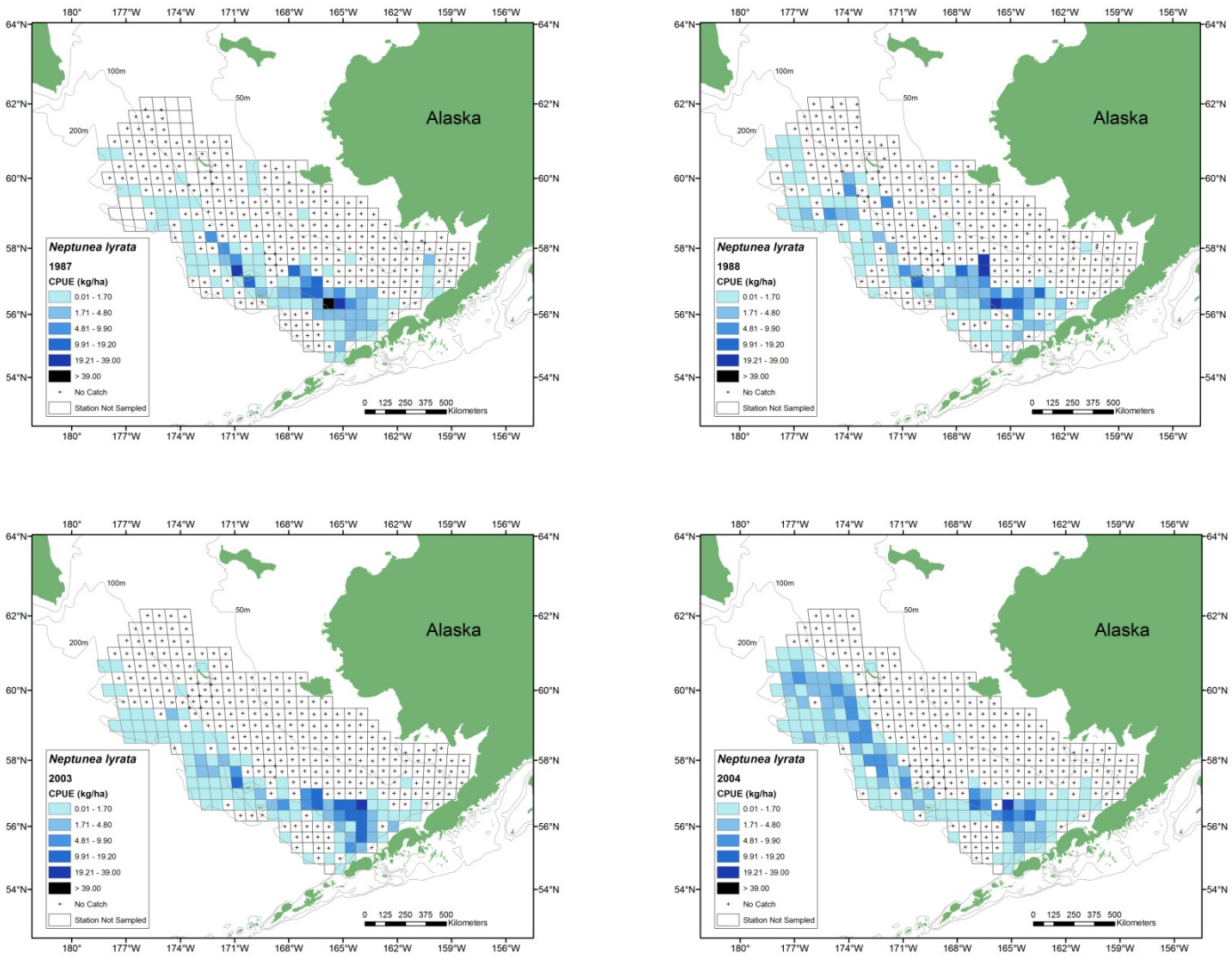


Figure 4. -- Abundance of *Neptunea lyrata* in the Eastern Bering Sea (EBS) shelf region as catch per unit effort (CPUE, kg/ha) by standard RACE annual bottom trawl sample surveys of groundfish and invertebrates for the select years 1983 through 1988 and 2003 through 2010. The grid of 20 nmi × 20 nmi contiguous squares represents the standard EBS shelf area covered by the surveys, with each square colored to represent the average CPUE of the species within that square.



