

Ecology of Cephalopod Early Life History in the Gulf of Alaska and Bering Sea

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Abstract

Ecology of Cephalopod Early Life History in the Gulf of Alaska and Bering Sea

Populations of cephalopods are known to exhibit boom-bust cycles however adult populations are difficult to study due to sampling limitations. This research was designed to investigate the causes for the interannual variation exhibited by these organisms. A spatially and temporally extensive collection of cephalopod paralarvae from the Gulf of Alaska and Bering Sea was analyzed and a rearing experiment was performed. The five most abundant species were: *Berryteuthis anonychus*, *Enteroctopus dofleini*, *Gonatus onyx*, *Berryteuthis magister*, and *Gonatopsis borealis*. *Berryteuthis anonychus*, *E. dofleini*, *B. magister*, and *G. borealis* appear to be hatching throughout the months of sampling (April – September), while *G. onyx* appears to be hatching in springtime. *Gonatus onyx* and *B. magister* have long planktonic duration (approximatley two months), during which time they develop characters of the juvenile stage. *Berryteuthis anonychus*, *E. dofleini*, and *G. borealis* planktonic durations appear to be much shorter which may be due to ontogenetic shift in depth or geography. MOCNESS sampling reveals that all species are common in the upper 100 m with highest abundances of all but *G. borealis* in the upper 20 m; highest abundances of *G. borealis* were at 70 m. These new insights into the spatial, temporal, and vertical distribution of these early life stages allowed informed investigations into the effects of bottom-up and top-down controls on their ecology. Canonical correspondence analysis was performed on the abundances of a spatial subset of the data constrained by climatic and oceanographic indices as well as pink salmon abundance. The indices that explained the most significant amount of variation in cephalopod paralarval abundance

were pink salmon, North Pacific Index, and mixing winds. The amount of variation in the cephalopod abundance matrix explained by the matrix of top-down and bottom-up controls was 79.7%, P-value 0.001. Further research is necessary to determine the mechanisms underlying these correlations however the data presented here represent significant advancements in our understanding of the ecology of the cephalopods from this region and provide direction for future research.

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Chapter I: Introduction

Ecologist and author Charles Krebs (1994) states that “Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms.” Krebs’ definition built on the previous definition of ecology put forth by Andrewartha (1961) which stated that “ecology is the scientific study of the distribution and abundance of organisms” with one important improvement, Krebs’ definition includes “interactions” that result in the observed distribution and abundances. These interactions can refer to many different scenarios, for instance how organisms relate to each other, how organisms relate to their environment, and how organisms relate to their prey, to name a few. The foundation of this body of work is to understand the relationships that drive the distribution and abundance of the early life stages of cephalopods in the Gulf of Alaska.

The Gulf of Alaska (Figure 1.1) extends north from approximately 54° N to Prince William Sound and west to Unimak Pass (~164° W). The Gulf of Alaska has a long, narrow shelf margin and a steep shelfbreak. At the southern portion of the Gulf of Alaska, the West Wind Drift or North Pacific Current flows eastward to the continent where it bifurcates into the northward flowing Alaska Current and the southward flowing California Current (Stabeno et al., 2004). The Alaska Current flows northeast along the continent until approximately Prince William Sound where its flow becomes southwesterly and it becomes the Alaska Stream current. Also near Prince William Sound, the Alaska Coastal Current forms. This current dominates the shelf region and is driven by winds and runoff (Royer, 1981; Stabeno et al., 2004). The Alaska Coastal Current bifurcates at the southern tip of the Kenai Peninsula, with approximately 70% flowing along Shelikof Strait and 30% joining the Alaska Stream (Stabeno et al., 2004). Severe weather due to the northern climate and mountain ranges that surround the Gulf of Alaska on three sides, affects the

amount of precipitation, cloud cover, runoff, and wind. In this case, the meteorology of the region has a profound impact on the oceanography especially in the Alaska Coastal Current. Royer (1981) found that this predominantly downwelling system experiences upwelling and an infusion of nutrients when winds and runoff relax in the summer months. Overland et al. (2000) found that in this region the coupled atmosphere and ocean exhibits chaotic traits, specifically, the system varies between two general states (warm and cool sea surface temperature) and that these states are stable. When the system is close to switching between states it is more vulnerable to external forcings and while the system is in one of the stable states, external forcings have less effect. Furthermore, the shift between states is rapid but the system can experience extreme anomalies during the shift (Overland et al., 2000).

External forces acting on the Gulf of Alaska come in the form of natural climatic and oceanographic cycles. In this region, the Pacific Decadal Oscillation (PDO), which is expressed by relatively warmer or cooler sea surface temperatures (Mantua et al., 1997), plays an important role. El Niño Southern Oscillation (ENSO) also affects sea surface temperatures (Wolter and Timlin, 1998); in the positive phase (El Niño) temperatures are warmer than average while in the negative phase (La Niña) temperatures are cooler than average. The ENSO is a perturbation of tropical winds near the equator and not as strongly experienced by the Gulf of Alaska ecosystem as the lower latitudes (N. Bond, personal communication). The Arctic Oscillation (AO), North Pacific (NP), and East Pacific North Pacific (EPNP) oscillations are all expressed as high or low sea level pressure anomalies. The AO oscillates between a high pressure cell over the Arctic and a low pressure cell over the North Pacific and vice versa (Thompson and Wallace, 1998). The NP is higher or lower than normal sea level pressure of the Aleutian Islands (Trenberth and Hurrell, 1994) and is a good indicator of the Aleutian Low, a semipermanent low

pressure cell over the Aleutian Islands (N. Bond, personal communication). The EPNP oscillates between the central North Pacific (lower than normal sea level pressure) and the Gulf of Alaska (higher than normal sea level pressure) in the positive phase and between the central North Pacific (higher than normal sea level pressure) and eastern North America (lower than normal sea level pressure) in the negative phase. These three anomalies directly affect winds in the region (Barnston and Livezey, 1987).

Cephalopods are marine mollusks found in all the world's oceans, from the shallow intertidal to the hydrothermal vents (*Vulcanoctopus hydrothermalis* Gonzalez and Guerra, 1998). They range in size from a total length of a few centimeters (*Idiosepius pygmaeus* Steenstrup, 1881) to 10 meters (*Mesonychoteuthis hamiltoni* Robson, 1925, (the colossal squid)). They are unlike any other organism on the planet and as such, present many mysteries to this day. On many continents (Europe, Asia, South America, Africa), cephalopods represent important commercial fisheries but in every ocean they are an important prey item for seabirds, fishes, and marine mammals. Commercially important species such as *Doryteuthis opalescens* (Berry, 1911) in California, *Illaix illecebrosus* (Lesueur, 1821) in New England, and *Todarodes pacificus* (Steenstrup, 1880) and *Watasenia scintillans* (Berry, 1911) in Japan, are well understood, including life histories, spawning grounds, and mating (Fields, 1965; Hayashi, 1993; O'Dor, 1983; Okutani, 1983; Sakurai et al., 1996; Sakurai et al., 2000; Yang et al., 1986); whereas the most basic information, e.g. life span, about the majority of cephalopods is unknown. It has been assumed that all squids and octopods have life history strategies similar to their shallow-water cousins (one-year life cycle for squid; four to six for octopods; semelparous for both) however, as information comes to light about underrepresented species, it is becoming clear that their life history strategies cannot simply be extrapolated from their shallow water cousins (Bjørke, 1995; Kubodera, 1981, Hunt and Seibel, 2000).

Investigations of the ecology of underrepresented cephalopods are difficult due to limited or no information on basic life history, difficulty in sampling, either due to geography or depth or both, and poor identification of species.

Jorgensen (2007 and 2009) was the first researcher to recognize the need for, and implement guides to, good taxonomic identifications of paralarval and adult stages of cephalopods of Alaskan waters. These guides and the resulting accurate identifications provide the foundation for ecological research on the diverse assemblage of cephalopods in the region. In Alaskan waters 23 described and one undescribed species of cephalopod in five Orders have been collected (Table 1.1) (Jorgensen, 2009). The life histories of all but two (*D. opalescens* and *Enteroctopus dofleini*) are largely unknown and what is known about these two species is based on populations in warmer waters and may not be directly translatable to northern populations.

The potential data available to study cephalopods comes from adult cephalopods collected during fisheries surveys and commercial fishing, all life stages from fish stomachs, and paralarvae from ichthyoplankton surveys. Surveys targeted at cephalopod collection are not presently conducted. Fisheries surveys and commercial fishing generally do not sample cephalopods well because cephalopods have fundamentally different swimming and escape behaviors from fish. Underwater video of commercial fishing trawls in use show that as the net approaches, most species of fish swim in a straight line, while squids dart in all directions, often escaping through the meshes. In this way, traditional trawling nets have built-in squid excluders (halibut, salmon, and turtle excluders built into commercial trawling gear work because they are based on behavioral differences between the target species and the species to be excluded. Halibut will, for instance, swim downwards when caught in a trawl so halibut excluders are wide, narrow openings placed at the bottom of the trawls. Few of the target species, walleye pollock (*Theragra*

chalcogramma (Pallas, 1814)) in this example, escapes because its behavior is to swim straight ahead when a trawl approaches.).

Cephalopods from predator stomachs can be very useful because fish generally swallow cephalopods whole or take big bites (recently consumed cephalopods from fish stomachs often will be in better condition than a trawl-caught cephalopod), fish can sample a variety of cephalopod life stages, and fish are relatively easy to collect using traditional methods. The limitations of this method are primarily that cephalopods digest very quickly and although many can be identified from beaks, this is a time consuming endeavor and requires intact beaks and accurate identifications. Also, the information about distribution and abundance of cephalopods is limited since the sampling device's movements cannot be tracked.

Due to the limitations in sampling adult populations, Vecchione (1987) concluded that the paralarval stage is the most efficient time to sample cephalopods. The term 'paralarvae' refers to distinction between true invertebrate 'larvae' which undergo a metamorphosis before assuming the adult form and cephalopod 'larvae' which do not undergo a metamorphosis (Young et al., 1988). Ichthyoplankton surveys targeting walleye pollock (*Theragra chalcogramma* (Pallas, 1814)) have been conducted in the Gulf of Alaska and Bering Sea since 1981 and are ongoing. Sampling months typically include April, May/June, and September. Sampling is conducted with a variety of nets, including MOCNESS, Tucker, and neuston, however the 60 cm bongo is used most often (Doyle et al., 2009). Samples are fixed in 5% formalin:buffered seawater solution and sorted for ichthyoplankton and cephalopod paralarvae. Cephalopod paralarvae were identified to species using Jorgensen (2007). Unlike ichthyoplankton samples which are fairly well represented by sampling, cephalopod paralarval data sets typically show many fewer individuals than would be expected given adult populations, the explanation for which is still unclear. Despite the limitations in sampling, Vecchione (1987) considered paralarval

sampling the most accurate and efficient method to understand adult populations. Paralarvae have the significant added benefit of being small enough in size and number, to easily and with minimal space, be kept as a sample archive. Adult specimens are typically identified at sea and not saved so that identifications cannot be verified. Of the 23 species collected in the region, only 12 species, mostly from the Family Gonatidae (Table 1.2) are known from the paralarval sample archive. Species which are not represented in the paralarval collection either are spawning elsewhere (possibly migrating to the region to feed) or have benthic paralarvae, e.g. many octopods. The notable exception to the rule of octopods producing benthic paralarvae is *E. dofleini*, which is also the highest latitude octopod with planktonic paralarvae.

Paralarvae are found throughout the sampling period (February to October) however peak abundances are found in May. Distribution varies by species, with many gonatid species experiencing highest abundances at the shelfbreak and *E. dofleini* more common on the shelf. Jorgensen (2007) found paralarval abundances in the Gulf of Alaska had high interannual variation in 2001 to 2003.

The goal of this research is to investigate the role environment plays in the early life history of cephalopods from the Gulf of Alaska. To approach this question the following research was conducted:

1. An experiment was designed to determine the response of paralarval *E. dofleini* to starvation. The results of the experiment would allow researchers to quantify patterns of starvation in the distribution of wild-caught paralarval specimens.
2. Archived samples of *E. dofleini* were analyzed for starvation using the criteria determined in the rearing experiment. The results of this analysis provide, for the first time, early life history information for this species in the Bering Sea and Gulf of Alaska as well as over 20 years worth of maps of the distribution of starved *E. dofleini* paralarvae throughout the seasons. Interestingly, only a single specimen

was found to meet the criteria of being starved so the following sections focus on the more abundant squid paralarvae of the region and their distribution and abundance.

3. The distribution and abundance of all squid paralarvae in the sample archive were analyzed and plotted. This work is the beginning of understanding the life history of these species, including timing and location of hatching, duration of the paralarval stage, and interannual trends in abundance.

4. A subset of squid and octopus data from the sample archive was analyzed in the framework of bottom-up and top-down controls. This synthesis work investigates correlations between variations in abundance of cephalopod paralarvae and climatic and oceanographic anomalies as well as predation by pink salmon.

Table 1.1. Cephalopods known from the study area (from Jorgensen, 2009).

Order	Family	Genus	Species
Myopsida	Loliginidae	<i>Doryteuthis</i>	<i>opalescens</i>
Oegopsida	Chiroteuthidae	<i>Chiroteuthis</i>	<i>calyx</i>
	Cranchiidae	<i>Belonella</i>	<i>borealis</i>
		<i>Galiteuthis</i>	<i>phyllura</i>
	Gonatidae	<i>Berryteuthis</i>	<i>anonychus</i>
			<i>magister</i>
		<i>Eogonatus</i>	<i>tinro</i>
		<i>Gonatopsis</i>	<i>borealis</i>
		<i>Gonatus</i>	<i>berryi</i>
			<i>madokai</i>
			<i>middendorffi</i>
			<i>onyx</i>
			<i>pyros</i>
	Histioteuthidae	<i>Stigmatoteuthis</i>	<i>dofleini</i>
	Octopoteuthidae	<i>Octopoteuthis</i>	<i>deletron</i>
	Onychoteuthidae	<i>Moroteuthis</i>	<i>robusta</i>
		<i>Onychoteuthis</i>	<i>borealijaponicus</i>
Sepioidea			
	Sepiolidae	<i>Rossia</i>	<i>pacifica</i>
Octopoda			
	Opisthoteuthidae	<i>Opisthoteuthis</i>	<i>californiana</i>
	Bolitaenidae	<i>Japetella</i>	<i>diaphana</i>
	Octopodidae	<i>Benthoctopus</i>	<i>leioderma</i>
		<i>Enteroctopus</i>	<i>dofleini</i>
Vampyromorpha			
	Vampyroteuthidae	<i>Vampyroteuthis</i>	<i>infernalis</i>

Table 1.2. Paralarval cephalopods known from the study area.

Order	Family	Genus	Species
Oegopsida			
	Chiroteuthidae	<i>Chiroteuthis</i>	<i>calyx</i>
	Cranchiidae	<i>Galiteuthis</i>	<i>phyllura</i>
	Gonatidae	<i>Berryteuthis</i>	<i>anonychus</i>
			<i>magister</i>
		<i>Gonatopsis</i>	<i>borealis</i>
		<i>Gonatus</i>	<i>berryi</i>
			<i>madokai</i>
			<i>middendorffi</i>
			<i>onyx</i>
			<i>pyros</i>
Octopoda			
	Bolitaenidae	<i>Japetella</i>	<i>diaphana</i>
	Octopodidae	<i>Enteroctopus</i>	<i>dofleini</i>

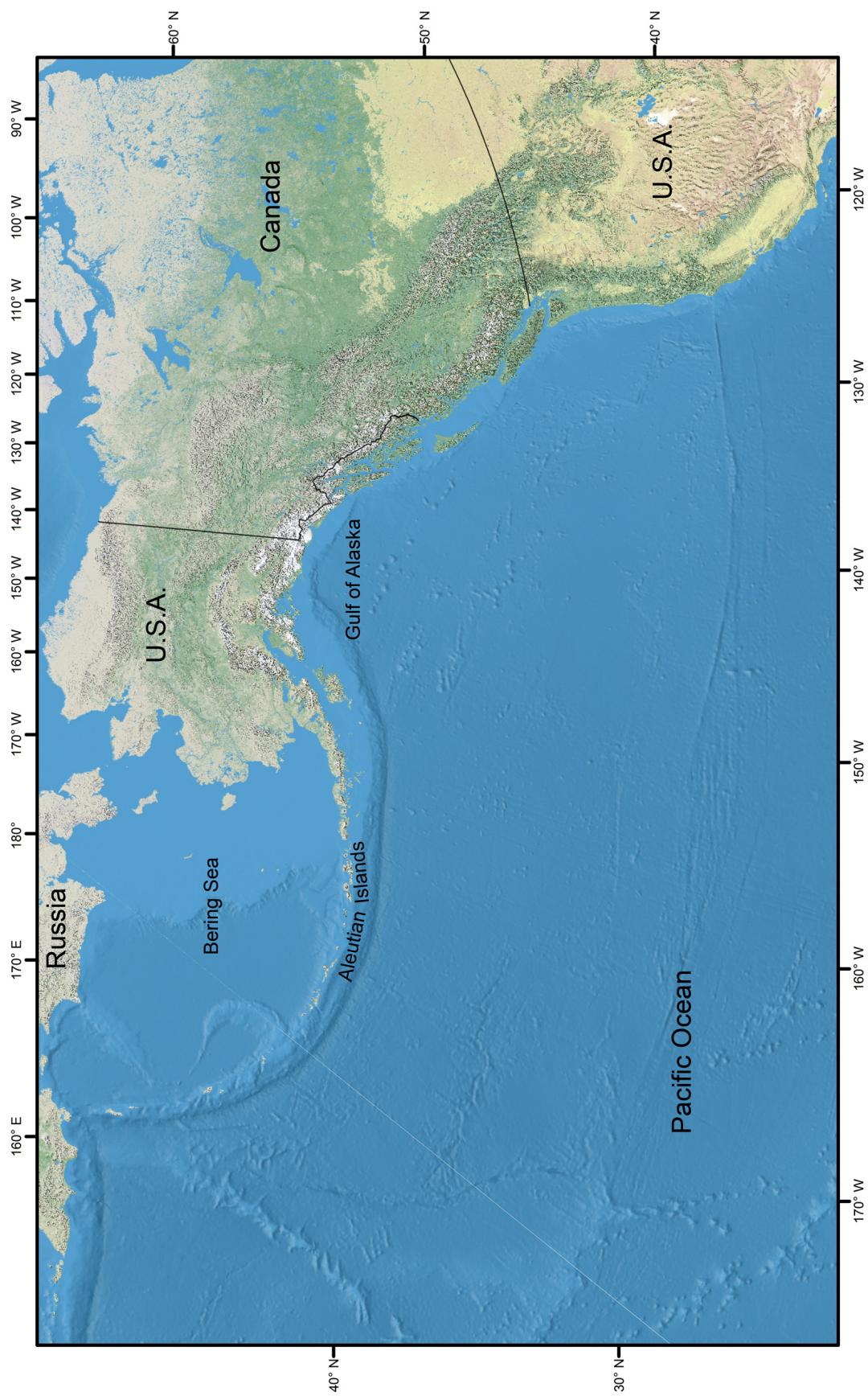


Figure 1.1. Map of study area.

Chapter II: *Enteroctopus dofleini* rearing methods and effects of starvation on the digestive gland of the paralarval stage

Abstract

A rearing experiment was conducted on the Pacific giant octopus, *Enteroctopus dofleini* (Wölker, 1910), to determine the role of the digestive gland in the survival of paralarval *E. dofleini* and how to quantify the response of paralarvae to starvation. Paralarvae were obtained from wild-caught eggs. Seven days after hatching began, paralarvae were separated into control and experimental groups. The control animals were fed every eight hours while the experimental animals were not fed. Three paralarvae were sampled from each planktonkreisel every eight hours for 14 days. Paralarval *E. dofleini* were successfully reared in planktonkreisel aquaria however high densities increased mortality. The digestive gland in both groups of animals decreased in size until age 19 days, after which the digestive gland of control animals significantly increased in size while that of starved animals continued to decrease. A digestive gland width to head width ratio of 50% or less indicates the paralarvae was starving at the time of collection.

Introduction

Cephalopods are important members of many marine ecosystems. In recent years, there has been increased pressure to commercially fish for cephalopods (Rodhouse et al., 1998; Jereb et al., 2005). Cephalopod populations tend to have high interannual variability (Otero et al., 2008) and are difficult to quantify. Multiple authors have concluded population estimates would best be made from paralarval distribution and abundance (Vecchione, 1987; Bower et al., 1999). The paralarval stage of cephalopods has long been believed to have the highest mortality of all the life stages (Vecchione, 1987). The source of this mortality has often been assumed

to be due to starvation (Vecchione, 1987); however initial abundance and mortality due to predation are also important considerations especially when attempting to understand how environment influences cephalopod population dynamics. To begin to address the question of how environment influences cephalopod population dynamics it is necessary to have an additional vital piece of information, the condition of the individual.