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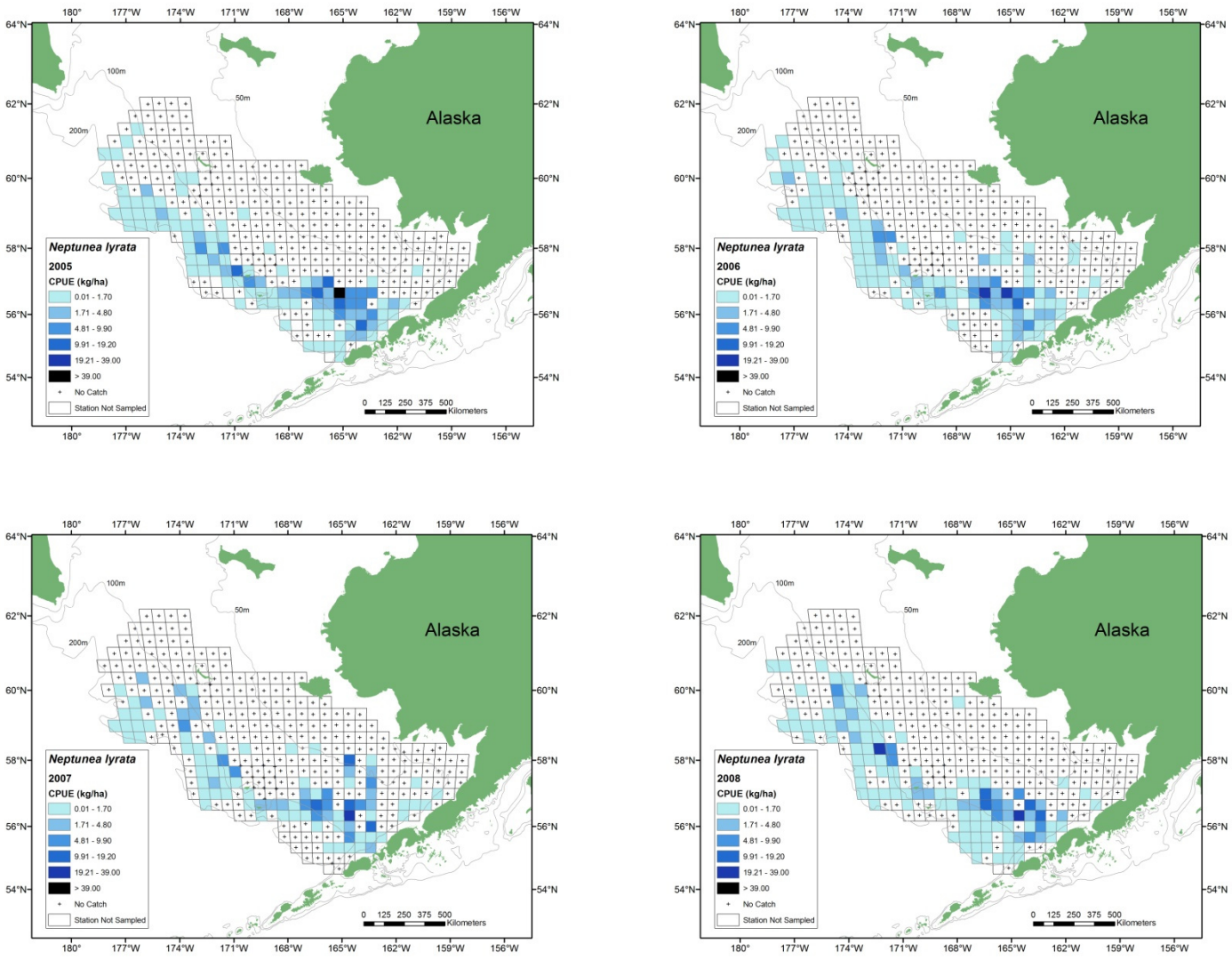

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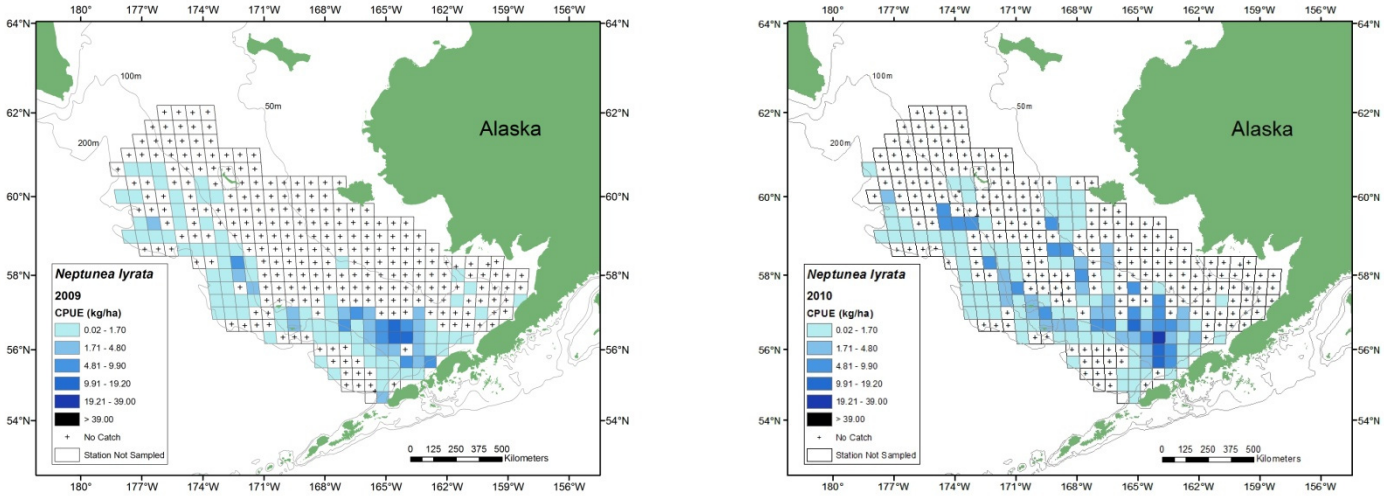

Figure 4. – Continued.

Regional Species Assemblages

Of the four species of *Neptunea* predominant in the EBS, *N. heros* and *N. ventricosa* both occur at depths generally exceeding 50 m, as part of the low-arctic-boreal species assemblage occupying the northern portion of the EBS shelf as well as northern and coastal waters of Bristol Bay (Shimek 1984). This is relatively cold water that nevertheless warms rapidly in summer. *Neptunea pribiloffensis* and *N. lyrata* are in the subarctic-boreal assemblage in the southern EBS, typically near the outer shelf edge in relatively deep water that is warmed by advection from the Pacific and fairly consistently at a temperature of 2-4°C (Shimek 1984). The latter two species also occur south of the Aleutian Islands and in shallow coastal areas south of the Alaska Peninsula. Their range extends south to at least the Washington coast.

In the EBS, the distributions of the four *Neptunea* species meet in a transition zone centered near the offshore western extremity of Bristol Bay (roughly 56° N, 165° W; Shimek 1984).

LIFE HISTORY AND ECOLOGY

Extent of Information

There have been relatively few biological studies of *Neptunea* species in the EBS, but a few specific aspects of the ecology and life history of *N. pribiloffensis*, *N. lyrata*, *N. heros*, and/or *N. ventricosa* in the region have been investigated (Kaimmer et al. 1976, MacIntosh and Paul 1977, Nagai 1974, Shimek 1981). In addition, many life history characteristics have been examined in species of *Neptunea* outside the region, including characteristics of some species also occurring in the EBS. Because life history characteristics are likely similar among the

various species of the genus as well as among regional populations within a species, available findings from all pertinent studies are included in this summary.

Growth and Development

Morphogenesis

Neptunea hatchlings emerge from the eggs at the juvenile stage, with the primary shell already developed (Fujinaga 2003), and unlike most prosobranchs which usually produce a free-swimming larva (veliger) they undergo no subsequent metamorphosis. MacIntosh (1976b) observed the following shell lengths for newly emerged hatchlings of the four major EBS species: *N. heros*, 6-8 mm; *N. ventricosa*, 8-11 mm; *N. pribiloffensis*, 7-11 mm; and *N. lyrata*, 8-12 mm. Power and Keegan (2001a) observed 50 newly-hatched juvenile *N. antiqua* from the Irish Sea to have an average shell length of 8.32 mm. Contrary to the limited dispersal expected of snails with direct development, the wide geographic distribution of the genus mirrors that of some genera of gastropods and bivalves having pelagic larvae (Nelson 1978).

Sexes

Neptunea are dioecious (individuals are either male or female throughout life). Nagai (1974) observed a sex ratio of 1:1 in *N. pribiloffensis* near the Pribilof Islands, and male-to-female ratios observed by Kaimmer et al. (1976) for the four major species of *Neptunea* in the EBS were *N. heros* (1.12), *N. ventricosa* (0.93), *N. pribiloffensis* (0.91), and *N. lyrata* (1.46). Sex ratios were approximately 1:1 in populations of non-EBS species *N. arthritica* in Japanese waters (Fujinaga 2003) and *N. antiqua* in the Irish Sea (Power and Keegan 2001a) and North Sea (Pearce and Thorson 1967).

Fujinaga (1987) found no secondary sexual dimorphism, such as overt differences in shell length (apex to end of anterior canal; *L*) versus shell width, in *N. arthritica* near Hokkaido, Japan. However, Power and Keegan (2001a) reported subtle but significant sex-related differences in *N. antiqua* in *L* versus such dimensions as aperture length and body whorl width.

Average Length

Average individual length (shell apex to end of anterior canal; *L*) for each of the four predominant *Neptunea* species was reported by MacIntosh (1976a) from the 1975 NMFS EBS bottom trawl survey as follows: *N. pribiloffensis* = 100 mm; *N. lyrata* = 115 mm; *N. heros* = 121 mm; *N. ventricosa* = 121 mm. As the 1 ¼-inch mesh of the codends retained few snails < 50 mm long, these averages generally apply to adults.

Maximum Length

Maximum *L* for each of the four predominant *Neptunea* species was reported from the 1975 EBS survey as follows: *N. pribiloffensis*, 150 mm; *N. lyrata*, 170 mm; *N. heros*, 170 mm; *N. ventricosa*, 150 mm (MacIntosh 1976a). These lengths fall within the range of reported maximums for non-EBS species as well. Borulya and Bregman (2002) observed specimens of *N. constricta* and *N. polycostata* from the Sea of Japan up to 220 mm and 184 mm long, respectively. *Neptunea antiqua* have been reported from waters near Great Britain exceeding 200 mm (Fretter and Graham 1962), and from the North Sea near Denmark up to 165 mm (Pearce and Thorson 1967). *Neptunea lyrata*, a species found in the western North Pacific as well as in the EBS, attained *L* = 161 mm in samples from the Sea of Japan (Borulya and Bregman 2002). *Neptunea arthritica*, a species possibly smaller than usual among *Neptunea*, was observed by Miranda et al. (2008) near Hokkaido, Japan, to attain *L* = 94.2 mm. At least one

other species of *Neptunea*, *N. borealis*, occurs in the EBS, but it is not common and reaches a maximum *L* of only about 60 mm (MacIntosh 1976a).

Weight Versus Length

Total weight (*W)* is a power function of *L* ($W = aL^b$) for individuals of the four major EBS *Neptunea* species. MacIntosh and Paul (1977) found the following best-fitting formulae for *W* (grams) relative to *L* (mm) of the respective species, based on least sum-of-squares: *N. pribiloffensis* ($W = 0.0381\ L^{3.41344}$); *N. lyrata* ($W = 0.0411\ L^{3.09406}$); *N. heros* ($W = 0.0347\ L^{3.63557}$) ; *N. ventricosa* ($W = 0.439\ L^{3.22321}$). Other investigators have fitted power functions for *W* versus *L* to data obtained for other species of *Neptunea* in other areas. In these studies values for parameter *b* ranged from 2.48 ($\pm$ 0.11; Borulya and Bregman 2002) to 2.8 (Miranda et al. 2008). Although *Neptunea* juveniles have shells with the same basic width-to-length ratio as do conspecific adults (Fujinaga 1987), Miranda et al. (2008) noted that the growth they observed of *N. arthritica* in *W* versus *L* was non-isometric ($b \neq 3$, $P < 0.001$). This may be the result of seasonal and/or permanent changes in anatomical proportions over the lifespan of individuals.

Growth Rate

Several studies have been made of individual growth rate within *Neptunea* species in various regions inhabited by the genus. All have shown growth to be self-limiting (i.e., approaching an asymptotic limit of average length-at-age, L_∞), but following different models or parameters within a model (Miranda et al. 2008, Fujinaga 2003, Borulya and Bregman 2002, Power and Keegan 2001a, Suzuki et al. 1996, Fujinaga 1987). Although no such investigations have been made in the EBS, together these studies provide a general picture of likely growth patterns of the four principal species in the EBS (Table 1).

In the life history of snails, various physical features appear to exhibit cyclical periodic change (e.g., straie deposition in opercula, change of Mg:Ca ratio in the chemistry of newly formed shell) and therefore to produce patterns that are potential age indicators (Richardson et al. 2005). However, little research has been done to verify and calibrate these methods for ageing *Neptunea* species. Nevertheless, investigations of populations of *Neptunea* species in various regions tentatively using these methods as well as one analyzing periodic changes in length frequency distributions (Fujinaga 1987) have shown some features of the growth rate over the individual lifespan (Table 1). The following is a brief summary of the methods used by these studies and some of the findings:

Fujinaga (2003, 1987) and Suzuki et al. (1996) used length frequency distributions observed during regular monthly sampling of *N. arthritica* populations near Hokkaido, Japan, to estimate age without relying on any morphological features. Using the method of Harding (1949) to examine each of these monthly distributions for the presence of multiple latent modal subsets, they estimated the composition of each sample by multiple year-class cohorts, "tracking" and identifying each cohort over a 4-year sampling period by comparison of the monthly frequency distributions. They then plotted average *L* against age (years), and used the criteria of least squares to find best-fitting growth formulae. Both found adult growth to slow with age after achieving a maximum rate, although Fujinaga's (1987) study indicated a Gompertz model while Suzuki et al. (1996) found a logistic model best.