To determine a quantifiable measure of the condition of individual paralarvae a rearing experiment was designed in which the control group was given copious amounts of food and the experimental group was unfed. Vecchione (1987) noted that rearing cephalopod paralarvae has been unsuccessful in the past so a new rearing tank was designed based on Raskoff et al. (2004) work on rearing gelatinous zooplankton. The rearing tanks, termed planktonkreisels, were designed so that the fragile organisms would be kept in suspension by the movement of water in the tank, thereby avoiding contact with the tank itself.

The species chosen for this experiment was *Enteroctopus dofleini* (Wülker, 1910). *Enteroctopus dofleini* is an epibenthic octopod that occurs from off the coast of California to the Gulf of Alaska, Bering Sea, and Japan. It occurs from the intertidal to 1000 m (Jorgensen, 2009) but is most abundant on rocky bottoms less than 200 m. After mating, the female attaches strands of eggs to the ceilings of rocky dens and blocks the entrance of the den with rocks. The female cleans and guards the eggs until hatching, approximately 5-7 months (Hartwick, 1987) and then dies. A female can lay up to 100,000 eggs but the average is 50,000 (Kanamaru, 1964; Kubodera, 1991). In Japan, spawning is believed to occur at depths less than 50 m (Hartwick, 1987; Kanamaru and Yamashita, 1967; Yamashita, 1975). The availability of eggs within SCUBA diving limits made this species an especially suitable study organism.

The geographic range of *E. dofleini* also contributed to its suitability as a

study organism. The facility where the rearing was conducted, Mukilteo Marine Laboratory, is located in Puget Sound. This experiment was designed with the goal of applying the results to specimens in an archived collection of cephalopod paralarvae from the Gulf of Alaska and Bering Sea which includes *E. dofleini*.

The most obvious organ in paralarval *E. dofleini* collected in plankton tows is the digestive gland. It is the largest organ in most paralarval cephalopods and it is one of only two opaque organs (the other being the eyes) in the otherwise transparent planktonic paralarvae, indicating its importance in the survival. It is located on the dorsal midline, just behind the head and anterior to the stomach and caecum. The digestive gland can be measured without damaging the specimen allowing the techniques developed from the experiment to be applied to the *E. dofleini* specimens in the 30 year sample archive from the region. For these reasons, the response variable chosen to investigate the condition of starvation of the individual was the digestive gland.

Several studies have already been conducted on cephalopod digestive glands. During post-embryonic development the digestive gland replaces the internal yolk sac as the yolk is used up in the first days after hatching. Boucher-Rodoni et al. (1987) found evidence that this post-embryonic development was triggered by first feeding. The digestive gland is characterized by a single type of cell, called the digestive cell, in multiple functional stages. The digestive cell has two main types of inclusions, boules and brown body vacuoles (Boucaud-Camou and Boucher-Rodoni, 1983). The boules contain digestive enzymes which are passed to the stomach for primary production. The brown-body vacuoles package cellular waste and then are excreted from the cells (Boucaud-Camou and Yim, 1980; Boucher-Rodoni et al., 1987). The role of the digestive gland is to aid in digestion, absorption of nutrients, and the storage of fuel reserves (Boucaud-Camou and Boucher-Rodoni, 1983; Boucher-Rodoni et al., 1987). Indeed, it is the efficiency

with which the digestive gland digests food and absorbs nutrients that allows cephalopods to achieve their high growth rate, >2% body weight per day (Castro and Lee, 1994), resulting in their unique position in the food web. Because of the importance of the digestive gland in the growth of cephalopods, it has received much attention from researchers in recent years.

Bidder (1957) was one of the first to experiment on the digestive system of cephalopods. By color coding prey items, the author determined that absorption took place predominantly in the digestive gland of *Sepia* and *Octopus* and mainly in the caecal sac of *Loligo*. Since Bidder's work, experiments on the digestive gland have focused on the effects of different food types on the structure of the digestive gland and the effects of starvation on the weight and volume of the digestive gland.

Vecchione and Hand (1981) analyzed the internal structure of the digestive gland of paralarval *Loligo* with different feeding histories (starved in aquaria vs. wild-caught) and found that the histological structure varied by food type. The constraints of the experimental design did not allow the author to draw conclusions about the ecological meaning of the differences that were observed except that different food resulted in a different structure of the digestive gland.

The cuttlefish *Sepia officinalis* dedicates most available energy to growth, not storage so that during long periods of starvation muscle protein was metabolized; however during short term starvation events (<5 days) the digestive gland supplied the needed energy (Castro et al., 1992). Similar results were found for juvenile *S. officinalis* by Melzner et al. (2005). The authors found that the weight of the digestive gland of juvenile *S. officinalis* showed a strong correlation to starvation. The results of their study indicate that the digestive gland of juvenile *S. officinalis* is capable of a high degree of plasticity in response to food availability and the digestive gland index (DGI) is a good indicator of recent growth. Furthermore, they found that the digestive gland is utilized during short-term starvation events (lasting

up to four days) while muscle protein is metabolized during long-term starvation.

Similar research on the role of the digestive gland in survival has not been conducted on members of the family Octopodidae. The objectives of this research are to determine the role of the digestive gland in the survival of *E. dofleini* paralarvae and quantify the response of the digestive gland of *E. dofleini* to starvation.

Methods

Enteroctopus dofleini eggs were collected on 7 December 2008 in 20 m water depth using SCUBA at 48° 37.1'N 123° 30.8'W (Figure 2.1). Water temperature at the den was 8.9°C. Eggs were transported from the collection site to the rearing facility in plastic containers with seawater which were then placed in a cooler with ice. At the rearing facility eggs were placed in a planktonkreisel, modified from Raskoff et al. (2004) with a 30.5 cm diameter and 10 cm width (Figure 2.2). The outflow screen was 153 µm. Eggs were reared at the Mukilteo Field Station which has a flow-through, gravity-fed seawater system. Water intake is at 20 m and the water is sand filtered to remove particulates. Water temperature was an average of 9.5 °C during the experiment.

The experiment began one week after collection, on 14 December 2008. From 7 - 14 December, hatchlings were given an abundance of food, allowing for first feeding. During the first week after hatching, all individuals were kept in one planktonkreisel. At initiation of the experiment, 200 individuals were removed from the original planktonkreisel and placed in each of five planktonkreisels, the sixth planktonkreisel contained the original hatchlings. There were three replicate control planktonkreisels and three replicate experimental planktonkreisels. The control animals were fed every eight hours (0000, 0800, and 1600) while the experimental animals were not fed. Food consisted of rotifers and artemia, enriched

with Instant Algae Nannochloropsis Premium 3600, and minced frozen mysid shrimp from Gamma frozen fish foods. Three individuals were sampled from each planktonkreisel every eight hours (0000, 0800, and 1600). Animals were placed in chilled carbonated seawater for anesthetization before they were placed in 4% formalin. Each planktonkreisel was cleaned every eight hours and dead animals were removed and quantified. The experiment was completed on 27 December 2008.

Upon completion of the experiment, specimens were placed in 100% glycerin to clear mantle tissues. After clearing, each specimen was photographed using a Leica DFC420 camera mounted on a Leica MZ9.5 microscope. Morphological measurements were recorded for individuals sampled at 0800 daily.

To be able to apply the results of the experiment to paralarvae of unknown age, the response variable needs to be a ratio of the digestive gland measurement to another morphological measurement that best estimates age of the individual. Therefore six morphological measurements were made for each specimen, measurements included the three possibilities to best represent the digestive gland: digestive gland length (DGL), digestive gland width (DGW), and digestive gland base width (DGBW); and the three best possibilities to represent age of the individual: the standard, dorsal mantle length (ML), mantle width (MW), and head width (HW) (Figure 2.3).

Results

Rearing paralarvae

Hatching began immediately after placement of eggs in the planktonkreisel which was likely due to the difference in temperature of the water in the transport containers and the planktonkreisels. Although some early hatchlings still had an external yolk present after hatching, indicating they had hatched prematurely, at the

start of the experiment all external yolks were gone.

The planktonkreisels were suitable aquaria in which to rear hatchling and paralarval *E. dofleini*. Control animals actively fed on non-living prey items. Animals in both experimental and control groups were successfully reared until the experiment was ended, 21 days after the eggs were introduced into the planktonkreisels, with relatively low mortality (16 - 65.1% in control tanks; 8.5 - 16% in experimental tanks) (Table 2.1). The planktonkreisel with the animals that experienced the highest mortality (65.1%) was the original location for the egg masses and it was determined that at the end of the experiment that planktonkreisel had 350 individuals not the intended 200 individuals that each of the other five planktonkreisels contained.

Experimental results

Measurements of HW, MW, and ML revealed that over the course of the 14 day experiment, control and experimental animals did not differ significantly and neither group changed in body size (Figure 2.4). Measurements of the digestive gland, however, revealed the digestive gland decreased in size for both the experimental and the control animals over the first 12 days (age 19 days), after which time the digestive gland of the control animals began to increase in size while that of the experimental animals continued to decrease in size (Figure 2.5).

A ratio of digestive gland width to head width (DGW:HW) of 50% or less was indicative of starved paralarvae (Table 2.3). A Paired Student's *t*-test was performed and the DGW of the two groups were found to be significantly different at the last two sampling times (days 13 and 14) ($P<0.001$).

Discussion

Control animals actively fed on non-living prey items. Although the

animals were given enriched rotifers and artemia, they appeared to eat mostly the minced mysid shrimp. The mysid shrimp were likely closest in size to normal prey of paralarval *E. dofleini* and the movement of the water current in the circular planktonkreisels kept the prey items moving. Prey items that fell to the bottom of the planktonkreisel were never eaten. It is likely that movement of prey items is more important than whether the prey is alive or not.

The presence of excess prey in the control tanks may have contributed to the higher mortalities in those tanks (Table 2.1) by adding to the overall density of items in the tanks and/or by the clogging the outflow screens with uneaten food. Left unattended, clogged screens would result in animals caught in the screens; the highest mortality events coincided with clogged screen events. Future rearing work with planktonkreisels should employ a larger mesh screen (>500 µm). In a properly functioning tank the flow of water will prevent loss of prey items through the outflow screen.

The low mortality of the experimental animals was unexpected. These individuals were closely monitored to record cannibalism however none was seen until, potentially, day 10. This incident was not believed to have impacted the experiment because the live animal was only holding a dead animal in its arms and the dead animal was completely intact. Furthermore, all planktonkreisels were inspected and cleaned every eight hours and none of the experimental planktonkreisels showed the presence of feces during the entire experiment. Therefore, the low mortality observed in the experimental animals is believed to be an accurate representation of the mortality of animals starved for 14 days. The outflow screens of the experimental tanks did not clog during the 14 days.

Paralarval *E. dofleini* appear to experience the ‘no net growth’ phase described by Vidal et al. (2002). Vidal et al. (2002) hypothesized that at the beginning of this phase hatchling *Doryteuthis opalescens* (Berry, 1911) decreased

in body weight, despite feeding, as the internal yolk was exhausted. The second half of this phase is marked by an increase in body weight as hatchlings continue to feed such that by the end of the ‘no net growth’ phase, animals are the same size as when they were hatched. Vidal et al. (2002) found that the length of the ‘no net growth’ phase was temperature dependent. Although body weight was not calculated in this experiment, measurement of the digestive gland is considered a parallel to body weights.

During the course of the experiment ML, MW, and HW measurements did not significantly vary while DGL, DGW, and DGBW measurements decreased during the first 12 days of the experiment. After the twelfth day, DGW and DGBW of control animals showed a marked increase in size but after 14 days were still significantly less than at the start of the experiment. Using digestive gland measurements as a proxy for weight, since HW, ML, and MW did not vary, indicates that first half of the ‘no net growth’ phase ended at approximately day 12 (19 days after hatching). Unfortunately the experiment did not capture the end of the ‘no net growth’ phase; however, given the rapid increase in DGW and DGBW seen in the control animals, the end of the ‘no net growth’ phase could be estimated to occur at day 16-18 (age 23-25 days).

The ‘no net growth’ phase described by Vidal et al. (2002; Figure 7) consists of two time periods. The first time period is the time it takes to use up the internal yolk, approximately 6 days in *D. opalescens* and approximately 19 days in *E. dofleini*, three times longer than for *D. opalescens*. The second time period is the growth period, which lasted another 6 days in *D. opalescens* but only an estimated 6 - 8 days in *E. dofleini*. The difference in water temperature between that in the experiment of Vidal et al. (2002) (12 and 16°C) and that of this experiment (9.5°C) may explain the much lower rate of utilization of internal yolk however the same decreased metabolism should have resulted in a much longer growth period for *E.*

dofleini. The cause of the discrepancy is unclear but may be linked to the lower mortalities experienced by the study organisms in this study.

It is unknown why paralarvae with internal yolks feed since they seem unable to incorporate the food into growth (M. Vecchione, personal communication). It is possible that the act of feeding even without direct benefit prepares them for feeding when the yolk is exhausted. Darmillacq et al. (2006) found that *S. officinalis* juveniles preferred food to which they had been visually imprinted and that visual imprinting was more important than prey at first feeding. Darmillacq et al. (2008) found this imprinting occurred as early as the embryonic stage in *S. officinalis*. It is possible that during the post-hatching stage when the internal yolk is being utilized, that hatchlings are learning what to eat. It is also possible that paralarvae with internal yolk that are actively feeding are practicing prey capture. It was observed during the experiment that the paralarvae assumed a distinctive posture prior to striking the prey. The relatively high success in rearing of post-hatching paralarval *E. dofleini* would allow more individuals to both learn what prey items were available and practice prey capture.

The period after hatching, while the internal yolk is being exhausted, should be a period of low mortality since starvation is not possible and predators are not present. The high mortality experienced by Vidal et al. (2002) may be more a reflection of rearing method than representative of vulnerability of this life stage. It should be noted that the complete ‘no net growth’ phase of *E. dofleini* is only estimated and future work should begin with rearing through the entire ‘no net growth’ phase to determine the actual time frame of the growth portion of the phase.

Vidal et al. (2002) found that immediately after hatching body weight of *D. opalescens* decreased due to the use of the internal yolk sac; *E. dofleini* experienced a similar phenomenon evidenced by the shrinking digestive gland. After the internal yolk was utilized, *D. opalescens* paralarvae increased in body weight; the digestive

gland of *E. dofleini* increased in size, while external morphometrics remained relatively unchanged. Growth in *E. dofleini* after the internal yolk sac is utilized, is in the digestive gland. The discrepancy in the size of the digestive glands of starved and fed animals after day 12 of the experiment may indicate that the digestive gland of *E. dofleini* paralarvae is used for energy storage.

The size discrepancies between the digestive glands of the control and experimental animals allows categorization of starved paralarvae however, due to the ‘no net growth’ phase, it does not allow categorization of the health of all paralarvae because individuals less than 19 days of age (7 days after hatching to allow for first feeding plus the first 12 days of the experiment) from both the control and experimental groups had similar DGW:HW ratios. Therefore, individuals with a DGW:HW ratio of 50% or less are known to be starving but individuals with a DGW:HW ratio of over 50% may or may not be well fed.

The ability of *E. dofleini* paralarvae to survive for 12 days without feeding is a significant factor in their ecology. Bailey and Macklin (1994) and Lasker (1981) determined that successful first feeding in fish larvae is an important factor in survival. By outfitting the paralarval stage with an internal yolk that can sustain the paralarvae for up to 19 days after hatching, the parent may be allowing the paralarvae to avoid this critical period.

Future work should aim at determining methods to non-destructively differentiate hatchlings (internal yolk sac present) from paralarvae (no internal yolk sac), testing the ability to withstand starvation of animals in the paralarval stage, and extending the timeframe of the experiment to include the full ‘no net growth’ stage. *Doryteuthis opalescens* paralarvae should be reared throughout their ‘no net growth’ stage in planktonkreisels to determine if the high mortality reported by Vidal et al. (2002) is an artifact of rearing technique.

Conclusions

This research represents the first attempt to explore the role of the digestive gland in the survival of paralarval *E. dofleini*. The use of planktonkreisels as rearing aquaria allowed successful long-term rearing of paralarval octopus with relatively low mortality. The unique design of the planktonkreisel induces a circular water current that prevents injury due to contact with the sides and bottom of the tank. This current also maintains inanimate prey items in the water column, allowing paralarvae to successfully feed on non-living prey. The experiment was successful in producing an index of starvation which can, non-destructively, be applied to archived specimens. A DGW:HW < 0.50 indicates the animal is starving. The index is limited due to the ‘no net growth’ phenomenon first described by Vidal et al. (2002) and experienced by *E. dofleini* immediately post-hatching when, during the first 19 days of age, the digestive glands of both starved and fed animals, shrank, resulting in similar DGW:HW. *Enteroctopus dofleini* experienced the ‘no net growth’ phase described by Vidal et al. (2002) however, the phase was three times longer in *E. dofleini* than that observed for *D. opalescens*, likely due to the cooler water temperatures in which *E. dofleini* live. The long ‘no net growth’ phase exhibited by post hatching *E. dofleini* have significant ramifications for survival in a highly variable environment and, at least for this life stage, indicates that it may be predation, not starvation that contributes most to the mortality of paralarval *E. dofleini*.

Table 2.1. Percent Mortality of each replicate in the Control and Experiment at the completion of the experiment (day 14 which was 21 days after hatching).

Percent Mortality	
Control	Experiment
16.0	16.0
65.1	13.5
44.0	8.5

Table 2.2. Average digestive gland width (mm), average head width (mm), and digestive gland width to head width ratio for control and experiment groups. Day is from the beginning of the experiment, which is day 7 after hatching.

Day	Control			Experiment		
	DGW	HW	DGW:HW	DGW	HW	DGW:HW
1	1.41	1.98	0.711	1.47	2.09	0.703
2	1.47	2.05	0.720	1.31	1.97	0.661
3	1.29	2.02	0.640	1.34	1.88	0.710
4	1.34	2.01	0.670	1.24	1.93	0.642
5	1.22	1.97	0.620	1.14	1.97	0.577
6	1.14	1.83	0.623	1.02	1.80	0.563
7	1.02	1.82	0.561	1.00	1.75	0.573
8	0.96	1.78	0.537	1.10	1.89	0.580
9	1.00	1.78	0.559	0.95	1.73	0.552
10	1.17	1.93	0.607	1.03	1.89	0.545
11	1.08	1.84	0.584	0.91	1.82	0.501
12	1.03	1.75	0.586	1.02	1.82	0.559
13	1.15	1.91	0.602	0.93	1.83	0.508
14	1.22	1.97	0.620	0.87	1.74	0.500

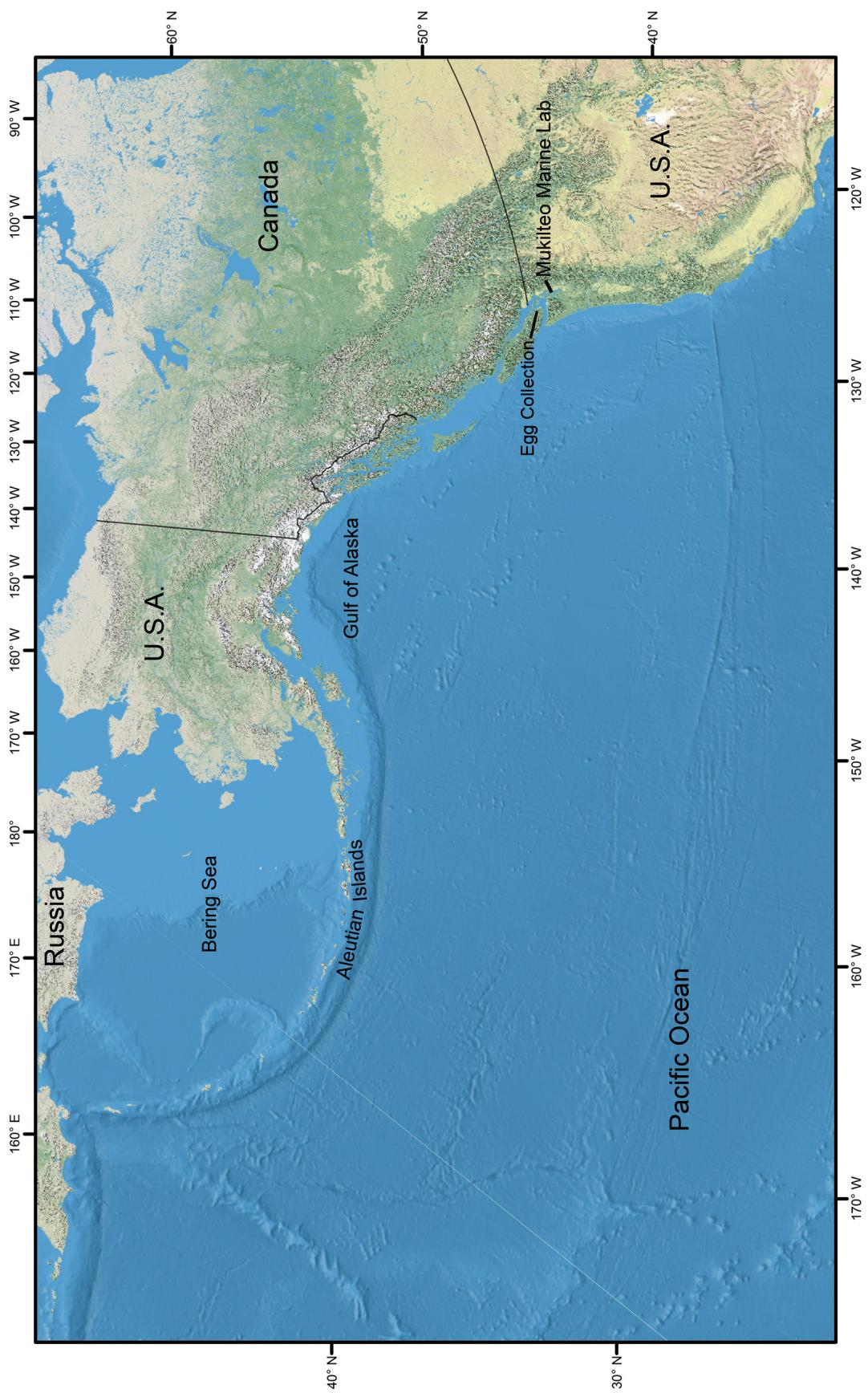


Figure 2.1. Map of northern North Pacific showing study area, location of egg collection, and location of rearing facility (Mukilteo Marine Laboratories).