Alternatively, Miranda et al. (2008) aged *N. arthritica* from the Hokkaido area by counting age-related opercula striae, estimating growth to follow a Gompertz model best. All three models developed for *N. arthritica* (Miranda et al. 2008, Suzuki et al. 1996, Fujinaga 1987) indicate a pattern of slower growth in the early juvenile stage, faster in late juvenile and early

adult stages, and slowing again in late adulthood while approaching an asymptotic limit. Borulya and Bregman (2002) used essentially the same ageing technique as Miranda et al. (2008), studying *N. constricta*, *N. polycostata* and *N. lyrata* in Ussuriisky Bay, Sea of Japan. Their observations in plotting *L* against operculum-derived age estimates and seeking the best-fit model indicated a von Bertalanffy growth pattern for those populations. Power and Keegan (2001a) endorsed a von Bertalanffy formula previously fitted to *L* versus operculum-striae-based ages of *N. antiqua*, using the formula to back-calculate age after measuring *L* in samples from the Irish Sea. In their separate studies referred to above, Fujinaga (2003, 1987) and Miranda et al. (2008) found no significant difference in growth rate between sexes of *N. arthritica* in waters near Hokkaido. However, in size distributions separated by sex, female *Neptunea* have tended to be larger than males in some populations in the EBS (Kaimmer et al. 1976, Nagai 1974), North Sea (Pearce and Thorson 1967), and Irish Sea (Power and Keegan 2001a). Aside from a possible difference in growth rates of sexes this could result from differing mortality rates at age.

Maximum Average Length-at-Age

For each of the growth studies of (non-EBS) populations of *Neptunea* mentioned above, the respective theoretical asymptotic upper limit of average *L* (L_∞) from the best-fit *L*-versus-age function is presented in Table 1. These values generally mirror the relative differences among greatest lengths reported above for the same species, for example showing the lowest values for *N. arthritica.*

Greatest Age Observed

In addition to the other morphological aging methods outlined above, Richardson et al. (2005), although not attempting an analysis of growth rate, used statoliths to age sampled *N. antiqua* of up to 148 mm *L* from the North Sea. The small (< 0.2 mm dia.) structures in the

gastropod anatomy, integral to an individual's orientation to gravity, present rings in which annually created patterns can be microscopically observed.

Although Golikov (1978) postulated a general age limit for *Neptunea* of 8 years, most of the above-mentioned ageing studies have indicated greater maximums. Maximum ages observed in these investigations are presented in Table 1 along with estimates of L_∞.

Table 1. -- Estimated asymptotic upper limit of average L-at-age (L_∞), greatest observed age, best-fit model type describing growth rate, and ageing method for some studied regional populations of *Neptunea* species. Information not obtained by the studies is designated by "NA".

Species	Area	L_∞ (mm)	Oldest	Model	Ageing method
N. arthritica	Usu Bay, Hokkaido	107.5	NA	Gompertz	*L* freq. dist. (Fujinaga 1987)
	Shiriuchi, Hokkaido	90.5	NA	Logistic	*L* freq. dist. (Suzuki et al. 1996)
	Saroma Lagoon, Hokkaido	96.5 (males) 91.6 (females)	13 yrs 10 yrs	Gompertz	Opercula striae (Miranda et al. 2008)
N. lyrata	Ussuriisky Bay, Sea of Japan	140.5	18 yrs	Von Bertalanffy	Opercula striae (Borulya and Bregman 2002)
N. polycostata		204.6	17 yrs		
N. constricta		213.1	16 yrs		
N. antiqua	Irish Sea	140	NA	Von Bertalanffy	Opercula striae (Power and Keegan 2001a)
N. antiqua	North Sea	NA	17 yrs	NA	Statolith striae (Richardson et al. 2005)

Maturation of Sexes

Length at Maturity

MacIntosh and Paul (1977) have examined data indicating L at onset of maturity (L_{mat}) for each sex of the four major *Neptunea* species in the EBS. Parameter estimates were based on the graphical nature of each of the eight best-fit regressions of sampled gonad weight as a power function of L for females, penis weight as a power function of L for males. Their study shows a general trend of greater L_{mat} for female *Neptunea* than for conspecific males, by roughly 10-15 mm (Table 2).

Other investigators have used different methods to determine L_{mat} for other populations of *Neptunea* species. Their results are consistent with those of MacIntosh and Paul (1977) in the EBS, after taking into consideration differences in asymptotic average length-at-age (L_{∞}) and maximum length observed among the species and populations involved (Table 2). Fujinaga (1987, 1985) determined L_{mat} for *N. arthritica* from Usu Bay, Hokkaido, Japan, based on histological observations of seminal vesicles and female gonads from measured individuals. For other Hokkaido waters, Fujinaga et al. (2006) and Fujinaga and Oyama (2007) variously estimated L_{mat} of *N. arthritica* and *N. polycostata* with a method similar to that of MacIntosh and Paul (1977), albeit without use of a regression formula. This consisted of inspecting scattergrams of penis index (PI)[4] and seminal vesicle index (SVI)[5] versus L for males, gonadosomatic index (GSI)[6] and pallial oviduct index (POI)[7] versus L for females. An abrupt general rate of increase in these indexes with increase in L, as observed in the scattergrams, indicated respective L_{mat}

[4] PI = ([penis weight]/[soft body weight]) × 100
[5] SVI = ([seminal vesicle weight]/[soft body weight]) × 100
[6] GSI = ([gonad weight]/[soft body weight]) × 100
[7] POI = ([pallial oviduct weight]/[soft body weight]) × 100

values. In a similar way, Power and Keegan (2001a) estimated L_{mat} for *N. antiqua* from the Irish Sea by plotting gonad weight and penis length separately against *L* for males and gonad weight against *L* for females. Lastly, Pearce and Thorson (1967), observing mating behavior of *N. antiqua* males and females from the Danish North Sea in an aquarium, estimated L_{mat} for each sex. The methods and results of these investigations are summarized in Table 2.