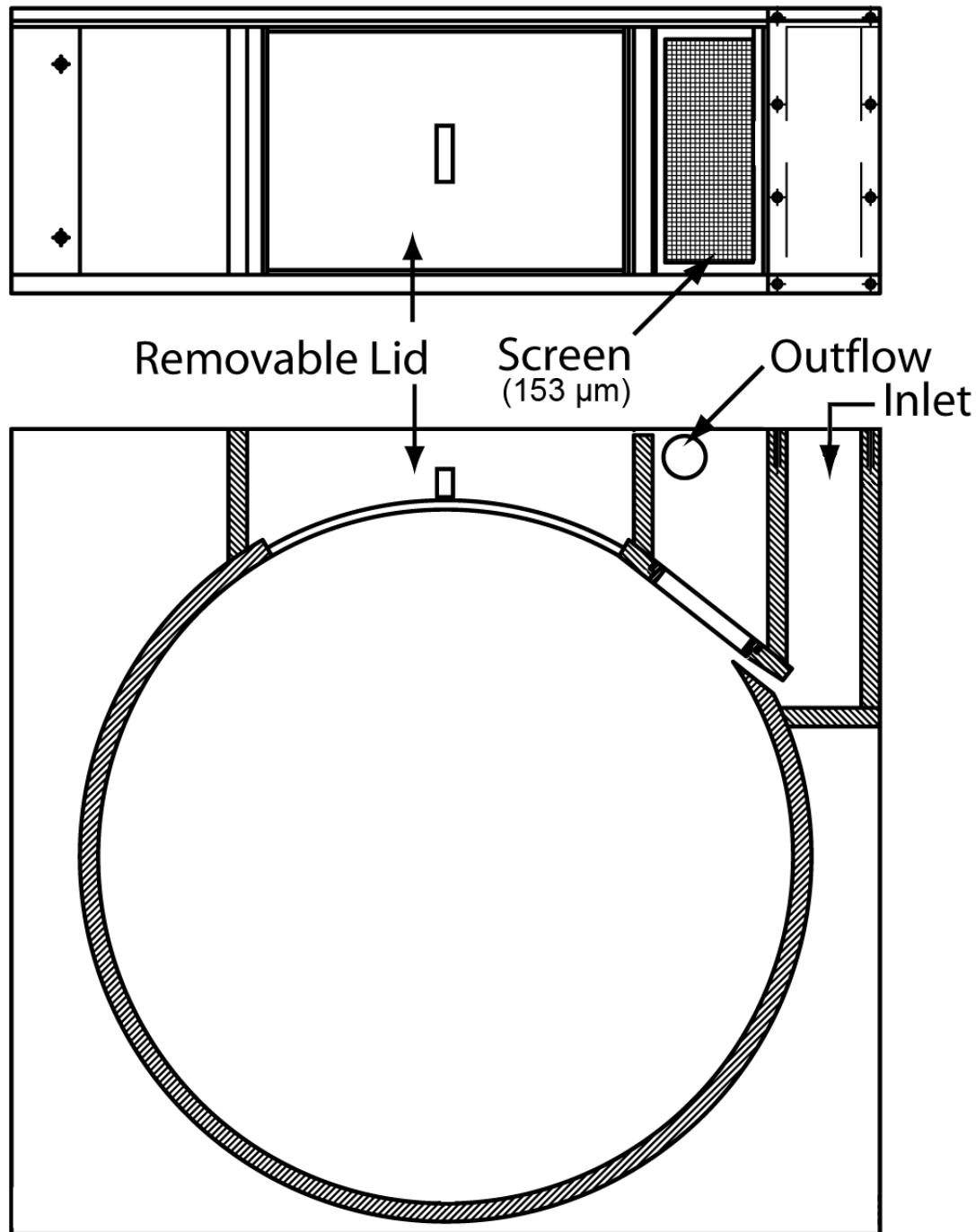


Figure 2.2. Planktonkreisel design from Raskoff et al. (2004) with modifications. Top illustrates view from above tank; bottom illustrates side view. From Raskoff et al., 2004.

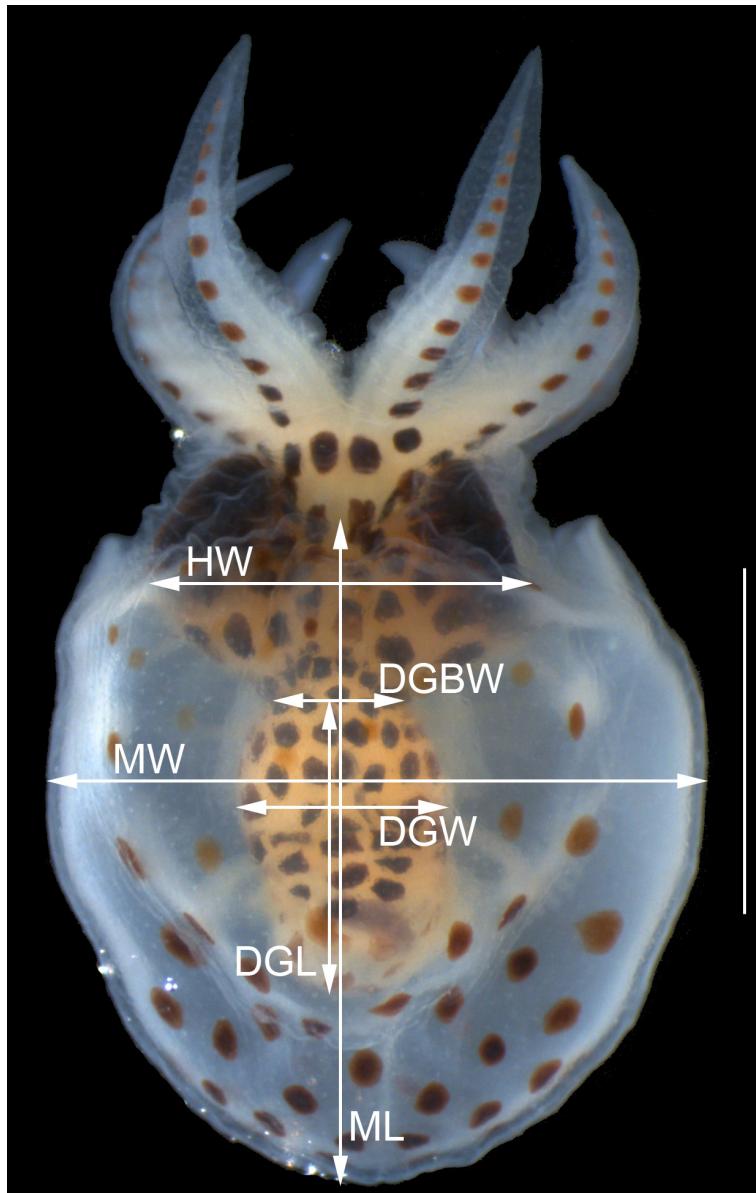


Figure 2.3. *Enteroctopus dofleini* paralarvae with measurements illustrated. HW = Head Width; DGBW = Digestive Gland Base Width; MW = Mantle Width; DGW = Digestive Gland Width; DGL = Digestive Gland Length; ML = Mantle Length. Scale bar = 2 mm.

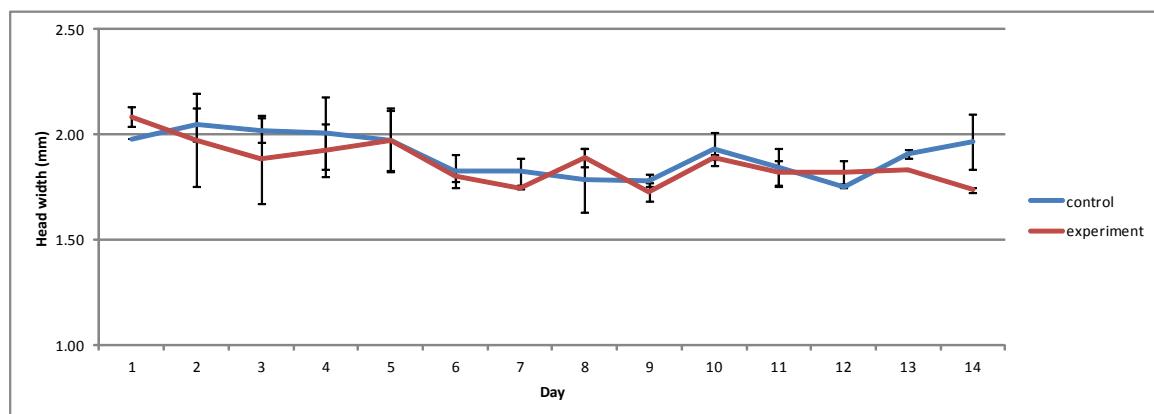
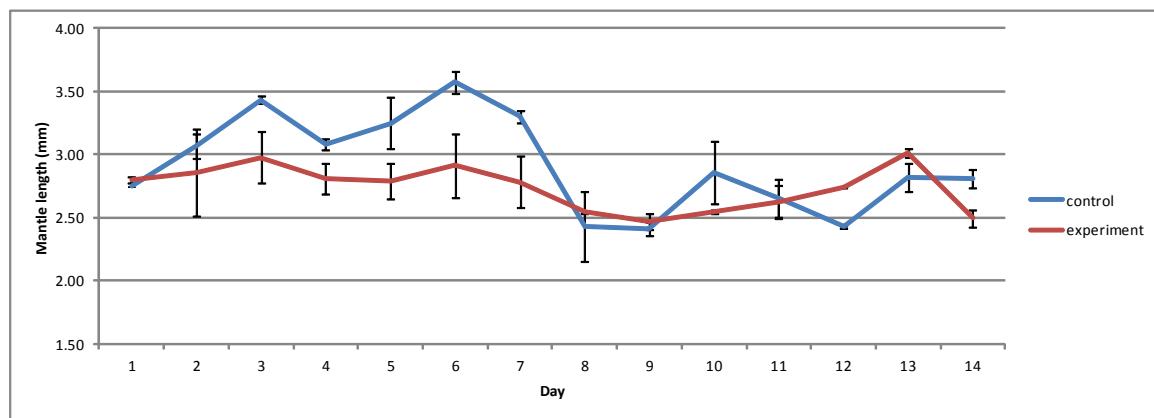
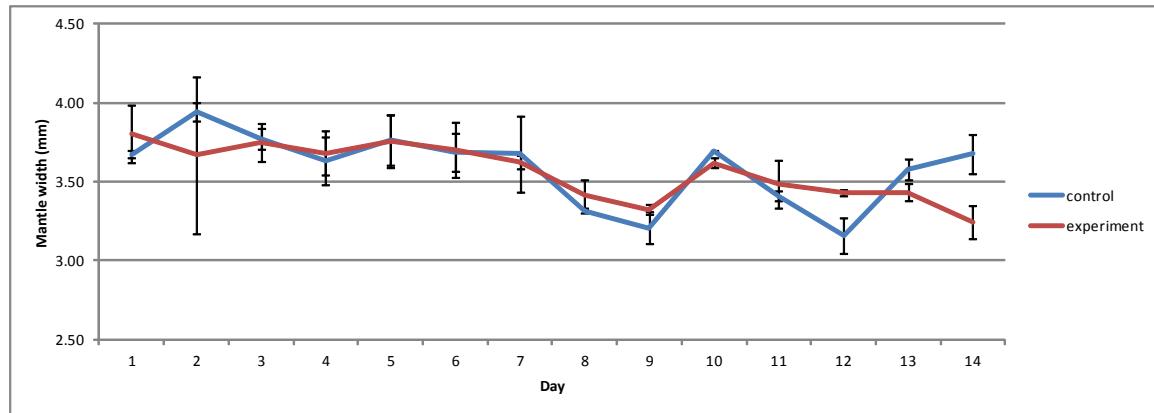
A**B****C**

Figure 2.4. External measurements. A. Head width (mm); B. Mantle length (mm); C. Mantle width (mm). Error bars represent the first standard deviation.

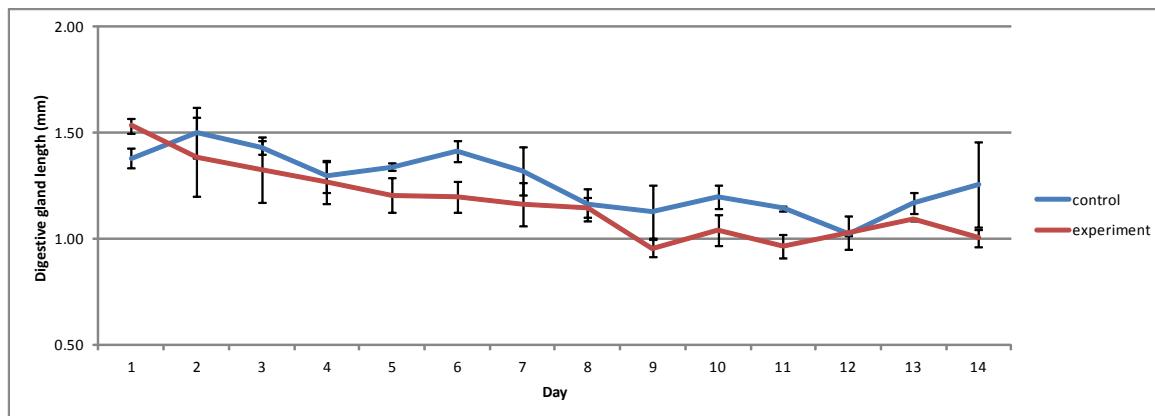
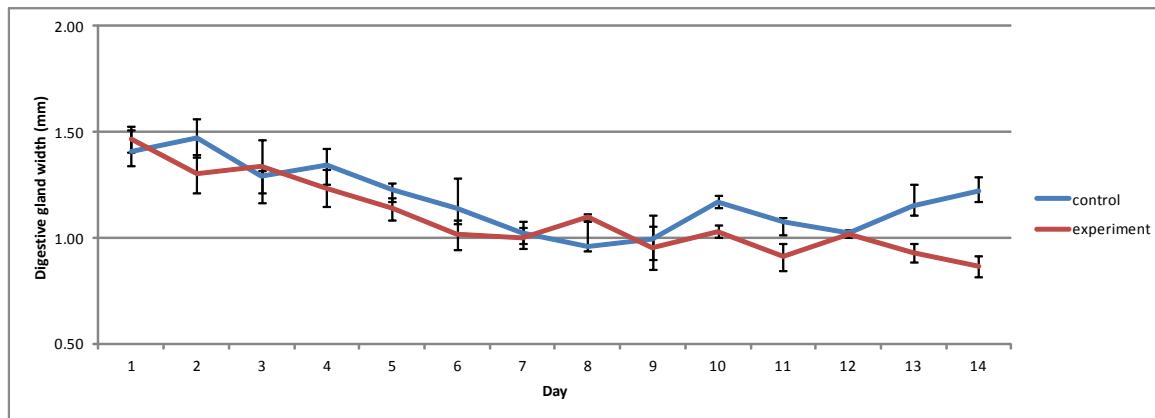
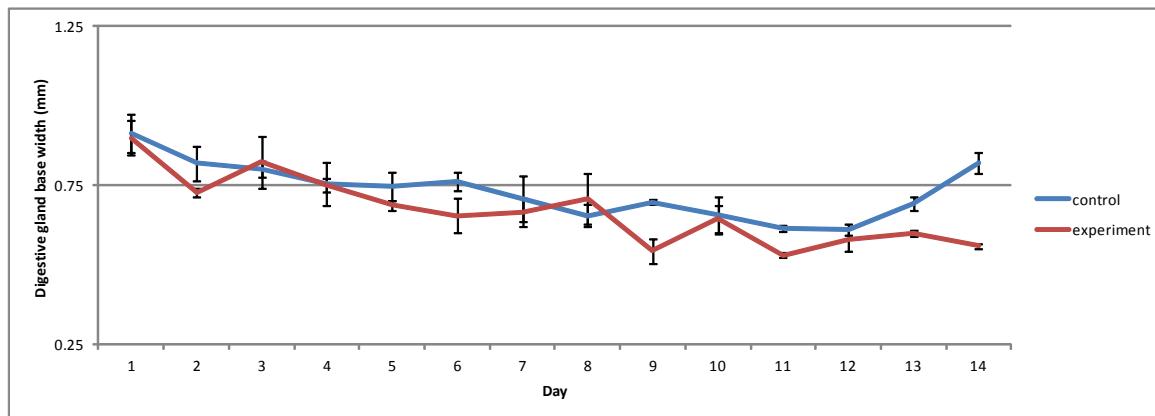
A**B****C**

Figure 2.5. Internal measurements. A. Digestive gland length (mm); B. Digestive gland width (mm); C. Digestive gland base width (mm). Error bars represent the first standard deviation.

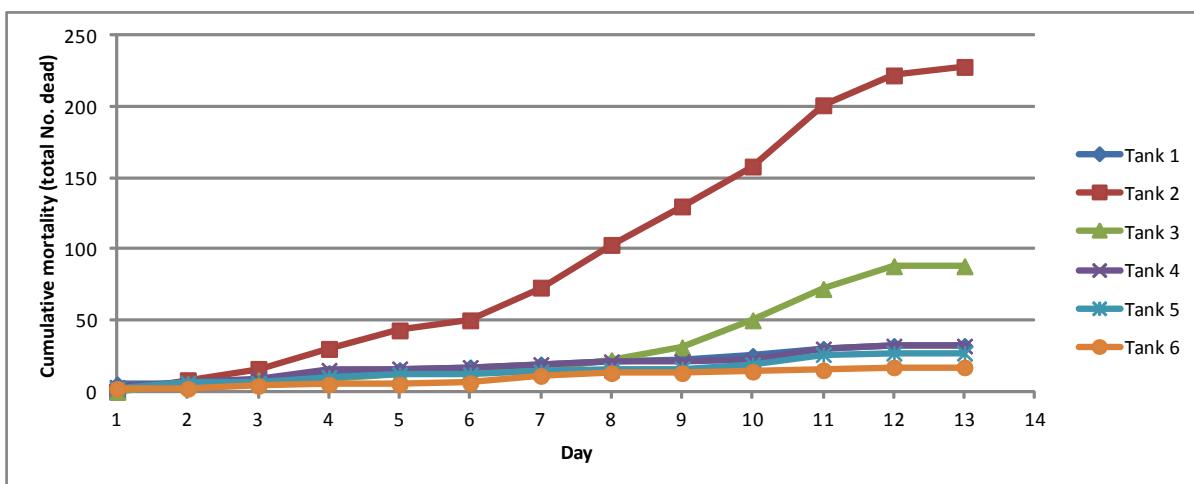


Figure 2.6. Cumulative mortality in each planktonkreisel. Tanks 1 - 3 are control (fed); tanks 4 - 6 are experiment (starved). Units are number of dead individuals removed daily from each tank.

Chapter III: Investigating the early life history and testing for the effects of starvation in wild-caught *Enteroctopus dofleini* (Wülker, 1910) paralarvae from the Bering Sea and Gulf of Alaska, 1991 to 2008

Abstract

Abundance, geographic and depth distribution, length frequency, and starvation index of wild-caught *Enteroctopus dofleini* (Wülker, 1910) paralarvae from the Bering Sea and Gulf of Alaska, 1991 to 2008, was investigated. Paralarval *E. dofleini* are part of a sample archive, the result of ongoing ichthyoplankton surveys in the region. Hatching occurred throughout the Gulf of Alaska shelf region and the shelfbreak region of the Bering Sea. Paralarvae were collected in plankton tows from 2.2 - 6.5 mm mantle length, with a peak at 3 mm mantle length. MOCNESS sampling reveals specimens were collected from the surface to 500 m with the majority of specimens occurring in the upper 100 m. Hatching occurs in February and appears to continue until September. Specimens were measured to test for the effects of starvation (previous chapter) however only a single individual, out of 760, was found to meet the criteria of starvation.

Introduction

Enteroctopus dofleini, the Pacific giant octopus, is found from the west coast of the United States to the Bering Sea and Japan (Jorgensen, 2009). It is considered a coastal species however in the Bering Sea it is most abundant at the shelfbreak and has been collected as deep as 1,000 m (Jorgensen, 2009). It is epibenthic after the paralarval stage but adults are known to forage in the water column (Rigby and Sakurai, 2005). Of the octopods, *E. dofleini* is the highest latitude species with a planktonic paralarval stage. Females lay several strands of

eggs from the ceilings of rock dens and clean and protect the eggs until hatching, estimated to be 5 - 7 months. Hatchlings are 2.2 - 3.5 mm mantle length, after swimming to the surface they spend 2 - 4 months as members of the plankton before settling to the seafloor and assuming the epibenthic lifestyle of the adults (Hartwick, 1983). The duration of the planktonic paralarval stage is estimated for west coast animals and may be temperature dependent. As the common name suggests, *E. dofleini* can reach very large sizes and is the world's largest octopod. Larger females can produce an estimated 100,000 eggs, however the average number is estimated at 50,000 (Kanamura, 1964; Kubodera, 1991). Mortality is highest during the planktonic period with an estimated 4% surviving to 6 mm mantle length (Mottet, 1975).

It is during this planktonic stage that *E. dofleini* is most available to scientific collection (Vecchione, 1987). *Enteroctopus dofleini* has been collected as bycatch in on-going ichthyoplankton surveys in the Gulf of Alaska and Bering Sea since 1981. The primary objective of this research was to investigate the early life history of *E. dofleini* from the region, in the form of quantifying abundance, spatial and vertical distribution, paralarval duration, and hatching location and timing, as well as testing for starvation using the digestive gland index (Chapter 2).

Methods

Planktonic sampling was conducted in the Bering Sea and Gulf of Alaska each year from 1981 to 2008 (Figure 3.1). Typically, sampling started as early as February to as late as September however some January and October sampling was also conducted. Sampling was conducted with several gear types: 60 cm bongo, calvet, neuston, Methot, tucker, MOCNESS (multiple opening close net environmental sampling system), and variations on these. The 60 cm bongo was used most often however all specimens collected from all sampling gears

were included. Net mesh was either 333 µm or 505 µm for all nets except the Methot, which was 1000 µm. All nets include a flowmeter to give an estimate of effort however the neuston net is sampled at the surface and its flowmeter is not submerged throughout sampling, resulting in very high catch per unit effort ((number collected/volume filtered)*100; units number per 100 m³) measurements.

All samples were fixed in 5% buffered formalin seawater solution and sent to Sea Fisheries Institute's Plankton Sorting and Identification Center in Szczecin, Poland for sorting of ichthyoplankton and cephalopod paralarvae. All cephalopod specimens were placed in vials according to their cruise, station, haul, gear, and net. These specimens were cleared, photographed, and measured using the techniques outlined in Chapter Two. The index of starvation is digestive gland width to head width ratio.

For ease of data visualization, all catch data from all years was summed spatially in 20 x 20 km cells and temporally into two week bins beginning at the earliest Julian day sampled. Mantle length data were condensed into half millimeter bins using standard rounding rules (e.g. 2.251 - 2.75 mm mantle was represented by 2.5 mm bin value).

Results

In the 20 years of the study, 760 *E. dofleini* paralarvae were collected. It was found as early as January and as late as September in the Gulf of Alaska and as early as February and as late as October in the Bering Sea. The number of stations sampled and their location varied from year to year, making comparisons between regions and between seasons difficult. For ease of visualization of seasonal trends, catch per unit effort for all years was summed up in 20 x 20 km grid cells for every two weeks. The first sampling bin was the third two weeks of the year (30 January - 11 February) and consisted of very few samples along the shelfbreak in the Gulf of

Alaska and one sample near Kodiak Island; a single specimen was found south of the Shumagin Islands (Figure 3.2A). Sampling intensity and spatial extent increased during 12 - 25 February and included the Bering Sea. During this time, *Enteroctopus dofleini* was collected from over the Bering Canyon and over the shelf of the Gulf of Alaska, south of Kodiak Island (Figure 3.2B). Specimens were absent from 26 February - 26 March (Figure 3.2C & D). Sampling from 27 March - 9 April was again limited to the Gulf of Alaska; *E. dofleini* was collected from Shelikof Strait (Figure 3.2E). Sampling increased again during 9 - 22 April; *E. dofleini* was abundant in the Bering Canyon and surrounding area; it was also collected from Shelikof Strait and Amatuli Trough (Figure 3.2F). *Enteroctopus dofleini* showed an increase in abundance and spatial extent from 23 April - 6 May; highest abundances were over the Bering Canyon and Shelikof Strait (Figure 3.2G). Highest abundances were on the shelf in the Gulf of Alaska and in the Bering Canyon from 7 - 20 May (Figure 3.2H). Sampling from 21 May - 3 June was focused on the Gulf of Alaska which showed high abundances on the shelf southwest of Kodiak Island and Shelikof Strait (Figure 3.2I). Sampling was relatively low for the remainder of the year, 4 June - 21 October, and *E. dofleini* abundances were relatively low (Figures 3.2J - S). One notable exception to the relatively low abundances found from June - October was a station in September (Figure 3.2Q) which had the highest abundance found in the entire study; however this represents a station at which only two individuals were collected using very little effort.

Mantle length frequency bins ranged from 2.0 to 6.5 mm, the majority of specimens fell between 2.5 and 4.5 mm ML with a peak at 3 mm ML (Figure 3.3). Mantle length data for all individuals in the Bering Sea (Figure 3.4) and Gulf of Alaska (Figure 3.5) illustrate that hatching-sized individuals were collected from as early as February to as late as October in both regions. The range of mantle lengths is greater in the Bering Sea samples during the fall than fall-caught specimens from

the Gulf of Alaska samples.

During the study, 313 stations were sampled using the MOCNESS; 58 *E. dofleini* were collected (Table 3.1). MOCNESS sampling occurred at least once per year from 1991 through 2008, except 2000 and 2001. A subsurface maximum in abundance was found in the 50 - 100 m depth bin; 20 - 50 m was the next most abundant depth bin, followed by 0 - 20 m (Table 3.2). The deepest depth bin in which paralarvae were collected was 550 - 650 m (Figure 3.6).

Of the 760 *E. dofleini* paralarvae analyzed for starvation, as indicated by the digestive gland index (Chapter 2), during this study (Table 3.3), only a single individual met the criteria of being starved (digestive gland width to head width ratio of less than or equal to 0.50). Digestive gland index values ranged from 0.44 - 1.14 with an average of 0.78 and standard deviation of 0.075.

Discussion

The collection of *E. dofleini* from the Gulf of Alaska and Bering Sea is the longest ongoing collection published for this species. Based on the distribution and abundance data of the paralarvae, it appears that *E. dofleini* hatches in both the Bering Sea and the Gulf of Alaska (Figures 3.2F-H). In the Bering Sea, the Bering Canyon and Unimak Pass likely represent the primary hatching areas however other shelfbreak locations cannot be ruled out because sampling was limited in the Bering Sea. The Bering Sea shelf was a region of low abundances and likely is not an area where *E. dofleini* are hatched.

The Gulf of Alaska, on the other hand, was well sampled and the highest abundances of *E. dofleini* likely represent primary hatching areas. Unlike in the Bering Sea, in the Gulf of Alaska, *E. dofleini* paralarvae had highest abundances on the shelf, with the region southwest of Shelikof Strait having the highest values. The discrepancy between spawning/hatching locations in the Bering Sea and Gulf

of Alaska is likely due to bottom type. After mating, female *Enteroctopus dofleini* lay their eggs under large rocks. The Bering Sea shelf has a sandy or muddy substrate making it ill-suited for denning octopods; the shelf in the Gulf of Alaska has more structure suitable for denning.

Kubodera (1991) sampled at night in the northern North Pacific, primarily near the Aleutian Islands, and Bering Sea, using a neuston net, from mid-April to mid-September, 1975-1979 and reported on the distribution and abundance of *E. dofleini* paralarvae. Kubodera (1991) samples were primarily taken offshore, highest abundances were found in July. Northern North Pacific samples contained more *E. dofleini* paralarvae than did Bering Sea samples. Bering Sea specimens were primarily found at the shelfbreak and over the abyss, though two shelf stations had *E. dofleini*. Where there is geographic overlap in sampling, the results of the Kubodera (1991) are similar to those found here with the notable exception that length frequency data for the specimens collected by Kubodera (1991) showed a peak in the 4-5 mm ML bin whereas the specimens collected in this study had a peak in the 3 mm ML bin. The larger specimens collected by Kubodera (1991) may be due to the larger sampling net or the presence of larger animals at night.

The work of Kubodera (1991) is the only other publication on *E. dofleini* paralarvae in the northern North Pacific and the sample locations and times do not match up well with this study. To interpret the distribution patterns of paralarval *E. dofleini*, they will be compared to the larval distributions of the kelp greenling (*Hexagrammos decagrammus* (Pallas, 1810)) (Figure 3.7, from Matarese et al., 2003), a shallow-water fish common in the Gulf of Alaska (Mecklenburg et al., 2002), that spawns its eggs in rocky crevices and exhibits parental care (Crow et al., 1997), similar to that of *E. dofleini* (Figure 3.8). In these figures, the distribution and abundance data for all years (1979 - 2000 for kelp greenling and 1991 - 2008 for *E. dofleini*) were condensed into a single figure to illustrate areas of highest

abundances. The larval distributions of both species show highest abundances on the shelf in the Gulf of Alaska, particularly Shelikof Strait for the kelp greenling and the Shelikof Sea Valley for *E. dofleini*. The presence of *E. dofleini* paralarvae far north in the Bering Sea, and not kelp greenling is further evidence that *E. dofleini* spawns in the Bering Sea and is not just transported there via currents.

In this region, the spawning locations of many cephalopod species are unknown while fish spawning locations are relatively well understood. Based on the similarities of the larval distributions of kelp greenling and *E. dofleini*, which have similar spawning habitat and location in the Gulf of Alaska, it is possible to use similarities in larval fish distributions, with known adult spawning locations to infer the spawning locations of cephalopods for which no information is available.

The mantle length frequency data (Figure 3.3) shows that the maximum number of paralarvae collected were in the 3 mm ML bin and that the number of individuals in larger sized bins have fewer individuals. Mottet (1975) found a similarly shaped mantle length frequency result for *E. dofleini* paralarvae collected in plankton tows in Washington State. Mottet (1975) concluded that the decreasing number of individuals in the larger sized bins represented mortality and estimated that *E. dofleini* paralarvae experience 96% mortality from hatching to 6 mm ML. It is also possible that *E. dofleini* paralarvae become better at avoiding sampling gear or move out of the study area by 6 mm, which would also decrease the number collected.

Enteroctopus dofleini is found at near-hatching size throughout the sampling period (February - October) in the Bering Sea and Gulf of Alaska (Figures 3.4 and 3.5). The presence of hatchlings in both regions for the majority of the year supports the conclusion that spawning in *E. dofleini* occurs throughout the year. Hartwick (1983) concluded spawning occurred throughout the year with peaks in the winter off the west coast of Canada and the summer Japan. Kubodera (1991) concluded

spawning peak in the winter in the region of the Aleutian Islands.

The range of sizes collected in Bering Sea was greater than those collected in the Gulf of Alaska however this is likely due to the use of different and larger sampling gears in the Bering Sea. The *E. dofleini* paralarvae collected using a neuston net in Kubodera (1991) were larger, on average, than the specimens collected in this study. Larger sampling gears would collect more *E. dofleini* paralarvae because they filter much more water and *E. dofleini* paralarvae have a patchy distribution. At these sizes it is not expected that *E. dofleini* is able to avoid the smaller sampling gears.

Kubodera (1991) noted that vertical distribution data for this species was an important missing piece of information. Vertical distribution data are available for this study however *E. dofleini* paralarvae are rare (only 760 specimens collected in 13,000 tows) and discrete depth sampling represents a small percentage of the samples taken during this study, therefore, the vertical distribution provides limited information. For the purposes of this work, the presence of this species mostly in the upper 50 m of the water column provides insight into the relative importance of the difference environmental influences.

The single animal that met the criteria for starvation (Chapter 2) was collected on 27 April 1994 (Table 3.3). It was interesting to discover that *E. dofleini* paralarvae appear to be not starving while in the plankton. Vidal et al. (2005) found that the California market squid, *Doryteuthis opalescens* (Berry, 1911), experienced a ‘no net growth’ phase after hatching and the authors concluded that in the few days after hatching, the paralarvae use up its internal yolk sac and therefore shrink in size. After the internal yolk is exhausted, the paralarvae begins to grow. The paralarvae feeds throughout this period but feeding seems not to influence size until after the internal yolk is exhausted. *Enteroctopus dofleini* paralarvae exhibited a similar ‘no net growth’ phase however, while *D. opalescens* completed this phase in 10 days, *E.*

dofleini took over three weeks (Chapter 2). It is likely that the majority of specimens from the archive were still within the period of feeding off internal yolks and therefore could not be starving. The period of time that newly hatched paralarvae can survive off the internal yolk sac would be extended during colder years since the metabolic demands would be decreased. This may be the primary reason why *E. dofleini* is able to hatch year round. In the winter, when food is not available, colder water temperatures would allow the paralarvae to survive longer on their internal yolk sac.

Conclusions

Enteroctopus dofleini paralarvae were collected as bycatch in ichthyoplankton surveys. Samples were collected using a variety of plankton nets which were designed and employed to do address a variety of different research questions. For these reasons, drawing strong conclusions about the data are difficult however the results further our understanding of this organism and provide a foundation on which to conduct future work.

This works provides strong evidence for spawning/hatching of *E. dofleini* in the Bering Sea. It was found at hatchling size from February to October at the shelfbreak in the Bering Sea and on the shelf in the Gulf of Alaska, with a peak in hatching in April and May. Discrete depth sampling reveals that it is found throughout the water column but mostly in the upper 100 m. In the size range collected by plankton sampling devices, *E. dofleini* may be still utilizing its internal yolk sac for survival.

Table 3.1. *Enteroctopus dofleini* paralarvae collected by MOCNESS.

Year	HaulID	Date	JulianDay	MinDepth	MaxDepth	BIN	Region	NoCollected
1991	3MF91 G109A 1 MOC1 4	5/10/91	130	45	60	-50	GOA	1
1991	3MF91 G124A 1 MOC1 1	5/13/91	133	0	15	0	GOA	1
1991	3MF91 G125A 1 MOC1 1	5/13/91	133	1	30	0	GOA	1
1991	3MF91 G125A 1 MOC1 3	5/13/91	133	30	37	-20	GOA	1
1991	3MF91 G126A 1 MOC1 1	5/13/91	133	1	15	0	GOA	1
1991	3MF91 G126A 1 MOC1 3	5/13/91	133	30	46	-20	GOA	1
1991	3MF91 G126A 1 MOC1 5	5/13/91	133	64	78	-50	GOA	1
1991	3MF91 G126A 1 MOC1 6	5/13/91	133	78	119	-50	GOA	1
1991	3MF91 G128A 1 MOC1 3	5/14/91	134	50	81	-50	GOA	2
1991	3MF91 G128A 1 MOC1 1	5/14/91	134	1	24	0	GOA	1
1991	3MF91 G128A 1 MOC1 5	5/14/91	134	119	139	-100	GOA	1
1992	3MF92 G172A 1 MOC1 2	5/12/92	133	80	100	-50	GOA	2
1993	3MF93 62 2 MOC1 4	4/21/93	111	97	195	-100	BS	1
1993	3MF93 91 12 MOC1 7	4/24/93	114	45	73	-50	BS	1
1993	3MF93 92 12 MOC1 3	4/25/93	115	86	117	-50	BS	1
1993	3MF93 92 12 MOC1 6	4/25/93	115	26	43	-20	BS	1
1993	3MF93 92 13 MOC1 3	4/25/93	115	87	121	-100	BS	1
1993	3MF93 92 13 MOC1 4	4/25/93	115	75	87	-50	BS	1
1993	3MF93 92 2 MOC1 4	4/25/93	115	68	84	-50	BS	1
1993	3MF93 92 2 MOC1 7	4/25/93	115	28	41	-20	BS	1
1993	4MF93 187 2 MOC1 8	5/15/93	135	20	40	-20	GOA	1
1993	4MF93 187 2 MOC1 9	5/15/93	135	0	20	0	GOA	1
1994	4MF94 135 1 MOC1 2	4/27/94	117	148	188	-100	BS	1
1995	7MF95 21 9 MOC1 2	5/5/95	125	41	50	-20	BS	1
1996	6MF96 105 1 MOC1 7	5/8/96	129	25	40	-20	GOA	1
1996	6MF96 153 1 MOC1 7	5/11/96	132	23	38	-20	GOA	1
1996	10MF96 48 2 MOC1 5	9/9/96	253	11	21	0	BS	1
1996	10MF96 71 3 MOC1 3	9/11/96	255	9	20	0	BS	1
1996	10MF96 102 18 MOC1 5	9/14/96	258	11	21	0	BS	1
1996	10MF96 102 27 MOC1 5	9/15/96	259	11	19	0	BS	1
1998	4MF98 71 1 MOC1 3	5/7/98	127	55	75	-50	GOA	2
2002	5MF02 1 8 MOC1 6	9/9/02	252	0	20	0	GOA	1
2003	1HX03 83 1 MOC1 3	5/1/03	121	61	81	-50	GOA	1
2003	1HX03 132 1 MOC1 7	5/4/03	124	21	41	-20	GOA	1
2003	1HX03 136 1 MOC1 6	5/5/03	125	20	40	-20	GOA	1
2003	1HX03 267 1 MOC1 7	5/12/03	132	0	10	0	GOA	1
2003	1HX03 309 1 MOC1 7	5/14/03	134	0	11	0	GOA	1
2003	1HX03 319 1 MOC1 3	5/14/03	134	82	102	-50	GOA	1
2003	1HX03 319 1 MOC1 6	5/14/03	134	21	42	-20	GOA	1
2003	1HX03 324 1 MOC1 5	5/14/03	134	41	62	-50	GOA	1
2003	2HX03 116 1 MOC1 2	7/26/03	207	543	649	-500	GOA	1
2003	2HX03 159 1 MOC1 2	7/28/03	209	80	99	-50	GOA	1
2004	7MF04 2 11 MOC1 2	9/10/04	254	70	82	-50	GOA	1
2006	3MF06 5 5 MOC1 5	5/9/06	129	40	50	-20	BS	1
2006	3MF06 8 4 MOC1 3	5/10/06	130	101	199	-100	BS	1
2006	3MF06 8 4 MOC1 4	5/10/06	130	50	101	-50	BS	1
2006	3MF06 24 4 MOC1 5	5/12/06	132	40	50	-20	BS	1
2006	3MF06 34 4 MOC1 4	5/13/06	133	50	100	-50	BS	2
2006	3MF06 34 4 MOC1 5	5/13/06	133	40	50	-20	BS	1
2006	3MF06 44 4 MOC1 2	5/14/06	134	50	103	-50	BS	1
2006	3MF06 51 4 MOC1 5	5/15/06	135	20	30	-20	BS	1
2006	6MF06 69 5 MOC1 4	9/20/06	263	50	100	-50	BS	1
2006	6MF06 75 4 MOC1 6	9/21/06	264	29	40	-20	BS	1
2008	1MF08 12 3 MOC1 2	2/19/08	50	297	389	-300	BS	1

Table 3.2. Summary of *Enteroctopus dofleini* collected by MOCNESS.