Table 2. -- Length (*L*) at maturity of males and females (with method of determination) observed in some regional populations of *Neptunea* species.

Species	Area	*L* at maturity (mm)		Method of determination
		Males	Females	
N. pribiloffensis	EBS	90	105	Regression plots: weight of reproductive organ vs. *L* (MacIntosh and Paul 1977)
N. lyrata		100	110	
N. heros		95	110	
N. ventricosa		87	102	
N. arthritica	Usu Bay, Hokkaido	~50	~60	Histology: seminal vesicles, female gonads (Fujinaga 1985)
	Saroma Lagoon, Hokkaido	60	75	Histology: reproductive organs (Miranda et al. 2008)
	Sarufutsu, Hokkaido	70	80-90	Scattergrams: PI[4] & SVI[5] vs. *L* for males, GSI[6] & POI[7] vs. *L* for females (Fujinaga et al. 2006)
	Notoro Lake, Hokkaido	50	70-80	
	Notsuke, Hokkaido	60	75	
	Erimo, Hokkaido	55-60	70	
	Mashike, Hokkaido	70	75	

N. polycostata	Erimo, Hokkaido	120-130	150-160	Scattergrams: PI & SVI vs. *L* for males, GSI & POI vs. *L* for females (Fujinaga and Oyama 2007)
N. antiqua	Irish Sea	75-90	95-110	Scattergrams: gonad wt. vs. *L* for both sexes, penis length vs. *L* for males (Power and Keegan 2001a)
	North Sea (Denmark)	50-60	79	Aquarium observation (Pearce and Thorson 1967)

Age at Maturity

Little work has been done to determine the age at which individuals become mature among *Neptunea*. Some estimates have been included as part of the above-mentioned studies investigating L_{mat} for non-EBS *Neptunea* species. Fujinaga (1987) estimated onset of maturity to occur at 2+ years (~ 29 months) for males, 3+ years (~ 42 months) for females of *N. arthritica* from Usu Bay, Hokkaido. Level of maturity estimated from the histology of gonads of individuals of different lengths (*L*) was combined with *L*-at-age inferences from multi-year trends in a monthly series of length frequency distributions displaying different year classes. However, Miranda et al. (2008) estimated maturation to occur at 4.6 years for males and 6.1 years for females of *N. arthritica* from Saroma Lagoon, Hokkaido. These values were estimated by finding L_{mat} (from the histology of gonads) for each sex, then projecting those lengths onto von Bertalanffy regressions of *L* on age (as indicated by the number of operculum striae). Power and Keegan (2001a) used the same method of back-calculating age-at-maturity for *N. antiqua* from the Irish Sea, estimating ages at 4-5 years for males and 6-9 years for females.

Wherever the studies included age estimations the data have indicated a greater age at onset of maturity for females than for males (Miranda et al. 2008, Power and Keegan 2001a, Fujinaga 1987). Thus the obvious similarity among the findings in the ubiquitously greater length at which this occurs for females, compared with males of the same species (Table 2; Miranda et al. 2008, Fujinaga and Oyama 2007, Fujinaga et al. 2006, Power and Keegan 2001a, Fujinaga 1985, MacIntosh and Paul 1977, Pearce and Thorson 1967) may be a result of this difference in age at maturity rather than a difference in growth rates.

Annual Cycles of Reproduction

Insemination of females is internal, via the male penis. Females store sperm in a seminal receptacle connected to the oviduct, for later fertilization of eggs released by the ovary (Ruppert et al. 2004). Spawning cycle schedules, fecundity, and other aspects of reproductive behavior of EBS *Neptunea* are poorly known, but pertinent observations of the same and congeneric species in other regions are available as indicators of general characteristics expected to occur among the EBS populations (below and Table 3):

Mate Selection

Neptunea antiqua (Pearce and Thorson 1967) from the Danish North Sea and *N. arthritica* (Miranda et al. 2008) from Hokkaido waters observed during mating were polygamous; that is, females sometimes copulated with multiple males.

Copulation and Spawning Seasons

Copulation timing among species of *Neptunea* in Alaskan waters has not been observed directly, but Shimek (1981) stated that intertidal female *N. pribiloffensis* and *N. lyrata* near Homer, Alaska, spawn from late April through early June. Based on the ~ 1-3 month copulation-

to-spawning interval observed for other *Neptunea* (Fujinaga and Oyama 2007, Fujinaga 2003, Power and Keegan 2001a), copulation could occur in these nearshore populations of the northwest Gulf of Alaska between late January and early May.

Copulation among *N. arthritica* near Hokkaido starts in April, peaking/ending in June (Fujinaga 2003). It starts in April as well for *N. antiqua* from the Irish Sea (Power and Keegan 2001a), with subsequent spawning from May to early summer in both populations. Spawning in *N. arthritica* from the Korean west coast is reported to be from May to August (Chung et al. 2006). Copulation appears to be somewhat earlier (late winter to early spring) for *N. antiqua* from the North Sea (Pearce and Thorson 1967), as in this case spawning itself occurs during February through April. For *N. polycostata* near Hokkaido, Fujinaga and Oyama (2007) report copulation from February to May, with spawning from March through August. Latitude varies considerably among the areas occupied by these regional populations, but the copulation and spawning dates mentioned above and in Table 3 do not present any obvious pattern relating to latitude as an influence on timing. However, egg incubation schedules do show a possible relationship with latitude.

Incubation

Shimek (1981) reported the time required for spawning by individual female *N. pribiloffensis* near Homer, Alaska, to be 2-3 days per cluster, and a spawning-to-hatching period of ~1 year. The average duration of spawning by each female *N. antiqua* from the North Sea was 21 days, and the incubation period was ~ 6 months (Pearce and Thorson 1967). This incubation period is similar to the 6-7 months observed for *N. antiqua* from the Irish Sea by Power and Keegan (2001a). Fujinaga (2003) estimated the process to take 3-4 months for *N. arthritica* from near Hokkaido. Thus the incubation period appears longest for the most northerly population,

Table 3. -- Spawning schedules and characteristics observed in studies of *Neptunea* species. Information not obtained by the studies is designated by "NA".