DepthBin	NoCollected
0	12
-20	16
-50	23
-100	5
-200	0
-300	1
-400	0
-500	1

Table 3.3. Digestive gland index for all *Enteroctopus dofleini* collected from 1991 to 2008. * denotes specimens that met criteria of starvation.

year	HaulID	Date	ML	DGI
1991	2MF91 G072A 1 60BON 1	22-Apr-91	4.59	0.84
1991	2MF91 G123A 1 60BON 1	26-Apr-91	2.57	0.67
1991	2MF91 G118A 1 60BON 1	26-Apr-91	3.15	0.79
1991	3MF91 G001A 1 60BON 1	1-May-91	3.57	0.69
1991	3MF91 G002A 1 60BON 1	1-May-91	2.88	0.73
1991	3MF91 G025A 1 60BON 1	3-May-91	2.82	0.81
1991	3MF91 G034A 1 60BON 1	4-May-91	2.71	0.82
1991	3MF91 G051A 1 60BON 1	5-May-91	2.63	0.75
1991	3MF91 G062A 1 60BON 1	6-May-91	2.69	0.72
1991	3MF91 G063A 1 60BON 1	6-May-91	3.46	0.80
1991	3MF91 G072A 1 60BON 1	7-May-91	3.07	0.66
1991	3MF91 G079A 1 60BON 1	7-May-91	3.07	0.71
1991	3MF91 G079A 1 60BON 1	7-May-91	3.02	0.79
1991	3MF91 G100A 1 60BON 1	9-May-91	3.17	0.74
1991	3MF91 G098A 1 60BON 1	9-May-91	3.26	0.76
1991	3MF91 G107A 1 60BON 1	10-May-91	2.90	0.85
1991	3MF91 G109A 1 MOC1 4	10-May-91	2.74	0.87
1991	3MF91 G121A 1 60BON 1	12-May-91	2.89	0.70
1991	3MF91 G126A 1 MOC1 1	13-May-91	3.35	0.69
1991	3MF91 G126A 1 MOC1 3	13-May-91	3.01	0.72
1991	3MF91 G126A 1 MOC1 5	13-May-91	2.80	0.72
1991	3MF91 G126A 1 MOC1 6	13-May-91	3.19	0.73
1991	3MF91 G125A 1 MOC1 3	13-May-91	2.81	0.75
1991	3MF91 G124A 1 MOC1 1	13-May-91	2.87	0.79
1991	3MF91 G125A 1 MOC1 1	13-May-91	2.55	0.93
1991	3MF91 G128A 1 MOC1 3	14-May-91	3.46	0.64
1991	3MF91 G128A 1 MOC1 3	14-May-91	3.40	0.65
1991	3MF91 G128A 1 MOC1 1	14-May-91	2.80	0.65
1991	3MF91 G128A 1 MOC1 5	14-May-91	2.60	0.70
1991	4MF91 G015A 1 60BON 1	20-May-91	2.66	0.78
1991	4MF91 G033A 1 60BON 1	21-May-91	3.10	0.84
1991	4MF91 G049A 1 60BON 1	22-May-91	3.31	0.66
1991	4MF91 G065A 1 60BON 1	23-May-91	3.05	0.72
1991	4MF91 G072A 1 60BON 1	23-May-91	3.45	0.77
1991	4MF91 G064A 1 60BON 1	23-May-91	3.18	0.81
1991	4MF91 G091A 1 60BON 1	24-May-91	2.80	0.64
1991	4MF91 G093A 1 60BON 1	25-May-91	3.18	0.91
1991	4MF91 G097A 1 60BON 1	25-May-91	2.94	0.99
1991	5MF91 G041A 1 METH 1	28-Jul-91	3.70	0.87
1991	5MF91 G041A 1 METH 1	28-Jul-91	3.47	0.95
1991	5MF91 G066A 1 METH 1	30-Jul-91	3.60	0.85
1991	5MF91 G066A 1 METH 1	30-Jul-91	4.45	0.86
1991	5MF91 G066A 1 METH 1	30-Jul-91	3.53	0.92
1992	1MF92 G016A 1 60BON 1	6-Apr-92	3.45	0.75
1992	1MF92 G029A 1 60BON 1	6-Apr-92	3.23	0.81
1992	1MF92 G043A 1 60BON 1	7-Apr-92	2.82	0.78
1992	1MF92 G057A 1 60BON 1	7-Apr-92	2.45	0.85
1992	1MF92 G051A 1 60BON 1	7-Apr-92	3.12	0.91
1992	1MF92 G057A 1 60BON 1	7-Apr-92	3.25	0.95
1992	1MF92 G080A 1 60BON 1	8-Apr-92	3.16	0.82
1992	1MF92 G091A 1 60BON 1	9-Apr-92	2.67	0.70
1992	2MF92 G037A 1 60BON 1	18-Apr-92	3.28	0.71
1992	3MF92 G013A 1 60BON 2	2-May-92	2.79	0.68
1992	3MF92 G011A 1 60BON 2	2-May-92	2.94	0.73
1992	3MF92 G011A 1 60BON 2	2-May-92	3.27	0.79
1992	3MF92 G021A 1 60BON 1	3-May-92	3.45	0.72
1992	3MF92 G024A 1 60BON 1	3-May-92	2.76	0.73
1992	3MF92 G016A 1 60BON 1	3-May-92	3.24	0.84

Table 3.3 continued.

1992	3MF92 G032A 1 60BON 1	4-May-92	3.70	0.84
1992	3MF92 G058A 1 60BON 2	5-May-92	2.69	0.74
1992	3MF92 G066A 1 60BON 1	6-May-92	3.29	0.76
1992	3MF92 G079A 1 60BON 1	6-May-92	3.44	0.78
1992	3MF92 G065A 1 60BON 2	6-May-92	3.69	0.80
1992	3MF92 G066A 1 60BON 1	6-May-92	2.54	0.86
1992	3MF92 G103A 1 60BON 1	8-May-92	3.57	0.71
1992	3MF92 G094A 1 60BON 1	8-May-92	3.24	0.74
1992	3MF92 G104A 1 60BON 1	8-May-92	3.65	0.77
1992	3MF92 G103A 1 60BON 1	8-May-92	2.74	0.81
1992	3MF92 G109A 1 60BON 1	9-May-92	3.26	0.70
1992	3MF92 G135A 1 60BON 1	10-May-92	3.10	0.74
1992	3MF92 G137B 1 TUCK1 1	10-May-92	3.09	0.77
1992	3MF92 G172A 1 MOC1 2	12-May-92	4.38	0.75
1992	3MF92 G172A 1 MOC1 2	12-May-92	4.25	0.78
1992	3MF92 G195A 1 60BON 1	13-May-92	2.97	0.73
1992	4MF92 G015A 1 60BON 1	19-May-92	3.88	0.90
1992	4MF92 G040A 1 60BON 1	20-May-92	2.86	0.77
1992	4MF92 G055A 1 60BON 1	21-May-92	3.31	0.78
1992	4MF92 G079A 1 60BON 1	22-May-92	2.66	0.74
1992	4MF92 G122A 1 60BON 1	25-May-92	3.38	0.72
1992	4MF92 G122A 1 60BON 1	25-May-92	4.57	0.73
1992	4MF92 G131A 1 60BON 1	26-May-92	3.49	0.74
1992	4MF92 G126A 1 60BON 1	26-May-92	3.60	0.74
1992	4MF92 G126A 1 60BON 1	26-May-92	3.36	0.75
1992	4MF92 G126A 1 60BON 1	26-May-92	3.54	0.78
1992	4MF92 G145A 1 60BON 1	27-May-92	3.90	0.80
1992	4MF92 G145A 1 60BON 1	27-May-92	3.50	0.91
1992	4MF92 G145A 1 60BON 1	27-May-92	3.50	0.91
1992	4MF92 G156A 1 60BON 1	28-May-92	3.64	0.72
1992	4MF92 G153D 1 60BON 1	28-May-92	2.78	0.77
1992	4MF92 G157A 1 60BON 1	28-May-92	3.88	0.80
1992	1MM92 2 1 METH 1	11-Jul-92	4.33	0.78
1992	1MM92 2 1 METH 1	11-Jul-92	4.29	0.94
1992	1MM92 3 1 METH 1	12-Jul-92	4.23	0.69
1992	1MM92 3 1 METH 1	12-Jul-92	2.97	0.73
1992	1MM92 3 1 METH 1	12-Jul-92	4.18	0.75
1992	1MM92 3 1 METH 1	12-Jul-92	4.64	0.79
1992	1MM92 3 1 METH 1	12-Jul-92	3.63	0.80
1992	1MM92 3 1 METH 1	12-Jul-92	5.14	0.80
1992	1MM92 3 1 METH 1	12-Jul-92	3.68	0.88
1992	1MM92 4 1 METH 1	14-Jul-92	3.58	0.68
1992	1MM92 5 1 METH 1	14-Jul-92	2.72	0.75
1992	1MM92 6 1 METH 1	17-Jul-92	3.82	0.83
1992	1MM92 13 1 METH 1	21-Jul-92	5.88	0.85
1993	2MF93 52 1 60BON 1	7-Apr-93	2.96	0.76
1993	2MF93 58 1 60BON 1	8-Apr-93	3.29	0.72
1993	2MF93 66 1 60BON 1	8-Apr-93	2.61	0.75
1993	2MF93 95 1 60BON 1	9-Apr-93	3.33	0.80
1993	2MF93 113 1 60BON 1	10-Apr-93	3.23	0.64
1993	2MF93 112 1 60BON 1	10-Apr-93	2.93	0.69
1993	2MF93 118 1 SLED 1	10-Apr-93	3.57	0.69
1993	2MF93 106 1 60BON 1	10-Apr-93	2.99	0.76
1993	2MF93 120 2 60BON 1	11-Apr-93	3.07	0.79
1993	3MF93 10 1 60BON 1	16-Apr-93	3.27	0.64
1993	3MF93 7 5 TUCK1 2	16-Apr-93	2.92	0.67
1993	3MF93 7 8 TUCK1 2	16-Apr-93	3.21	0.67
1993	3MF93 10 1 60BON 1	16-Apr-93	2.93	0.74
1993	3MF93 7 8 TUCK1 2	16-Apr-93	3.57	0.74

1993	3MF93 7 8 TUCK1 2	16-Apr-93	2.61	0.77
1993	3MF93 7 5 TUCK1 2	16-Apr-93	3.38	0.79
1993	3MF93 7 5 TUCK1 2	16-Apr-93	3.74	0.81
1993	3MF93 22 1 60BON 1	17-Apr-93	3.85	0.63
1993	3MF93 22 1 60BON 1	17-Apr-93	2.98	0.71
1993	3MF93 21 1 60BON 1	17-Apr-93	3.13	0.77
1993	3MF93 24 1 60BON 1	18-Apr-93	3.10	0.71
1993	3MF93 25 1 60BON 1	18-Apr-93	2.69	0.73
1993	3MF93 24 1 60BON 1	18-Apr-93	3.29	0.79
1993	3MF93 24 1 60BON 1	18-Apr-93	2.95	0.91
1993	3MF93 45 1 60BON 1	19-Apr-93	3.23	0.74
1993	3MF93 38 1 60BON 1	19-Apr-93	3.01	0.84
1993	3MF93 45 1 60BON 1	19-Apr-93	3.07	0.93
1993	3MF93 62 2 MOC1 4	21-Apr-93	3.16	0.74
1993	3MF93 61 1 60BON 1	21-Apr-93	3.75	0.85
1993	3MF93 91 12 MOC1 7	24-Apr-93	3.42	0.70
1993	3MF93 92 12 MOC1 3	25-Apr-93	2.60	0.81
1993	3MF93 93 1 60BON 1	25-Apr-93	3.45	0.81
1993	3MF93 92 12 MOC1 6	25-Apr-93	3.11	0.82
1993	3MF93 92 13 MOC1 4	25-Apr-93	3.81	0.84
1993	3MF93 92 2 MOC1 4	25-Apr-93	4.92	0.84
1993	3MF93 92 2 MOC1 7	25-Apr-93	3.28	0.85
1993	3MF93 92 13 MOC1 3	25-Apr-93	3.22	0.86
1993	3MF93 115 1 60BON 1	29-Apr-93	3.44	0.78
1993	3MF93 114 1 60BON 1	29-Apr-93	3.01	0.83
1993	3MF93 114 1 60BON 1	29-Apr-93	2.88	0.84
1993	3MF93 121 1 60BON 1	30-Apr-93	3.12	0.68
1993	3MF93 124 1 60BON 1	30-Apr-93	3.27	0.74
1993	3MF93 122 1 60BON 1	30-Apr-93	2.90	0.75
1993	3MF93 124 1 60BON 1	30-Apr-93	3.61	0.77
1993	4MF93 3 1 60BON 1	3-May-93	2.83	0.69
1993	4MF93 27 1 60BON 1	5-May-93	2.94	0.74
1993	4MF93 29 1 60BON 1	5-May-93	2.92	0.78
1993	4MF93 68 1 60BON 1	7-May-93	3.71	0.73
1993	4MF93 70 1 60BON 1	7-May-93	2.98	0.80
1993	4MF93 70 1 60BON 1	7-May-93	3.22	0.82
1993	4MF93 79 1 60BON 1	8-May-93	3.33	0.72
1993	4MF93 93 1 60BON 1	9-May-93	3.42	0.80
1993	4MF93 135 1 60BON 1	11-May-93	3.31	0.74
1993	4MF93 156 1 60BON 1	13-May-93	3.18	0.70
1993	4MF93 159 1 60BON 1	13-May-93	2.84	0.75
1993	4MF93 159 1 60BON 1	13-May-93	3.24	0.89
1993	4MF93 187 2 MOC1 9	15-May-93	2.71	0.74
1993	4MF93 187 2 MOC1 8	15-May-93	3.43	0.82
1993	5MF93 31 1 60BON 1	28-May-93	3.32	0.75
1993	5MF93 41 1 60BON 1	28-May-93	3.01	0.76
1993	5MF93 38 2 60BON 1	28-May-93	3.21	0.81
1993	5MF93 63 1 60BON 1	29-May-93	3.10	0.69
1993	5MF93 61 1 60BON 1	29-May-93	3.00	0.71
1993	5MF93 59 5 60BON 1	29-May-93	3.24	0.81
1993	5MF93 49 1 60BON 1	29-May-93	2.93	0.82
1993	5MF93 76 5 METH 1	30-May-93	2.95	0.57
1993	5MF93 76 5 METH 1	30-May-93	2.80	0.67
1993	5MF93 68 1 60BON 1	30-May-93	2.97	0.69
1993	5MF93 79 2 METH 1	30-May-93	3.50	0.73
1993	5MF93 66 3 60BON 1	30-May-93	3.11	0.74
1993	5MF93 79 2 METH 1	30-May-93	3.67	0.77
1993	5MF93 79 2 METH 1	30-May-93	3.24	0.86
1993	5MF93 79 2 METH 1	30-May-93	3.80	0.89

1993	5MF93 79 2 METH 1	30-May-93	3.40	0.91
1993	5MF93 89 11 METH 1	31-May-93	3.15	0.76
1993	5MF93 93 1 60BON 1	1-Jun-93	3.70	0.72
1993	5MF93 93 1 60BON 1	1-Jun-93	3.82	0.72
1993	5MF93 93 1 60BON 1	1-Jun-93	3.68	0.76
1993	5MF93 93 1 60BON 1	1-Jun-93	3.65	0.76
1993	5MF93 93 1 60BON 1	1-Jun-93	3.82	0.83
1994	4MF94 7 1 60BON 1	15-Apr-94	3.02	0.66
1994	4MF94 14 1 60BON 1	16-Apr-94	3.36	0.71
1994	4MF94 24 1 60BON 1	17-Apr-94	4.51	0.78
1994	4MF94 15 2 60BON 1	17-Apr-94	3.90	0.79
1994	4MF94 40 1 60BON 1	19-Apr-94	6.65	0.69
1994	4MF94 44 2 60BON 1	19-Apr-94	3.24	0.73
1994	4MF94 54 1 60BON 1	20-Apr-94	3.08	0.69
1994	4MF94 50 1 60BON 1	20-Apr-94	3.24	0.80
1994	4MF94 63 2 60BON 1	21-Apr-94	2.99	0.87
1994	4MF94 105 2 TUCK1 1	23-Apr-94	3.46	0.75
1994	4MF94 88 2 TUCK1 1	23-Apr-94	3.44	0.83
1994	4MF94 135 1 MOC1 2	27-Apr-94	2.58	0.44 *
1994	4MF94 139 5 60BON 1	27-Apr-94	3.64	0.71
1994	4MF94 135 2 TUCK1 2	27-Apr-94	3.11	0.78
1994	4MF94 135 2 TUCK1 1	27-Apr-94	3.32	0.78
1994	4MF94 145 4 60BON 1	28-Apr-94	3.41	0.65
1994	4MF94 146 1 60BON 1	28-Apr-94	3.64	0.69
1994	4MF94 145 4 60BON 1	28-Apr-94	4.24	0.69
1994	4MF94 146 2 60BON 1	28-Apr-94	3.47	0.72
1994	4MF94 145 6 60BON 1	28-Apr-94	3.10	0.72
1994	4MF94 147 6 60BON 1	28-Apr-94	3.38	0.73
1994	4MF94 147 4 60BON 1	28-Apr-94	3.11	0.73
1994	4MF94 147 4 60BON 1	28-Apr-94	2.45	0.74
1994	4MF94 145 4 60BON 1	28-Apr-94	3.54	0.74
1994	4MF94 144 3 60BON 1	28-Apr-94	3.64	0.75
1994	4MF94 143 4 60BON 1	28-Apr-94	3.26	0.75
1994	4MF94 145 6 60BON 1	28-Apr-94	2.90	0.76
1994	4MF94 147 4 60BON 1	28-Apr-94	3.01	0.76
1994	4MF94 144 3 60BON 1	28-Apr-94	3.60	0.77
1994	4MF94 144 2 60BON 1	28-Apr-94	4.31	0.79
1994	4MF94 141 4 60BON 1	28-Apr-94	3.04	0.81
1994	4MF94 142 3 60BON 1	28-Apr-94	3.46	0.82
1994	4MF94 144 3 60BON 1	28-Apr-94	3.56	0.83
1994	4MF94 146 3 60BON 1	28-Apr-94	3.06	0.87
1994	4MF94 149 5 60BON 1	29-Apr-94	2.92	0.64
1994	4MF94 148 1 60BON 1	29-Apr-94	3.63	0.68
1994	4MF94 148 1 60BON 1	29-Apr-94	3.15	0.70
1994	4MF94 148 2 60BON 1	29-Apr-94	2.91	0.72
1994	4MF94 151 6 60BON 1	29-Apr-94	3.55	0.72
1994	4MF94 149 7 60BON 1	29-Apr-94	2.88	0.72
1994	4MF94 152 1 60BON 1	29-Apr-94	3.32	0.73
1994	4MF94 149 7 60BON 1	29-Apr-94	3.13	0.73
1994	4MF94 149 7 60BON 1	29-Apr-94	3.46	0.76
1994	4MF94 148 3 60BON 1	29-Apr-94	3.53	0.76
1994	4MF94 149 5 60BON 1	29-Apr-94	2.93	0.77
1994	4MF94 148 1 60BON 1	29-Apr-94	3.17	0.78
1994	4MF94 152 3 60BON 1	29-Apr-94	2.78	0.80
1994	4MF94 148 3 60BON 1	29-Apr-94	3.19	0.84
1994	4MF94 154 3 60BON 1	30-Apr-94	3.21	0.69
1994	5MF94 23 1 60BON 1	5-May-94	2.90	0.71
1994	5MF94 43 1 60BON 1	6-May-94	2.67	0.75
1994	5MF94 103 2 TUCK1 1	10-May-94	2.71	0.70

1994	6MF94 29 1 60BON 1	25-May-94	3.70	0.80
1994	6MF94 48 1 60BON 1	26-May-94	2.98	0.74
1994	6MF94 62 1 60BON 1	27-May-94	2.76	0.78
1994	6MF94 106 1 60BON 1	30-May-94	2.63	0.76
1994	7MF94 6 1 METH 1	23-Jul-94	3.81	0.87
1994	1SU94 69 2 60BON 1	8-Sep-94	4.15	0.80
1994	1SU94 68 2 60BON 1	8-Sep-94	3.11	0.86
1995	6MF95 150 11 TUCK1 1	1-May-95	3.17	0.79
1995	6MF95 150 7 TUCK1 2	1-May-95	2.75	0.85
1995	7MF95 4 2 60BON 1	4-May-95	3.16	0.73
1995	7MF95 21 9 MOC1 2	5-May-95	2.63	0.67
1995	7MF95 97 2 60BON 1	13-May-95	3.24	0.68
1995	7MF95 116 1 60BON 1	14-May-95	3.30	0.81
1995	7MF95 158 2 60BON 1	18-May-95	3.04	0.78
1995	7MF95 158 2 60BON 1	18-May-95	3.57	0.85
1995	8MF95 8 1 60BON 1	22-May-95	3.02	0.79
1995	8MF95 20 1 60BON 1	23-May-95	3.35	0.75
1995	8MF95 18 1 60BON 1	23-May-95	3.17	0.81
1995	8MF95 44 2 60BON 2	24-May-95	3.10	0.73
1995	8MF95 57 2 60BON 2	25-May-95	3.24	0.72
1995	8MF95 51 2 METH 1	25-May-95	3.65	0.81
1995	8MF95 51 2 METH 1	25-May-95	3.37	0.90
1995	8MF95 63 1 60BON 1	26-May-95	3.29	0.70
1995	8MF95 80 1 60BON 1	27-May-95	3.46	1.05
1996	1DI96 1 2 60BON 1	26-Apr-96	2.76	0.71
1996	1DI96 1 2 60BON 1	26-Apr-96	2.92	0.75
1996	1DI96 29 2 60BON 1	28-Apr-96	3.53	0.69
1996	1DI96 19 3 60BON 1	28-Apr-96	3.68	0.80
1996	1DI96 38 3 60BON 1	29-Apr-96	3.20	0.78
1996	1DI96 53 1 60BON 1	30-Apr-96	3.32	0.73
1996	1DI96 59 1 60BON 1	1-May-96	2.94	0.73
1996	1DI96 61 1 60BON 1	1-May-96	2.86	0.77
1996	1DI96 59 1 60BON 1	1-May-96	3.48	0.83
1996	6MF96 5 2 60BON 1	2-May-96	3.12	0.72
1996	1DI96 78 1 60BON 1	2-May-96	3.24	0.79
1996	6MF96 21 1 60BON 1	3-May-96	3.33	0.66
1996	6MF96 18 2 60BON 1	3-May-96	3.19	0.75
1996	6MF96 18 2 60BON 1	3-May-96	3.09	0.77
1996	1DI96 104 1 60BON 1	3-May-96	3.30	0.77
1996	6MF96 16 2 60BON 1	3-May-96	3.08	0.78
1996	6MF96 21 1 60BON 1	3-May-96	3.58	0.79
1996	1DI96 93 1 60BON 1	3-May-96	2.71	0.81
1996	6MF96 31 2 60BON 1	4-May-96	3.54	0.76
1996	6MF96 31 1 60BON 1	4-May-96	3.47	0.78
1996	1DI96 119 1 60BON 1	4-May-96	2.90	0.79
1996	6MF96 30 4 60BON 2	4-May-96	3.76	0.80
1996	1DI96 115 1 60BON 1	4-May-96	3.00	0.80
1996	6MF96 30 3 60BON 2	4-May-96	3.63	0.82
1996	6MF96 45 1 60BON 1	5-May-96	2.60	0.69
1996	6MF96 53 1 60BON 1	5-May-96	3.24	0.75
1996	1DI96 144 1 60BON 1	5-May-96	3.18	0.79
1996	6MF96 64 1 60BON 1	6-May-96	3.04	0.75
1996	1DI96 149 1 60BON 1	6-May-96	2.76	0.82
1996	6MF96 94 1 60BON 1	7-May-96	3.40	0.68
1996	6MF96 94 1 60BON 1	7-May-96	2.87	0.70
1996	6MF96 94 1 60BON 1	7-May-96	2.64	0.71
1996	6MF96 94 1 60BON 1	7-May-96	3.63	0.74
1996	6MF96 86 2 60BON 1	7-May-96	2.71	0.86
1996	6MF96 105 1 MOC1 7	8-May-96	2.92	0.91

1996	6MF96 113 2 60BON 1	9-May-96	3.21	0.74
1996	6MF96 120 2 60BON 1	9-May-96	3.35	0.78
1996	6MF96 153 1 MOC1 7	11-May-96	3.42	0.74
1996	6MF96 160 1 60BON 2	11-May-96	3.39	0.76
1996	6MF96 164 2 60BON 1	11-May-96	3.13	0.94
1996	6MF96 175 1 60BON 2	12-May-96	3.25	0.72
1996	6MF96 174 1 60BON 1	12-May-96	3.54	0.77
1996	6MF96 187 1 60BON 1	13-May-96	3.75	0.74
1996	6MF96 187 1 60BON 1	13-May-96	2.74	0.77
1996	6MF96 192 1 60BON 2	13-May-96	3.80	0.78
1996	6MF96 187 1 60BON 1	13-May-96	3.34	0.78
1996	6MF96 191 1 60BON 2	13-May-96	3.47	0.80
1996	6MF96 200 1 60BON 1	14-May-96	3.48	0.75
1996	6MF96 194 1 60BON 1	14-May-96	2.91	0.79
1996	6MF96 201 1 60BON 1	14-May-96	3.29	0.86
1996	6MF96 210 2 60BON 1	15-May-96	3.16	0.71
1996	6MF96 210 2 60BON 1	15-May-96	3.99	0.78
1996	8MF96 3 1 60BON 1	24-May-96	3.58	0.71
1996	8MF96 2 1 60BON 1	24-May-96	3.49	0.81
1996	8MF96 2 1 60BON 1	24-May-96	3.46	0.87
1996	8MF96 32 1 60BON 1	26-May-96	3.12	0.76
1996	8MF96 25 1 60BON 1	26-May-96	3.56	0.82
1996	8MF96 44 1 60BON 1	27-May-96	3.43	0.72
1996	8MF96 72 1 60BON 1	28-May-96	3.17	0.74
1996	8MF96 63 1 60BON 1	28-May-96	2.82	0.75
1996	8MF96 62 1 60BON 1	28-May-96	2.90	0.77
1996	8MF96 85 1 60BON 1	29-May-96	3.50	0.80
1996	8MF96 91 1 60BON 1	29-May-96	3.43	0.83
1996	8MF96 81 1 60BON 1	29-May-96	3.35	0.83
1996	8MF96 110 1 60BON 1	30-May-96	4.06	0.81
1996	8MF96 99 1 60BON 1	30-May-96	3.01	0.82
1996	8MF96 120 2 60BON 1	31-May-96	4.19	0.89
1997	5MF97 1 2 60BON 1	16-Apr-97	2.75	0.82
1997	5MF97 15 2 60BON 1	18-Apr-97	2.90	0.78
1997	5MF97 15 2 60BON 1	18-Apr-97	4.00	0.86
1997	5MF97 69 2 60BON 1	25-Apr-97	2.76	0.70
1997	5MF97 69 2 60BON 1	25-Apr-97	3.14	0.72
1997	5MF97 65 2 60BON 1	25-Apr-97	2.87	0.76
1997	5MF97 69 2 60BON 1	25-Apr-97	3.26	0.77
1997	5MF97 69 2 60BON 1	25-Apr-97	2.68	0.78
1997	5MF97 68 3 60BON 1	25-Apr-97	3.09	0.79
1997	8MF97 17 1 60BON 1	25-May-97	3.15	0.70
1997	8MF97 36 1 60BON 1	26-May-97	2.71	0.69
1997	8MF97 41 1 60BON 1	26-May-97	3.00	0.70
1997	8MF97 30 1 60BON 1	26-May-97	2.92	0.71
1997	8MF97 41 1 60BON 1	26-May-97	2.90	0.72
1997	8MF97 30 1 60BON 1	26-May-97	3.62	0.73
1997	8MF97 43 1 60BON 1	27-May-97	2.99	0.72
1997	8MF97 58 1 60BON 1	27-May-97	2.49	0.79
1997	8MF97 54 1 60BON 1	27-May-97	3.52	0.88
1997	8MF97 73 1 60BON 1	28-May-97	2.96	0.71
1997	8MF97 75 1 60BON 1	28-May-97	2.84	0.78
1997	8MF97 95 1 60BON 1	29-May-97	3.27	0.72
1997	8MF97 79 1 60BON 1	29-May-97	2.83	0.76
1997	8MF97 105 1 60BON 1	30-May-97	3.76	0.71
1997	8MF97 100 1 60BON 1	30-May-97	3.64	0.89
1997	4WE97 2 2 60BON 1	1-Jul-97	3.21	0.88
1997	4WE97 67 2 60BON 1	6-Jul-97	3.19	0.90
1997	4WE97 57 1 METH 1	6-Jul-97	3.00	0.90

1997	4WE97 83 1 METH 1	8-Jul-97	3.31	0.96
1998	2MF98 24 1 60BON 1	11-Apr-98	2.43	0.85
1998	4MF98 8 1 60BON 1	3-May-98	3.85	0.74
1998	4MF98 1 4 60BON 1	3-May-98	3.06	0.75
1998	4MF98 2 1 60BON 1	3-May-98	3.27	0.79
1998	4MF98 2 1 60BON 1	3-May-98	3.46	0.79
1998	4MF98 1 4 60BON 1	3-May-98	2.93	0.80
1998	4MF98 3 1 60BON 1	3-May-98	3.30	0.80
1998	4MF98 10 1 60BON 1	3-May-98	2.69	0.89
1998	4MF98 17 1 60BON 1	4-May-98	2.80	0.71
1998	4MF98 21 1 60BON 1	4-May-98	3.28	0.75
1998	4MF98 23 1 60BON 1	4-May-98	3.76	0.77
1998	4MF98 42 1 60BON 1	5-May-98	3.77	0.73
1998	4MF98 38 1 60BON 1	5-May-98	2.85	0.73
1998	4MF98 45 1 60BON 1	5-May-98	3.29	0.74
1998	4MF98 41 1 60BON 1	5-May-98	3.66	1.14
1998	4MF98 62 1 TUCK1 1	6-May-98	2.78	0.66
1998	4MF98 63 1 TUCK1 2	6-May-98	3.40	0.73
1998	4MF98 63 1 TUCK1 2	6-May-98	3.38	0.76
1998	4MF98 58 1 TUCK1 2	6-May-98	2.68	0.84
1998	4MF98 71 1 MOC1 3	7-May-98	3.17	0.64
1998	4MF98 67 1 TUCK1 2	7-May-98	3.22	0.68
1998	4MF98 67 1 TUCK1 2	7-May-98	3.38	0.69
1998	4MF98 68 1 TUCK1 2	7-May-98	3.28	0.69
1998	4MF98 68 1 TUCK1 2	7-May-98	3.24	0.72
1998	4MF98 68 1 TUCK1 2	7-May-98	2.84	0.74
1998	4MF98 69 1 TUCK1 2	7-May-98	3.06	0.74
1998	4MF98 71 1 MOC1 3	7-May-98	3.51	0.74
1998	4MF98 69 1 TUCK1 2	7-May-98	3.40	0.77
1998	4MF98 69 1 TUCK1 2	7-May-98	3.81	0.78
1998	4MF98 76 2 60BON 1	8-May-98	2.82	0.63
1998	4MF98 82 3 60BON 1	8-May-98	3.44	0.67
1998	4MF98 77 2 60BON 1	8-May-98	2.85	0.78
1998	4MF98 87 2 60BON 1	9-May-98	2.94	0.71
1998	4MF98 90 2 60BON 1	9-May-98	2.57	0.71
1998	4MF98 93 2 60BON 1	9-May-98	3.64	0.75
1998	4MF98 93 2 60BON 1	9-May-98	3.58	0.77
1998	4MF98 93 2 60BON 1	9-May-98	3.68	0.81
1998	5MF98 2 1 60BON 1	22-May-98	3.26	0.80
1998	5MF98 27 1 60BON 1	23-May-98	2.60	0.79
1998	5MF98 27 1 60BON 1	23-May-98	2.71	0.81
1998	5MF98 21 1 60BON 2	23-May-98	3.89	0.86
1998	5MF98 36 1 60BON 1	24-May-98	3.07	0.62
1998	5MF98 42 1 60BON 1	24-May-98	3.26	0.70
1998	5MF98 40 1 60BON 1	24-May-98	2.48	0.77
1998	5MF98 42 1 60BON 1	24-May-98	3.18	0.81
1998	5MF98 56 1 TUCK1 2	25-May-98	3.24	0.73
1998	5MF98 66 1 60BON 1	25-May-98	2.82	0.74
1998	5MF98 53 1 60BON 1	25-May-98	3.73	0.89
1998	5MF98 68 2 TUCK1 2	26-May-98	3.63	0.80
1998	5MF98 68 2 TUCK1 2	26-May-98	3.65	0.81
1998	5MF98 71 2 TUCK1 2	26-May-98	3.96	0.85
1998	5MF98 101 1 60BON 1	28-May-98	3.82	0.80
1998	5MF98 101 1 60BON 1	28-May-98	4.45	0.84
1998	5MF98 102 1 60BON 1	28-May-98	3.67	0.85
1998	5MF98 115 2 TUCK1 2	29-May-98	3.45	0.69
1998	5MF98 115 2 TUCK1 2	29-May-98	3.47	0.77
1998	3WE98 6 1 METH 1	19-Jun-98	3.51	0.71
1998	3WE98 6 1 METH 1	19-Jun-98	3.31	0.87

1998	3WE98 14 1 METH 1	20-Jun-98	3.35	0.75
1998	3WE98 14 1 METH 1	20-Jun-98	3.54	0.77
1998	3WE98 12 1 METH 1	20-Jun-98	2.43	0.82
1998	3WE98 7 1 METH 1	20-Jun-98	3.38	0.84
1998	3WE98 7 1 METH 1	20-Jun-98	2.85	0.84
1998	3WE98 7 1 METH 1	20-Jun-98	2.79	0.89
1998	3WE98 7 1 METH 1	20-Jun-98	3.12	0.96
1998	3WE98 44 1 METH 1	23-Jun-98	3.78	0.91
1998	3WE98 59 1 METH 1	24-Jun-98	3.73	0.80
1998	3WE98 57 1 METH 1	24-Jun-98	4.16	0.91
1998	3WE98 50 1 METH 1	24-Jun-98	3.85	0.92
1998	3WE98 57 1 METH 1	24-Jun-98	4.29	0.93
1998	3WE98 84 1 METH 1	26-Jun-98	4.09	0.84
1998	3WE98 77 1 METH 1	26-Jun-98	4.77	0.84
1998	3WE98 77 1 METH 1	26-Jun-98	4.19	0.86
1998	3WE98 86 1 METH 1	26-Jun-98	4.10	0.87
1998	3WE98 84 1 METH 1	26-Jun-98	3.52	0.88
1998	3WE98 84 1 METH 1	26-Jun-98	4.18	0.89
1998	3WE98 89 1 METH 1	27-Jun-98	3.98	0.92
1998	3WE98 89 1 METH 1	27-Jun-98	4.63	1.01
1998	3WE98 108 1 TUCK1 1	28-Jun-98	4.18	0.86
1998	3WE98 108 1 TUCK1 1	28-Jun-98	2.90	0.90
1998	3WE98 118 1 TUCK1 2	29-Jun-98	3.79	0.82
1999	4MF99 9 1 60BON 1	19-May-99	2.82	0.66
1999	4MF99 15 1 60BON 1	19-May-99	3.82	0.71
1999	4MF99 11 1 60BON 1	19-May-99	3.85	0.72
1999	5MF99 8 1 60BON 1	22-May-99	3.00	0.59
1999	5MF99 8 1 60BON 1	22-May-99	3.33	0.71
1999	5MF99 8 1 60BON 1	22-May-99	3.40	0.86
1999	5MF99 2 1 60BON 1	22-May-99	3.43	0.86
1999	5MF99 25 1 60BON 1	23-May-99	2.57	0.70
1999	5MF99 21 1 60BON 1	23-May-99	2.77	0.76
1999	5MF99 21 1 60BON 1	23-May-99	2.52	0.78
1999	2WE99 35 1 60BON 1	25-May-99	2.96	0.80
1999	5MF99 35 1 60BON 1	26-May-99	3.04	0.68
1999	5MF99 29 1 60BON 1	26-May-99	3.66	0.71
1999	2WE99 46 1 60BON 1	26-May-99	3.13	0.78
1999	5MF99 30 1 60BON 1	26-May-99	3.40	0.78
1999	5MF99 28 1 60BON 1	26-May-99	3.04	0.83
1999	2WE99 68 1 60BON 1	27-May-99	2.94	0.65
1999	2WE99 66 1 60BON 1	27-May-99	2.78	0.75
1999	5MF99 43 1 60BON 1	27-May-99	2.99	0.79
1999	5MF99 54 2 MOC1 7	27-May-99	4.03	0.80
1999	5MF99 54 2 MOC1 4	27-May-99	2.82	0.80
1999	2WE99 65 1 60BON 1	27-May-99	3.42	0.83
1999	5MF99 70 1 60BON 1	28-May-99	3.01	0.63
1999	2WE99 95 1 60BON 1	28-May-99	3.99	0.66
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1999	2WE99 95 1 60BON 1	28-May-99	3.55	0.70
1999	2WE99 89 1 60BON 1	28-May-99	2.92	0.72
1999	2WE99 95 1 60BON 1	28-May-99	3.16	0.74
1999	5MF99 67 1 60BON 1	28-May-99	3.65	0.76
1999	2WE99 87 1 60BON 2	28-May-99	3.18	0.76
1999	2WE99 80 1 60BON 1	28-May-99	3.27	0.77
1999	2WE99 95 1 60BON 1	28-May-99	3.16	0.79
1999	2WE99 93 1 60BON 1	28-May-99	4.07	0.79
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1999	2WE99 95 1 60BON 1	28-May-99	2.95	0.87

1999	2WE99 105 1 60BON 1	29-May-99	3.04	0.73
1999	2WE99 113 1 60BON 1	30-May-99	3.27	0.78
1999	2WE99 123 1 60BON 1	31-May-99	3.05	0.69
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1999	2WE99 167 1 60BON 1	2-Jun-99	2.90	0.70
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2000	6MF00 19 1 60BON 1	27-May-00	3.05	0.82
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2000	6MF00 51 1 60BON 1	29-May-00	3.18	0.75
2000	6MF00 55 1 60BON 1	29-May-00	3.29	0.78
2000	6MF00 55 1 60BON 1	29-May-00	3.54	0.89
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2000	6MF00 69 1 60BON 1	30-May-00	4.16	0.85
2000	6MF00 94 1 60BON 1	31-May-00	3.59	0.77
2000	6MF00 93 1 60BON 1	31-May-00	3.71	0.80
2000	6MF00 115 1 60BON 1	1-Jun-00	3.34	0.80
2000	6MF00 104 1 60BON 1	1-Jun-00	3.96	0.82
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2000	8MF00 33 1 TUCK1 2	8-Sep-00	2.99	0.63
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2001	3MF01 45 1 60BON 1	28-May-01	2.79	0.74
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2001	3MF01 101 1 60BON 1	30-May-01	3.39	0.79

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2001	3MF01 117 1 60BON 1	31-May-01	3.67	0.72
2001	3MF01 126 1 60BON 1	1-Jun-01	3.58	0.85
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2001	3MF01 145 1 60BON 1	2-Jun-01	3.02	0.80
2001	4MF01 1 3 TUCK1 2	3-Sep-01	3.15	0.76
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2002	3MF02 7 2 60BON 1	13-May-02	3.22	0.73
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2002	3MF02 11 2 60BON 1	14-May-02	2.97	0.77
2002	3MF02 81 2 60BON 1	21-May-02	3.59	0.77
2002	3MF02 79 2 60BON 1	21-May-02	3.14	0.78
2002	4MF02 17 1 60BON 1	26-May-02	3.29	0.73
2002	1EW02 16 2 60BON 1	27-May-02	2.84	0.70
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2002	1EW02 12 3 60BON 1	27-May-02	3.03	0.72
2002	1EW02 2 3 60BON 1	27-May-02	3.52	0.75
2002	1EW02 6 2 60BON 2	27-May-02	3.08	0.75
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2002	4MF02 42 1 60BON 1	27-May-02	3.49	0.79
2002	4MF02 33 1 60BON 1	27-May-02	3.02	0.82
2002	1EW02 16 2 60BON 1	27-May-02	3.25	0.85
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2002	4MF02 127 1 60BON 1	1-Jun-02	2.32	0.78
2002	5MF02 1 8 MOC1 6	9-Sep-02	2.81	0.90
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2003	2KM03 67 2 60BON 1	3-May-03	2.73	0.75
2003	2KM03 59 2 60BON 1	3-May-03	2.55	0.76
2003	2KM03 51 2 60BON 1	3-May-03	2.76	0.83
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2003	2KM03 71 2 60BON 1	4-May-03	2.82	0.73
2003	1HX03 132 1 MOC1 7	4-May-03	2.50	0.88
2003	2KM03 104 2 60BON 1	5-May-03	3.19	0.73
2003	1HX03 136 1 MOC1 6	5-May-03	2.74	0.79