Species	Area	Spawning season	Incubation period	Egg capsules per cluster	Embryos per capsule	Source
N. pribiloffensis	EBS	NA	NA	103	3.2	MacIntosh and Somerton (1981)
N. heros		NA	NA	34	3.4	MacIntosh and Somerton (1981)
N. ventricosa		NA	NA	81	2.9	MacIntosh and Somerton (1981)
N. pribiloffensis	Homer AK	Late April – early June	~ 1 year	46	2.46	Shimek (1981)
N. lyrata		Late April – early June	NA	NA	NA	Shimek (1981)
N. antiqua	Denmark	February - April	~ 6 months	~21	NA	Pearce and Thorson (1967)
N. antiqua	Irish Sea	May – early summer	6-7 months	40.37	1.58	Power and Keegan (2001a)
N. arthritica	Hokkaido	May - June	3-4 months	41.9	1.01	Fujinaga (2003)
N. polycostata	Hokkaido	March - August	NA	NA	NA	Fujinaga and Oyama (2007)
N. arthritica	Korea, east coast	May – August	NA	NA	NA	Chung et al. (2006)
N. lamellosa	NA	NA	NA	NA	2.6	Ovsyannikov (2007)

and to decrease as the latitude occupied by the population decreases. Further observations would be necessary to determine whether or not such an influence actually exists.

Spawning Physiology

Females possess a series of organs for applying nutritive and protective materials (e.g., albumin, protein) to the outsides of the fertilized ova passing through the oviduct, encasing the eggs in capsules prior to spawning (Ruppert et al. 2004). This system includes albumin and capsule forming glands, as well as a pedal gland where the capsules are shaped after exiting the gonopore. Females lay capsules in clusters, the size and shape of which are distinctive for a species and which have been described for *N. lyrata*, *N. pribiloffensis*, *N. heros*, and *N. ventricosa* by Golikov (1961) and Shimek (1981).

Brood Size

Egg capsules each contain 1-4 (usually ~3) developing embryos and 1,000-5,000 immature oocytes as nurse eggs, which do not develop into embryos but rather provide food for the latter. Females laid clusters averaging 103 capsules with 3.2 embryos each for *N. pribiloffensis*, 34 capsules with 3.4 embryos each for *N. heros*, and 81 capsules with 2.9 embryos each for *N. ventricosa* as observed in small samples of each of the three species from the EBS (MacIntosh and Somerton 1981). Power and Keegan (2001a) observed female *Neptunea antiqua* from the Irish Sea to lay egg clusters averaging 40.37 egg capsules per cluster. These capsules contained an average of 1.58 developing juveniles for an average of 63.78 juveniles per cluster. Estimations of actual fecundity, however, are hampered by lack of information on the number of clusters laid per season per female (MacIntosh and Somerton 1981). Pearce and Thorson (1967) observed 11 female *N. antiqua* from the North Sea to lay, on average, 1.6 clusters each,

containing an average of 37 total capsules per female. Several capsules taken from multiple clusters each contained one or two embryos.

Spawning Habitat

Egg-capsule clusters are deposited on relatively solid substrate, as opposed to unconsolidated material. Such surfaces include dead and living snail shells (conspecific or otherwise), upper and upper-lateral surfaces of high-relief bottom structure greater than 50 cm height, and upper surfaces of boulders at less than 50 cm height (Fujinaga 2003). This anchoring probably mitigates egg mortality caused by displacement by waves or currents. Clusters are often located so as to minimize predation, such as on vertical or underside surfaces, in cracks, or in some cases near commensal organisms, such as the anemone *Tealia crassicornis*, which have been shown to provide protection by preying on would-be egg predators such as *Strongylocentrotus droebachiensis* (Shimek 1981).

Feeding Methods and Diet

In general, species of *Neptunea* are carnivorous, as are other buccinids and most other gastropods in the order Neogastropoda. Buccinidae feed via an eversible proboscis that extends the mouth. The mouth carries a relatively unspecialized radula having three teeth per row, which can be protruded from the mouth (Ruppert et al. 2004). Species of *Neptunea* are able to evert the proboscis ~ two times the length of the shell, into tubes as narrow as 4.5 mm in diameter, to access bait (Pearce and Thorson 1967, Avery 1961). The radula is used to cut or rasp food, and to pull it into the mouth.

The *Neptunea* are primarily predators. Although individuals have been observed naturally or in experiments to be feeding on or attracted to carrion, the few systematic studies to date of

feeding behavior among the species mostly suggest that they scavenge only opportunistically, and that their metabolic needs are modest. Direct observations of *Neptunea* in the field indicate most feeding is on live prey (Fujinaga 2003, Shimek 1984).

Surveys of stomach and gut contents of populations of the four major species from the EBS, as well as *N. pribiloffensis* and *N. lyrata* from near Homer, Alaska, and *N. antiqua* from the Clyde Sea, have indicated feeding to be infrequent, with most guts containing no food remains (Shimek 1984, Taylor 1978). The responses and feeding by individuals of non-EBS populations of *N. lyrata*, *N. tabulata*, *N. antiqua*, and *N. amianta,* experimentally exposed to live bait, carrion, or the scents thereof, have been relatively sluggish and limited when compared with behaviors of other co-occurring invertebrate scavengers and predators (Bergmann et al. 2002, Power et al. 2002, Tamburri and Barry 1999, Pearce and Thorson 1967, Avery 1961). Specimens of the bathyal *N. amianta* from Monterey Canyon, CA, survived 12 months without food until observation ceased in a deprivation experiment (Tamburri and Barry 1999).

Neptunea produce relatively high concentrations of the neurotoxin tetramine (tetramethyl-ammonium chloride) in the salivary gland, a possible adaptation for subduing live prey. *Neptunea antiqua* specimens have been observed in feeding experiments probing the hinge-side juncture of the closed valves of a live mussel with the proboscis, ultimately feeding on the opened bivalve. Possibly, the snails use salivary toxin to paralyze bivalves and access the inside of the shell, or use it to arrest flight response in other prey (Kawashima et al. 2002, Power et al. 2002, Shiomi et al. 1994).