2003	2KM03 91 2 60BON 1	5-May-03	3.07	0.88
2003	2KM03 112 2 60BON 1	6-May-03	2.97	0.77
2003	2KM03 122 2 60BON 1	7-May-03	3.09	0.85
2003	2KM03 163 2 60BON 1	9-May-03	3.25	0.81
2003	1HX03 267 1 MOC1 7	12-May-03	4.21	0.82
2003	2KM03 188 2 60BON 1	12-May-03	3.35	0.87
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2003	1HX03 319 1 MOC1 6	14-May-03	2.43	0.65
2003	1HX03 309 1 MOC1 7	14-May-03	3.40	0.79
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2003	1HX03 324 1 MOC1 5	14-May-03	2.60	0.80
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2003	4MF03 8 2 60BON 1	18-May-03	2.55	0.62
2003	4MF03 1 3 60BON 1	18-May-03	2.90	0.64
2003	4MF03 5 1 NEU 1	18-May-03	2.26	0.68
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2003	4MF03 7 2 60BON 1	18-May-03	3.09	0.78
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2003	5MF03 24 1 60BON 1	28-May-03	2.84	0.91
2003	5MF03 43 1 60BON 1	29-May-03	2.79	0.80
2003	5MF03 66 1 60BON 1	30-May-03	2.61	0.81
2003	5MF03 99 1 60BON 1	1-Jun-03	3.21	0.72
2003	5MF03 99 1 60BON 1	1-Jun-03	3.39	0.75
2003	5MF03 99 1 60BON 1	1-Jun-03	3.34	0.77
2003	5MF03 98 1 60BON 2	1-Jun-03	3.76	0.81
2003	5MF03 95 1 60BON 1	1-Jun-03	3.70	0.82
2003	2HX03 116 1 MOC1 2	26-Jul-03	4.46	0.77
2003	2HX03 159 1 MOC1 2	28-Jul-03	2.20	0.87
2003	7MF03 48 1 TUCK1 1	16-Sep-03	2.93	0.75
2004	5MF04 81 1 60BON 1	28-May-04	3.13	0.77
2004	5MF04 105 1 60BON 1	29-May-04	3.12	0.78
2004	5MF04 93 1 60BON 1	29-May-04	3.14	0.84
2004	5MF04 93 1 60BON 1	29-May-04	2.64	0.87
2004	5MF04 114 1 60BON 1	30-May-04	2.91	0.74
2004	5MF04 125 1 60BON 1	30-May-04	3.43	0.99
2004	5MF04 135 1 60BON 1	31-May-04	3.10	0.75
2004	7MF04 2 11 MOC1 2	10-Sep-04	2.26	0.92
2005	1TT05 1 2 60BON 1	28-Apr-05	3.79	0.81
2005	1TT05 1 2 60BON 1	28-Apr-05	3.88	0.89
2005	1TT05 15 2 60BON 1	1-May-05	4.04	0.78
2005	1TT05 28 2 60BON 1	3-May-05	3.34	0.92
2005	1TT05 37 2 60BON 1	4-May-05	4.04	0.68
2005	1TT05 43 2 60BON 1	5-May-05	4.18	0.85
2005	5MF05 1 3 60BON 1	10-May-05	3.45	0.87
2005	5MF05 66 2 60BON 1	16-May-05	3.75	0.66
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2005	5MF05 132 1 60BON 1	19-May-05	4.13	0.70

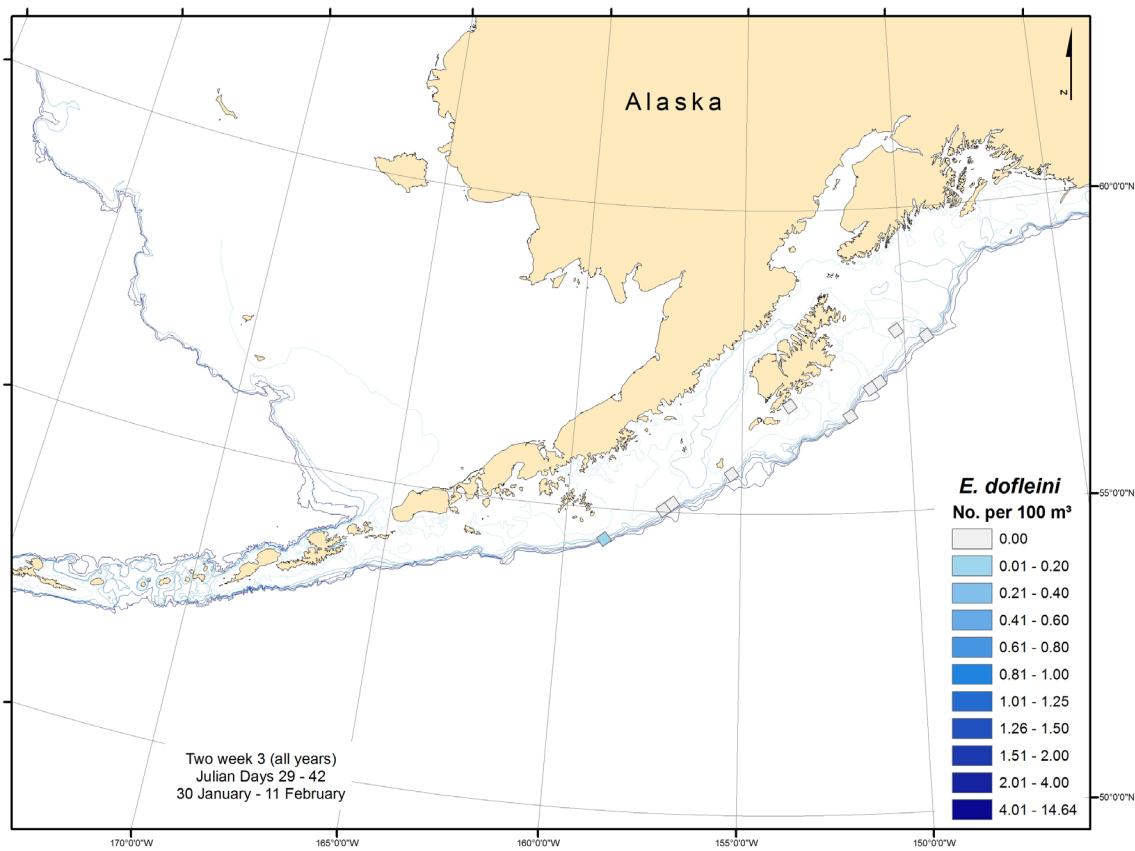
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2005	6MF05 86 1 60BON 1	27-May-05	2.46	0.78
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2005	1FA05 71 2 60BON 2	25-Jul-05	3.29	0.76
2006	1TT06 110 2 60BON 1	9-May-06	3.27	0.79
2006	3MF06 12 3 60BON 1	10-May-06	3.10	0.71
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2006	3MF06 15 2 60BON 1	11-May-06	4.43	0.77
2006	3MF06 24 2 60BON 1	12-May-06	3.23	0.70
2006	3MF06 24 4 MOC1 5	12-May-06	3.59	0.82
2006	3MF06 35 3 60BON 1	13-May-06	3.12	0.75
2006	3MF06 34 2 60BON 1	13-May-06	3.13	0.76
2006	3MF06 35 3 60BON 1	13-May-06	3.51	0.78
2006	3MF06 34 4 MOC1 5	13-May-06	3.24	0.78
2006	3MF06 35 3 60BON 1	13-May-06	2.82	0.80
2006	3MF06 34 4 MOC1 4	13-May-06	2.93	0.80
2006	3MF06 35 3 60BON 1	13-May-06	3.60	0.83
2006	3MF06 34 4 MOC1 4	13-May-06	3.26	0.84
2006	3MF06 35 3 60BON 1	13-May-06	2.93	0.85
2006	3MF06 44 4 MOC1 2	14-May-06	3.01	0.74
2006	3MF06 51 4 MOC1 5	15-May-06	2.66	0.79
2006	4MF06 2 1 60BON 1	22-May-06	2.89	0.69
2006	4MF06 3 1 60BON 1	22-May-06	2.78	0.80
2006	4MF06 43 1 60BON 1	25-May-06	3.48	0.77
2006	4MF06 49 1 60BON 1	25-May-06	3.16	0.80
2006	4MF06 104 1 60BON 1	28-May-06	3.04	0.76
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2006	4MF06 125 1 60BON 1	29-May-06	3.18	0.81
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2007	2MF07 83 2 60BON 1	11-Apr-07	4.01	0.89
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2007	4MF07 8 2 60BON 1	9-May-07	2.78	0.82
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2007	4MF07 40 2 60BON 1	12-May-07	3.26	0.71
2007	4MF07 57 3 60BON 1	13-May-07	6.63	0.80
2007	4MF07 90 1 60BON 1	17-May-07	3.24	0.74
2007	4MF07 94 1 60BON 1	18-May-07	3.01	0.85
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2007	5MF07 15 1 60BON 1	21-May-07	2.75	0.76
2007	5MF07 61 1 60BON 1	24-May-07	3.30	0.76
2007	5MF07 75 1 60BON 1	25-May-07	2.63	0.72
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2007	5MF07 93 1 60BON 1	26-May-07	2.41	0.73
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2008	3DY08 10 2 60BON 1	14-May-08	3.22	0.83
2008	3DY08 33 1 60BON 1	16-May-08	2.94	0.81
2008	3DY08 60 2 60BON 1	20-May-08	3.23	0.74
2008	3DY08 65 2 60BON 1	21-May-08	3.07	0.78
2008	3DY08 66 1 60BON 1	21-May-08	3.03	0.69
2008	4DY08 30 1 60BON 1	26-May-08	3.10	0.68
2008	4DY08 41 1 60BON 1	26-May-08	2.91	0.70
2008	4DY08 57 1 60BON 1	27-May-08	3.54	0.74
2008	4DY08 51 1 60BON 1	27-May-08	2.54	0.75
2008	4DY08 57 1 60BON 1	27-May-08	2.76	0.75
2008	4DY08 58 1 60BON 1	27-May-08	2.79	0.85
2008	4DY08 66 1 60BON 1	28-May-08	2.69	0.78
2008	4DY08 74 1 60BON 1	28-May-08	3.54	0.80
2008	4DY08 66 1 60BON 1	28-May-08	2.65	0.81
2008	1ME08 3 3 60BON 1	26-Aug-08	2.84	0.79
2008	1ME08 140 2 60BON 1	7-Sep-08	2.53	0.82
2008	1ME08 142 2 60BON 1	8-Sep-08	3.00	0.75
2008	1ME08 157 2 60BON 1	9-Sep-08	3.68	0.70
2008	1ME08 157 2 60BON 1	9-Sep-08	3.93	0.81

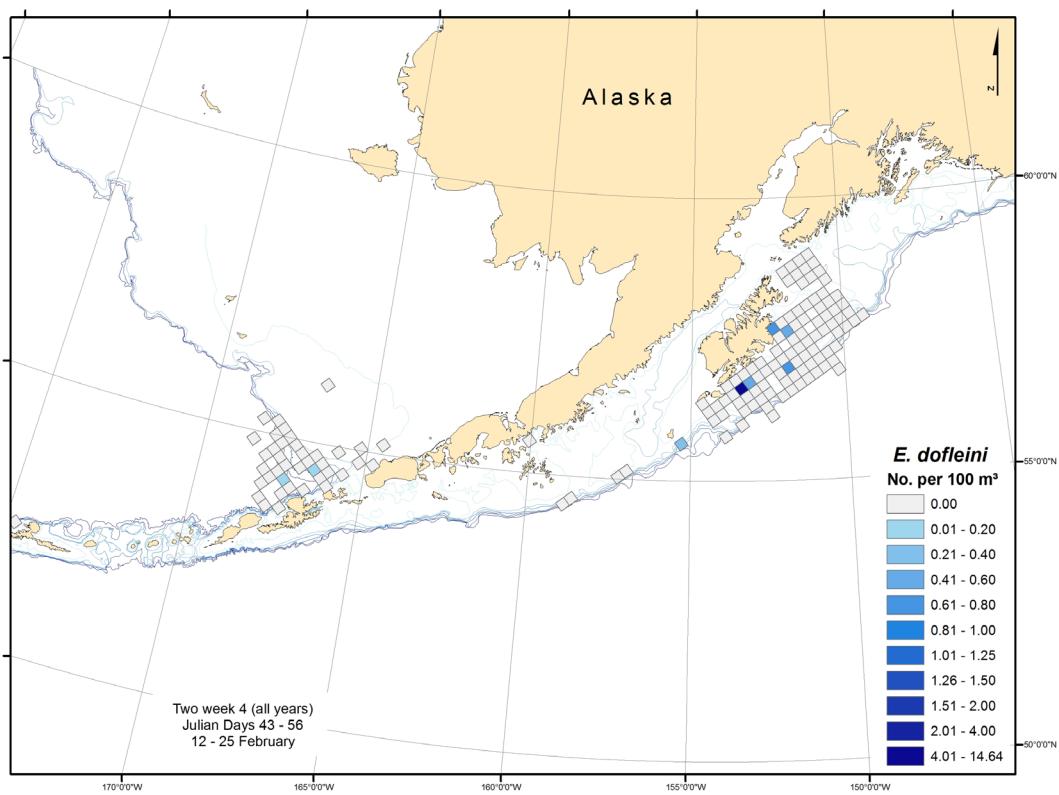
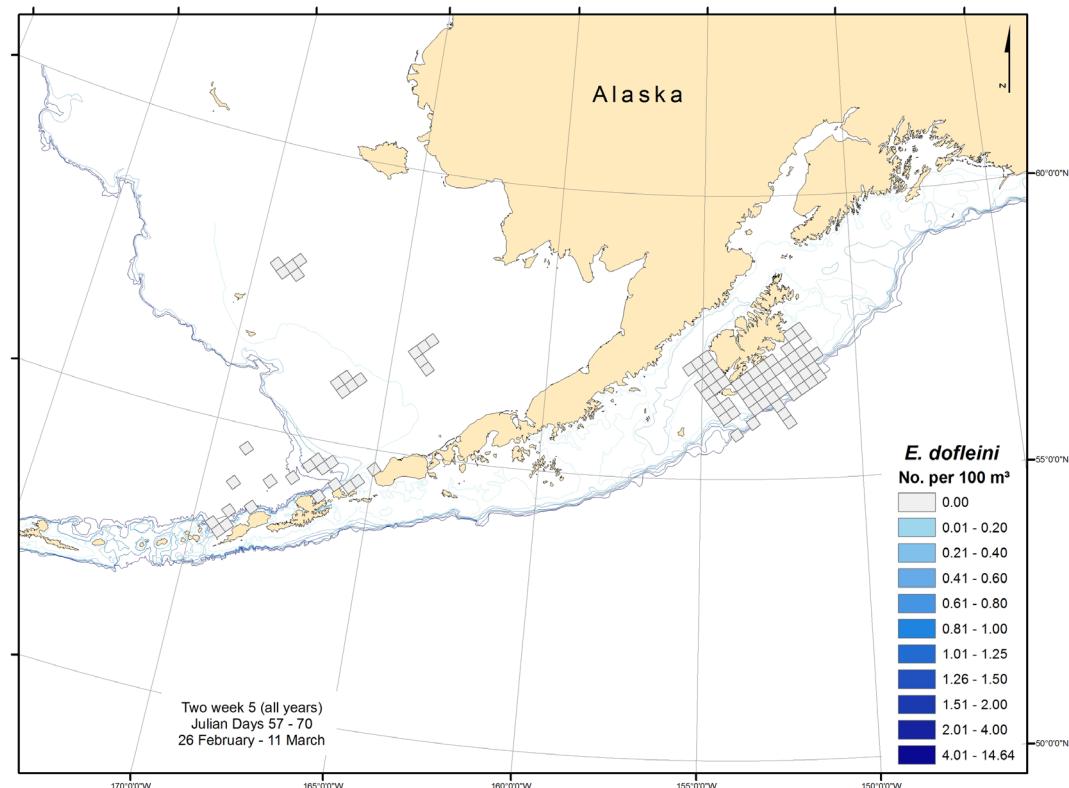


Figure 3.1. Map of the study area.

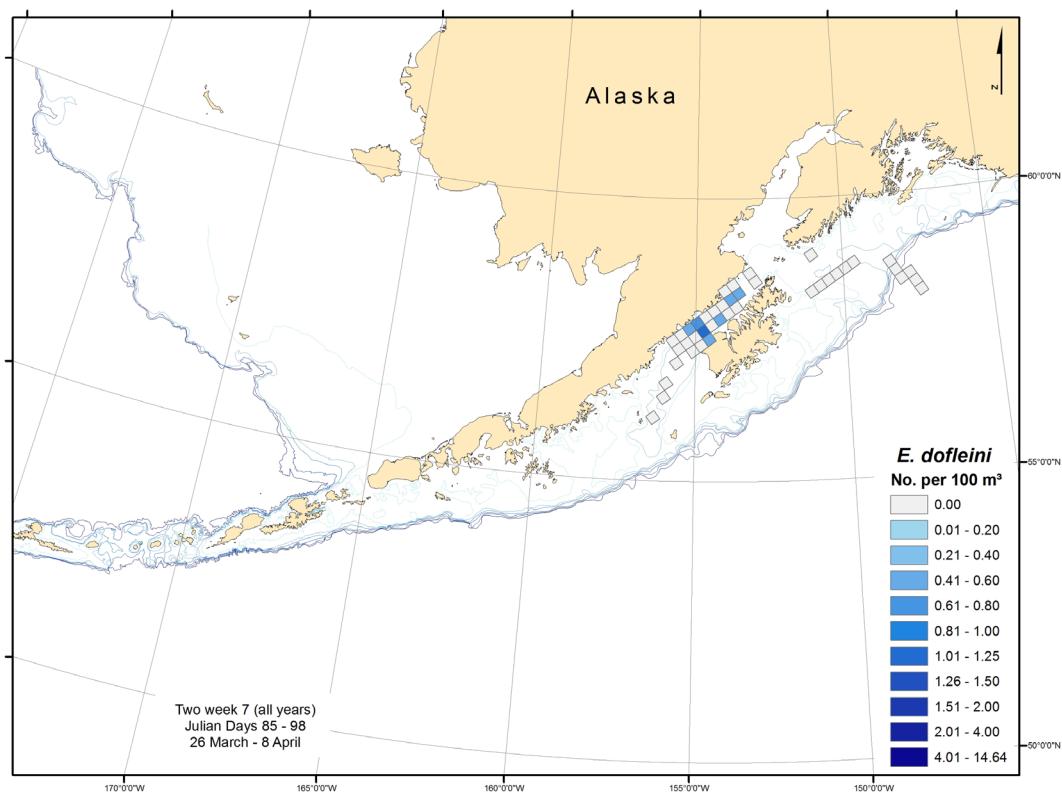
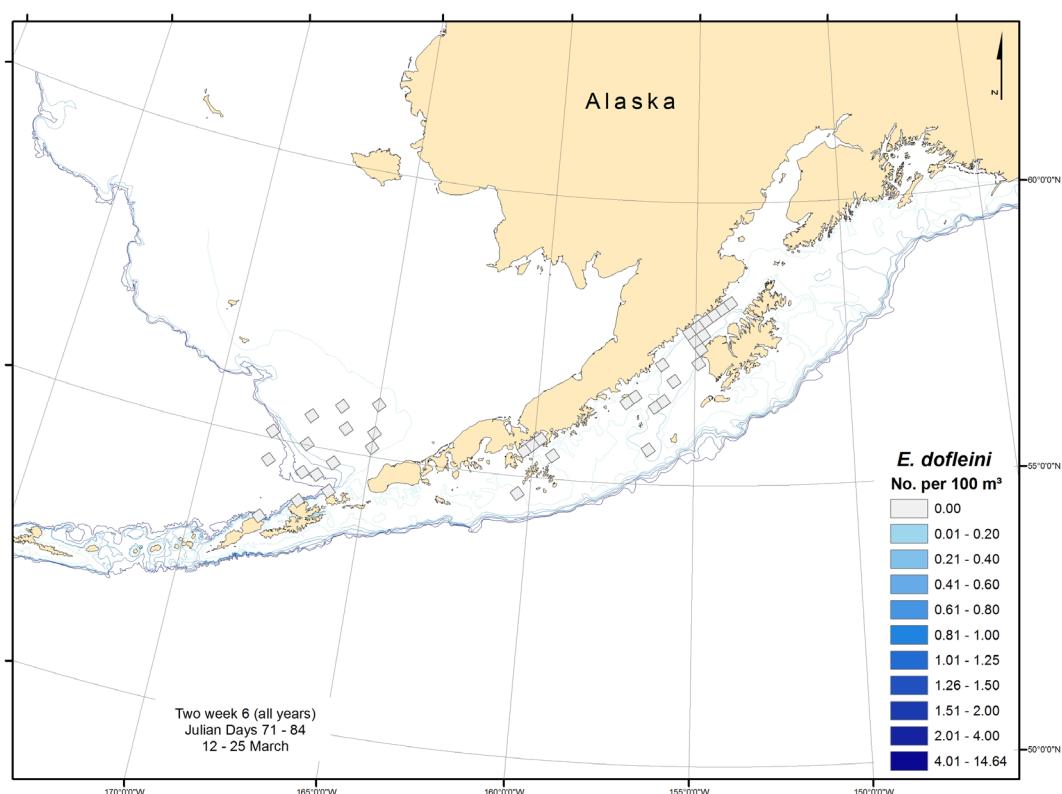
A