Prey

Shimek (1984) observed the diet of populations of *N. pribiloffensis*, *N. lyrata*, *N. heros*, and *N. ventricosa* in the EBS, as well as a mixed aggregation of the first two species occurring

intertidally near Homer, Alaska. Identifiable food items consisted of: 1) primarily live polychaetes; 2) somewhat less frequently bivalves and barnacles (*Cirripedia*); and 3) trace occurrences of gastropods, decapods, fish (probably carrion), and ophiuroids. Comparison of the distributions of *N. pribiloffensis* and *N. lyrata* with those of prey species in intertidal water near Homer showed little or no effect on the total prey population, suggesting the two *Neptunea* species are not food-limited at this location (Shimek 1984). *Neptunea arthritica* observed in Usu Bay, Hokkaido, ate mostly live *Mytilus* spp., followed less frequently by carrion and other live bivalves (Fujinaga 2003). Feeding on infauna such as tubiculous polychaetes may be less apparent to divers, as snails may be able to use proboscides to locate and ingest prey hidden in the substrate. Among gut contents of *N. antiqua* from the Clyde Sea, identifiable food items were usually indeterminate bivalve remnants or the bivalve *Abra alba*, followed less frequently by *Priapulus caudatus*, Polychaeta, and Decapoda (Taylor 1978).

Diet Strategies

Classifying prey items generally by class, Shimek (1984) compared diet compositions among allopatric and sympatric EBS populations of the four major *Neptunea* species in a southern and a northern assemblage region, respectively, and in a transitional zone between the regions near the mouth of Bristol Bay. He found considerable diet-composition overlap within each of the two intra-assemblage species pairs (*N. heros*/*N. ventricosa* and *N. pribiloffensis*/*N. lyrata*) within each of the assemblage regions, and also overlap between the two species pairs when allopatric (i.e., in separate assemblage regions). However, he found less diet overlap between the same two pairs in the inter-assemblage transition zone, or when comparing each pair in the transition-zone with either pair in its customary assemblage area. Thus he observed possible niche partitioning between sympatric species, which might result from selective

pressures on respective non-interbreeding populations. Such partitioning according to species does not by itself seem consistent with Shimek's observations of diet overlap within sympatric-species pairs in the respective assemblage areas, unless the partitioning is only triggered by a larger number of species present within the relatively small transition zone compared with either assemblage area. Alternatively, there could be more hybridization occurring within each of the species pairs than between pairs.

Mortality

Mortality rates among *Neptunea* populations are likely to vary with the season, with life stage, and with biotic and abiotic elements of the local environment. Pre-recruit mortality can occur through displacement of egg clusters by turbulence, encumbrance by epifauna (e.g., sponges), or by consumption of egg clusters or individual embryos by such predators as echinoids, asteroids, or other gastropods (Fujinaga 2003, Shimek 1984).

Rates

In some populations of *N. antiqua* and *N. arthritica*, mortality rate decreases after age 1 and before maturity but increases for mature adults during and immediately after the spawning season. Feeding activity decreases during the copulation-through-spawning period, when both sexes, particularly females, have recently expended considerable energy in reproduction. In fact, one or both sexes may often die after spawning (Fujinaga 2003, Pearce and Thorson 1967).

In addition to providing the species with solid substrate on which to attach egg capsules, the post-mortem durability and persistence of snail shells in the environment may be of use as an indicator of relative population viability. Sampling *Neptunea antiqua* with a beam trawl, Ten Hallers-Tjabbes et al. (2003) calculated the percentage that live shells constituted of all shells

taken (alive or empty) at each of 11 stations in the North Sea. The results, averaging 56 ± 8% and ranging from 4% in the Skagerrak to 93% in the open sea, were used as one parameter relating to population health.

Predators

Little is known of the extent and influence of predation-induced mortality in the life cycle of large prosobranchs such as *Neptunea* in the EBS. Consequently, there are gaps in the knowledge of their exact role in the benthic food webs. Taxonomic identification of gastropods, more specifically than at the level of class, among stomach contents from potential predators is difficult in the absence of shell remains. Even opercula are often morphologically indistinct among related taxa, with some exceptions (e.g., the distinctive oblong operculum with centered nucleus exhibited by *Buccinum* species uniquely among Buccinidae). However, observations have shown several types of predators are capable of feeding upon large gastropods like Neptunea, such predators including Asteroidea, larger species of Decapoda, and *Octopus* (Ruppert et al. 2004, Shimek and Gardner 1979, MacIntosh 1976b). *Neptunea* remains have been identified in stomach contents of a few fish, invertebrate, and marine mammal species occurring in the EBS, from samples taken in the region or in other Alaskan waters. These include *Gadus macrocephalus* (Pacific cod; Jewett 1978), *Paralithodes camtschaticus* (red king crab; Feder and Paul 1979, Feder et al. 1978, Feder et al. 1977), *Pycnopodia helianthoides* (sunflower starfish; Feder et al. 1980), *Hippoglossus stenolepis* (Pacific halibut; Rosenthal 1979), *Hemilepidotus jordani* (yellow Irish lord; Feder et al. 1979), *Cancer magister* (Dungeness crab; Feder and Paul 1979), *Odobenus rosmarus* (Pacific walrus; Fay and Burns 1988, Lowry and Frost 1981), and *Erignathus barbatus* (bearded seal; Dehn et al. 2007). None of the data in these investigations

indicated large gastropods such as *Neptunea* were a major component of the predator's diet. Rather, they seemed to be taken opportunistically.

ANTHROPOGENIIC INTERACTIONS

Incidental Results of Commercial Fishing

Snail Bycatch

Commercial bottom-trawling for demersal fish species in the EBS captures numerous snails among the bycatch. From 23 June 1986 to 30 July 2011 domestic fishing vessels in the EBS caught an estimated 2,601,898 kg of unidentified snails in 61,190 hauls [8], according to fishery observers reporting the catch for NOAA's Alaska Fisheries Science Center, division of Fisheries Monitoring and Analysis (FMA). Although fishery observers generally do not identify snail taxa more specifically than "snail unidentified", the preponderance of *Neptunea* among snails in RACE bottom trawl surveys in the same area indicates that a considerable portion of this catch was likely *Neptunea.*

Even with subsequent discard at sea, mortality or lessened viability as a direct result of capture and discard has potential significance. Although these effects are not easily quantified, at least one study has directly evaluated some of them in a non-EBS fishery. Bergmann et al. (2001) studied severity and frequency of injury to individuals of invertebrate species among the bycatch in commercial otter trawls targeting Norway lobster (*Nephrops norvegicus*) in the Scottish Clyde Sea. Although faring better than some species, approximately 40% of *Neptunea antiqua* thus taken sustained at least mild shell damage. It should be noted that hypoxia,

[8] Narita, R. 2011. Personal communication, data from the NORPAC database of the Fisheries Monitoring and Analysis Division (FMA), Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration.

temperature change, or pressure change may also contribute to or compound mortality associated with capture/discard.

Changes to the Benthos

In addition to collateral mortality, fishing could have several other less direct (negative or positive) affects on *Neptunea*, altering demographics, selecting for physical traits among survivors, or physically altering substrates and the availability of infauna prey. For example, invertebrate catch of experimental bottom-trawl samples from a heavily fished (HF) area of the EBS was compared with that of samples from an adjacent area where bottom trawling had never occurred (unfished, UF; McConnaughey et al. 2005, McConnaughey et al. 2000). The study found individuals of the genus *Neptunea* as a whole to be significantly more abundant as measured by CPUE, as well as significantly larger by average individual weight, in the UF area.

Food windfalls from fishing discards may also be important. Substantial amounts of carrion or moribund organisms discarded as fishing bycatch in the EBS may constitute a significant supplement to the nutrition of *Neptunea* species through opportunistic scavenging. The extent to which this incidental nutrition mitigates negative effects of the industry on *Neptunea* populations due to injury, mortality, or environmental damage by the gear is unknown. Although *N. antiqua*, *N. lyrata*, and *N. tabulata* in laboratory experiments have shown more limited response to olfactory signals than other prosobranch species in finding live bait or carrion (Pearce and Thorson 1967, Avery 1961), Bergmann et al. (2002) found *N. antiqua* among scavengers in traps baited and placed to approximate typical discarded bycatch from the *Nephrops norvegicus* trawl fishery in the Scottish Clyde Sea. The species showed a clear preference for crustacean bait (*Munida rugosa*, *Liocarcinus depurator*) over echinoderm bait (*Asterias rubens* and *Ophiura ophiura*). In a separate study of the *Nephrops norvegicus* trawl

fishery in the English North Sea, Catchpole et al. (2006) estimated that *Neptunea antiqua*, among other identified scavenger species, could receive as much as 21% of their annual energy requirement from fishery discards.

Pollution-induced Imposex

Exposure to organotins, especially tributyltin (TBT), has been shown to cause abnormal development in female *Neptunea*. The affected individuals develop homologues of the male penis and/or vas deferens (imposex), in addition to the regular female characteristics. This compound has been used in paint on vessel hulls to minimize fouling by periphyton or epifauna. In certain gastropod species the deformation results in female sterility and/or the higher TBT concentrations are associated with lower female/male ratios. In one study in the offshore Irish Sea, Power and Keegan (2001b) found incidences of TBT-induced imposex in monthly samples of female *N. antiqua* to be 90-100% of individuals but detected no related sterility or higher female mortality. Conversely, Bright and Ellis (1990) found female *N. phoenicia* from Howe Sound, British Columbia, exhibiting signs of TBT-induced imposex, seemingly rendered sterile by the development of an aberrant vas deferens, which in this species tended to occlude the gonopore and would thus preclude egress of egg capsules at spawning. In general, organotin concentrations in snail soft tissue and also in bottom sediments decrease with increasing distance and isolation from marine shipping traffic. Large-scale restrictions on marine use of TBT in paint, instituted internationally since 1989 (Champ 2000), have effectively reduced both TBT concentrations and related incidence of imposex. Nevertheless, some fairly recent monitoring has still detected the disease (e.g., Fujinaga et al. 2006). No information is available concerning past or present TBT concentrations, nor any related imposex, in the benthos of the EBS.

Human Consumption

Among gastropods popular in the human diet, several *Neptunea* species have been harvested commercially or by subsistence fishing in various parts of the range of the genus. In the EBS this has included commercial harvesting, principally of *N. pribiloffensis* (Bowers et al. 2008, MacIntosh 1980, Nagai and Suda 1976, Nagai 1974). No commercial targeting is known to have occurred in Alaskan waters since 1997, the last year in which any such catch was reported (Bowers et al. 2008). *Neptunea* species previously or presently harvested in areas outside of Alaska include: 1) *N. arthritica*, *N. polycostata*, *N. constricta*, and *N. lyrata* in the western North Pacific (Borulya and Bregman 2002, Suzuki et al. 2002, Kato 1979, Fujiwara and Ashino 1972); and 2) *N. antiqua* in the North Sea (Anthoni et al. 1989).

Potential Effects on Demographics of *Neptunea*

Using multiple tagging, Suzuki et al. (2002) in 1994 estimated a total annual mortality of 86% for a population of *N. arthritica* near Hokkaido exposed to commercial pot fishing. Their calculations attributed 53% of that mortality to the fishery, which retained individuals ≥ 60 mm long. As Fujinaga (1985) had previously estimated L_{mat} of female *N. arthritica* at 60 mm, Suzuki et al. (2002) postulated that such a low minimum-size-retained would cause the population to decline.

Food Poisoning

Incidents of human poisoning by ingestion of tetramine have been reported for certain *Neptunea* species that were otherwise thought to be edible (including some fished commercially). Among species involved are *N. arthritica* and *N. intersculpta* from the western North Pacific (Saitoh et al. 1983) and *N. antiqua* from the eastern North Atlantic (Reid et al.

1988, Ayres and Wood 1973, Fleming 1971). Unlike the report of Saitoh et al. (1983) concerning *N. arthritica*, Anthoni et al. (1989) found tetramine in tissue of *N. antiqua* was not confined to the salivary gland. Based on their findings of the characteristics and *in vivo* concentration of the compound, they classified *N. antiqua* as unfit for human consumption. As such, use of any *Neptunea* species as human food must be subject to controlled testing and other practices intended to minimize the risk

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