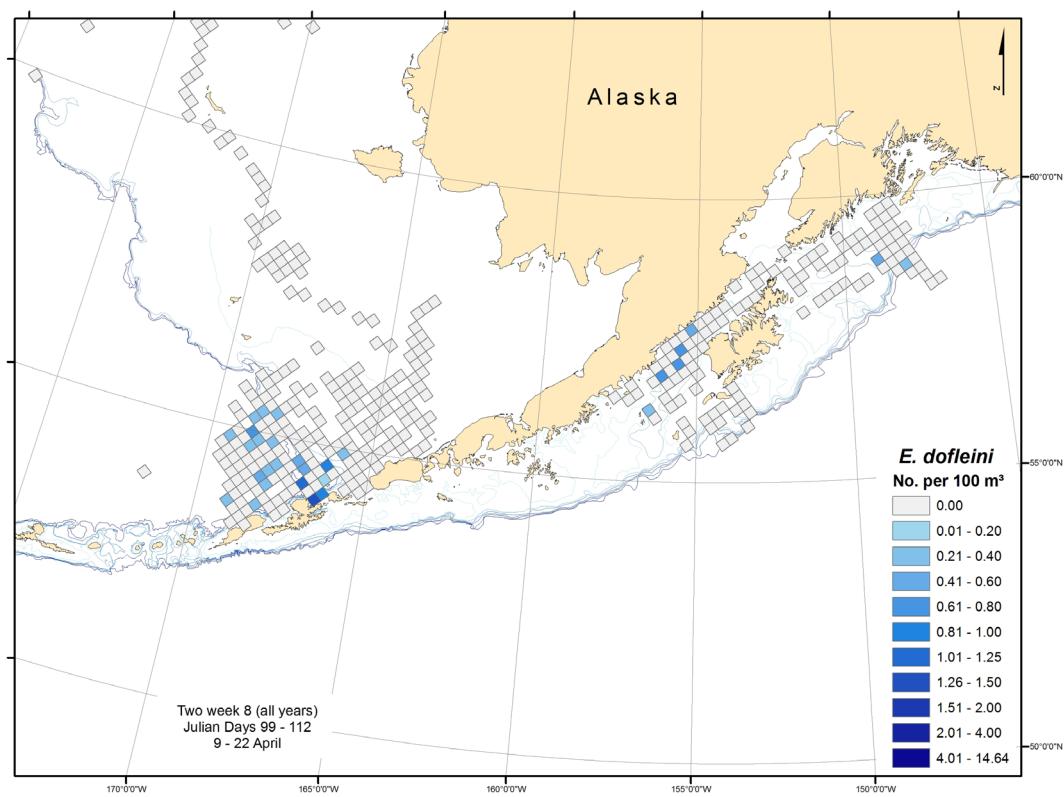
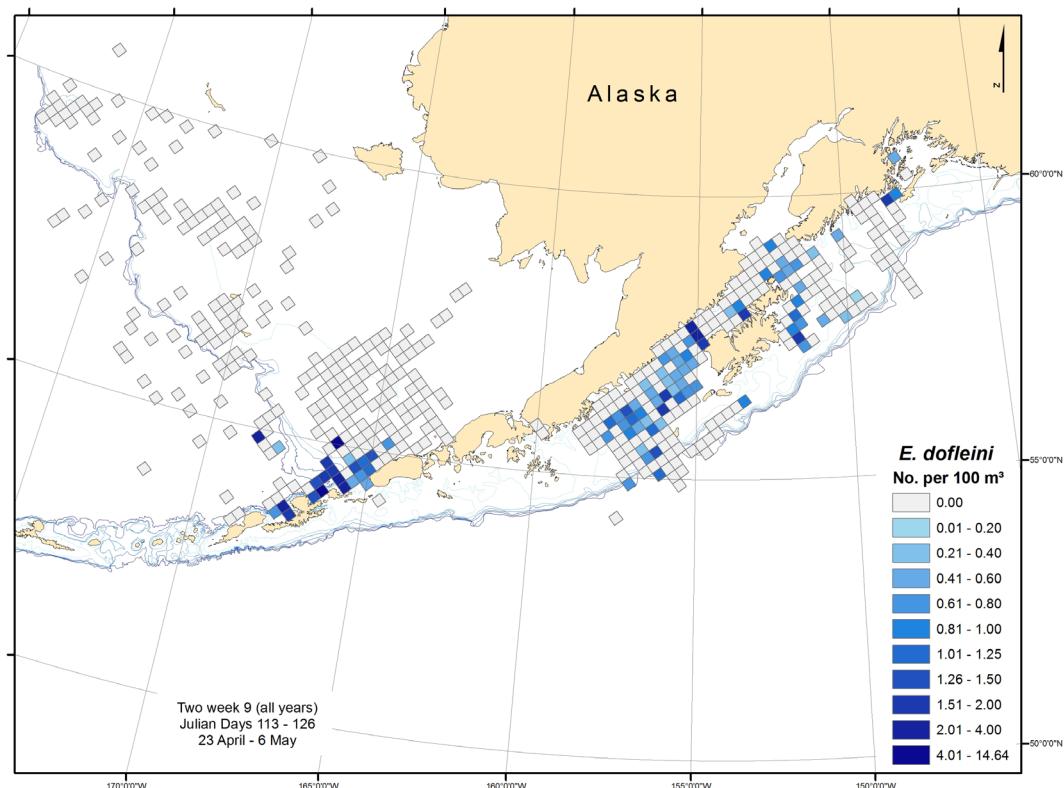
Figures 3.2A-S. Maps of *Enteroctopus dofleini* distribution and abundance. Each cell represents a 20 x 20 km region within which at least one station was occupied. Grey grid cells indicate that the cell was sampled but no *E. dofleini* were collected. Colors are according to legend and represent the summed number per 100 cubic meters at each station within each cell for the two-week period listed on the individual maps.

B**C**

Figures 3.2A-S continued.

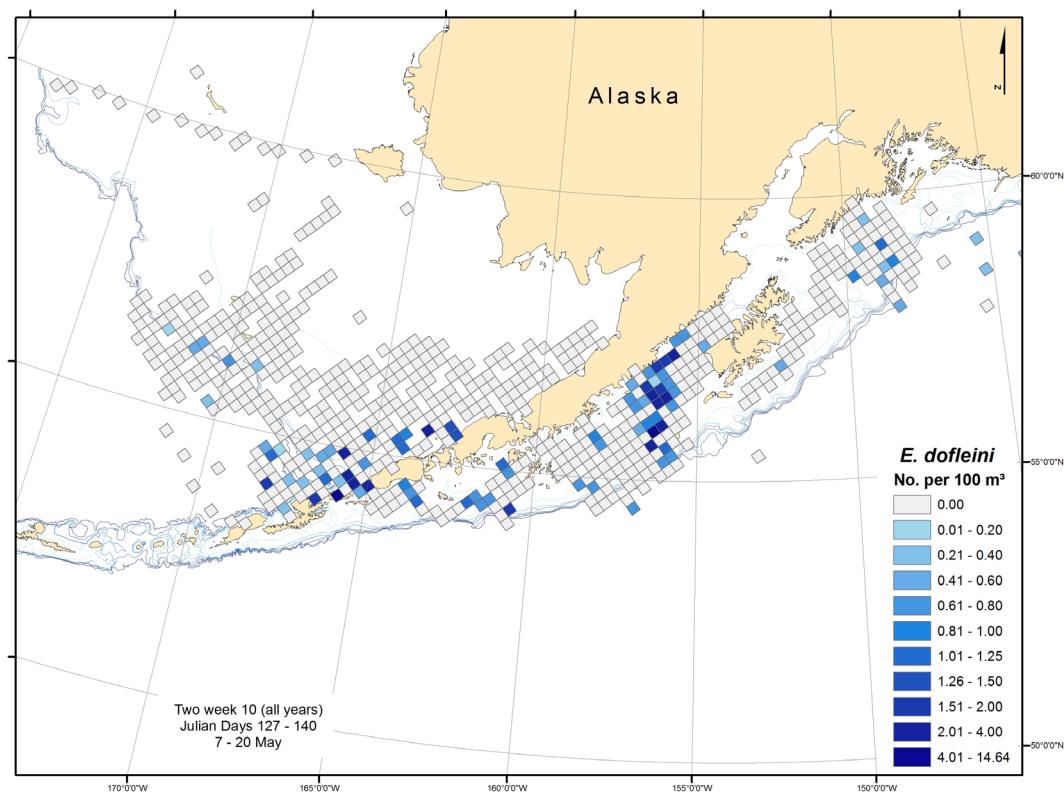
E**D**

Figures 3.2A-S continued.

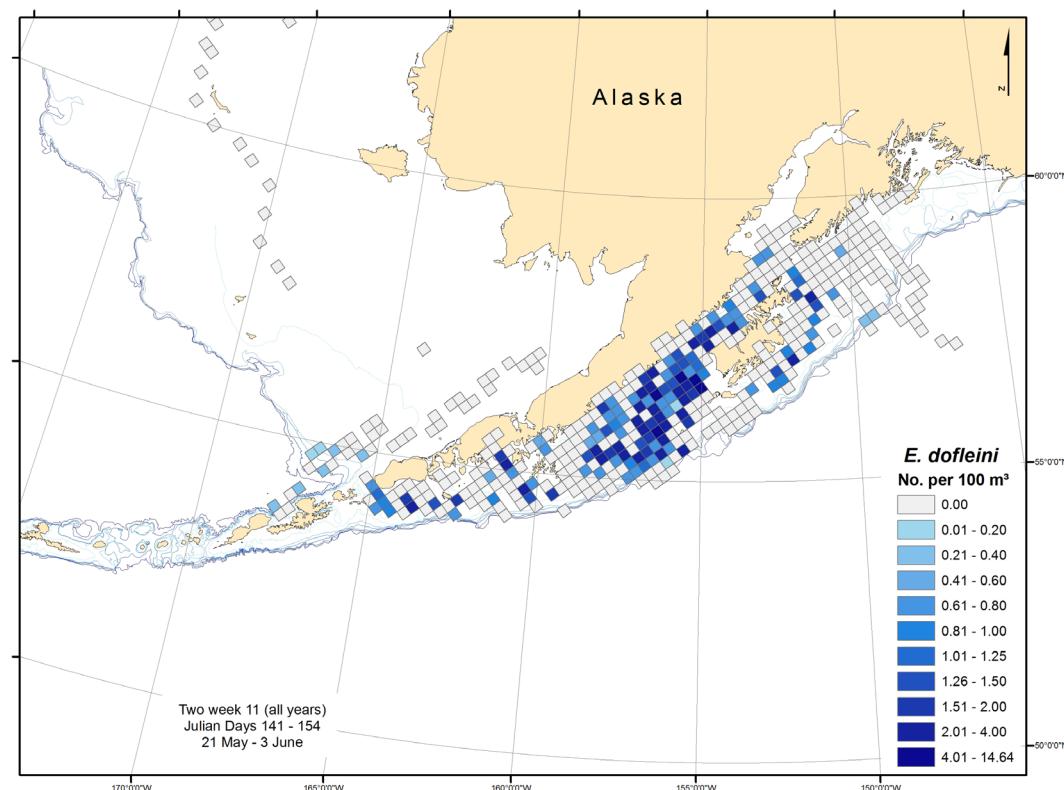
F**G**

Figures 3.2A-S continued.

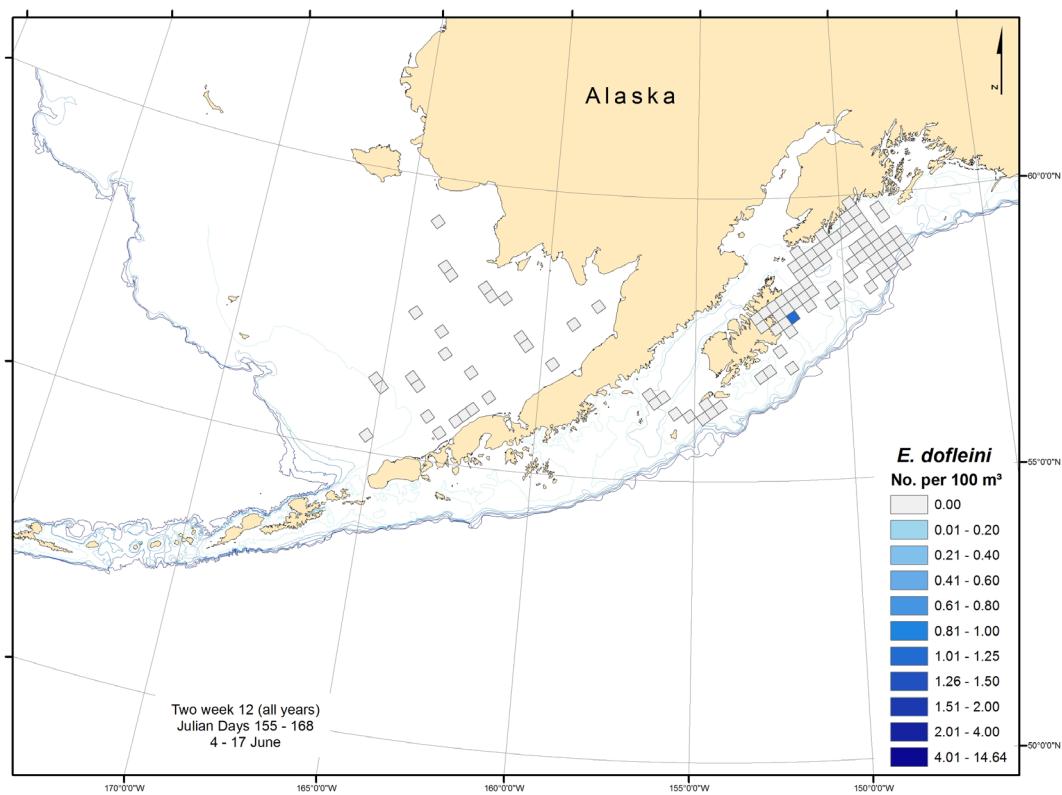
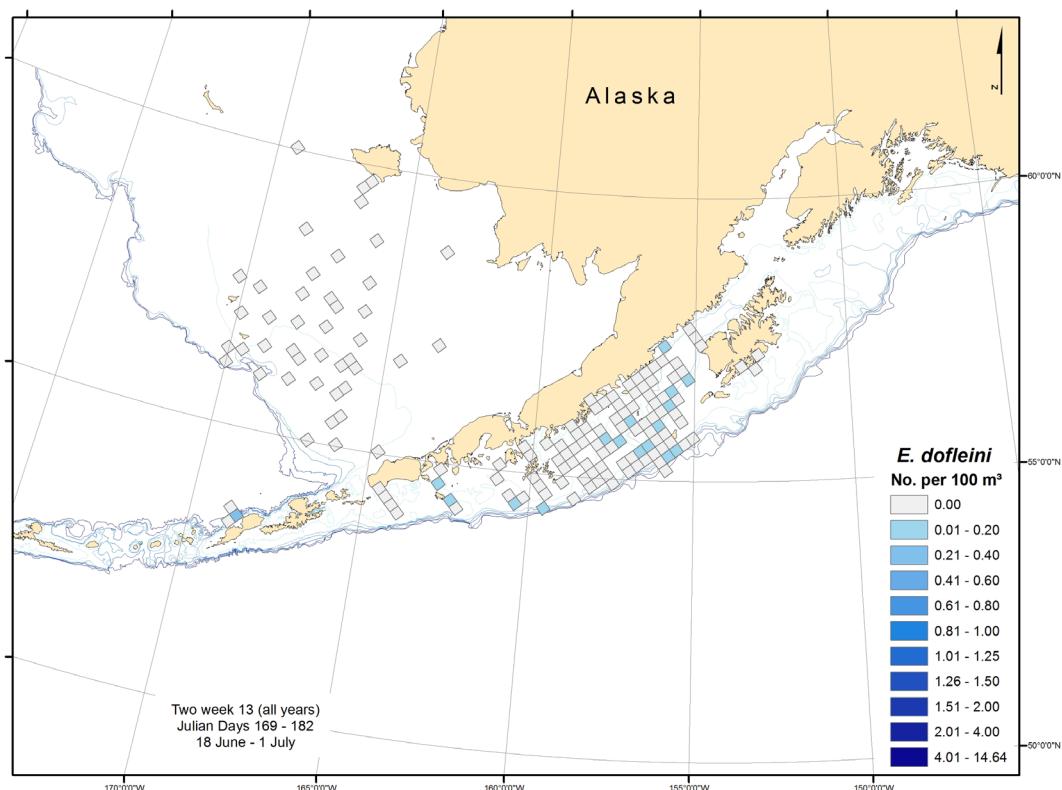
H



I

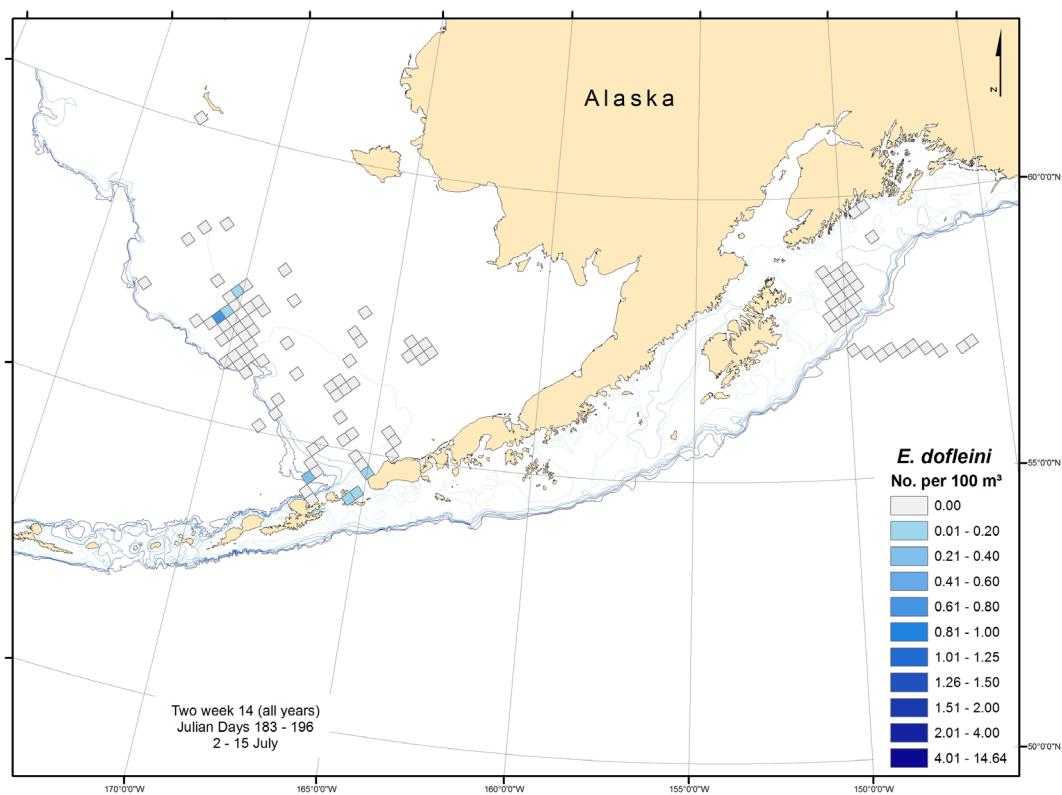


Figures 3.2A-S continued.

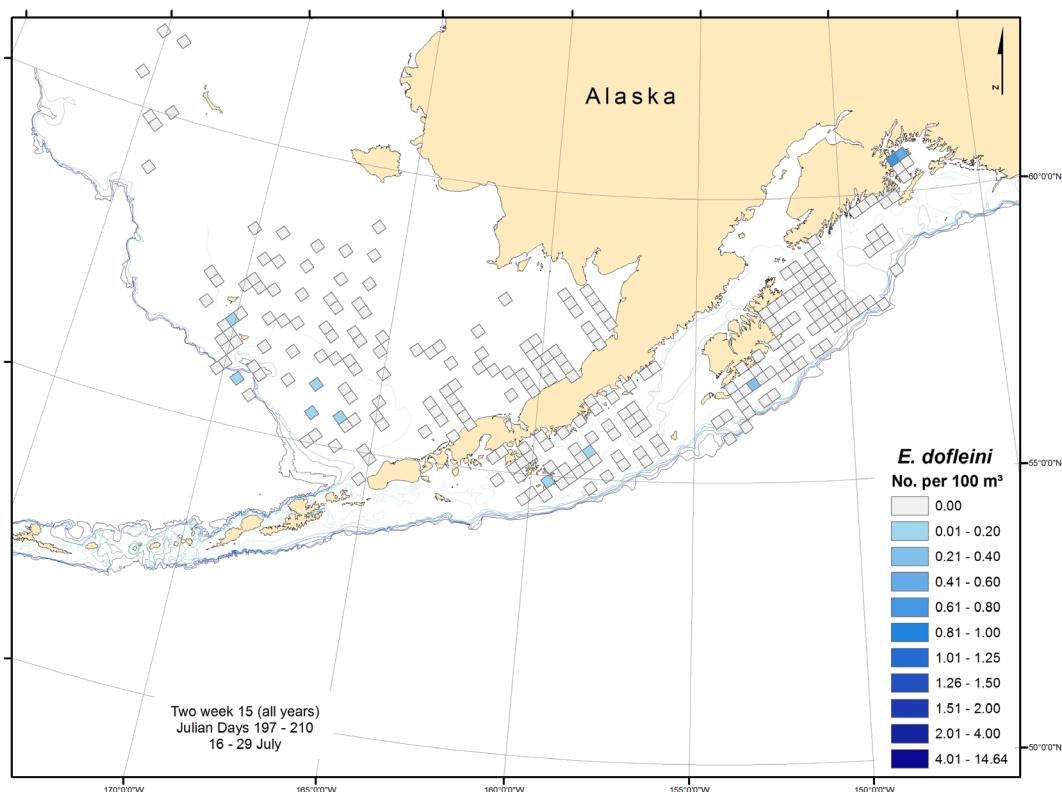
J**K**

Figures 3.2A-S continued.

L

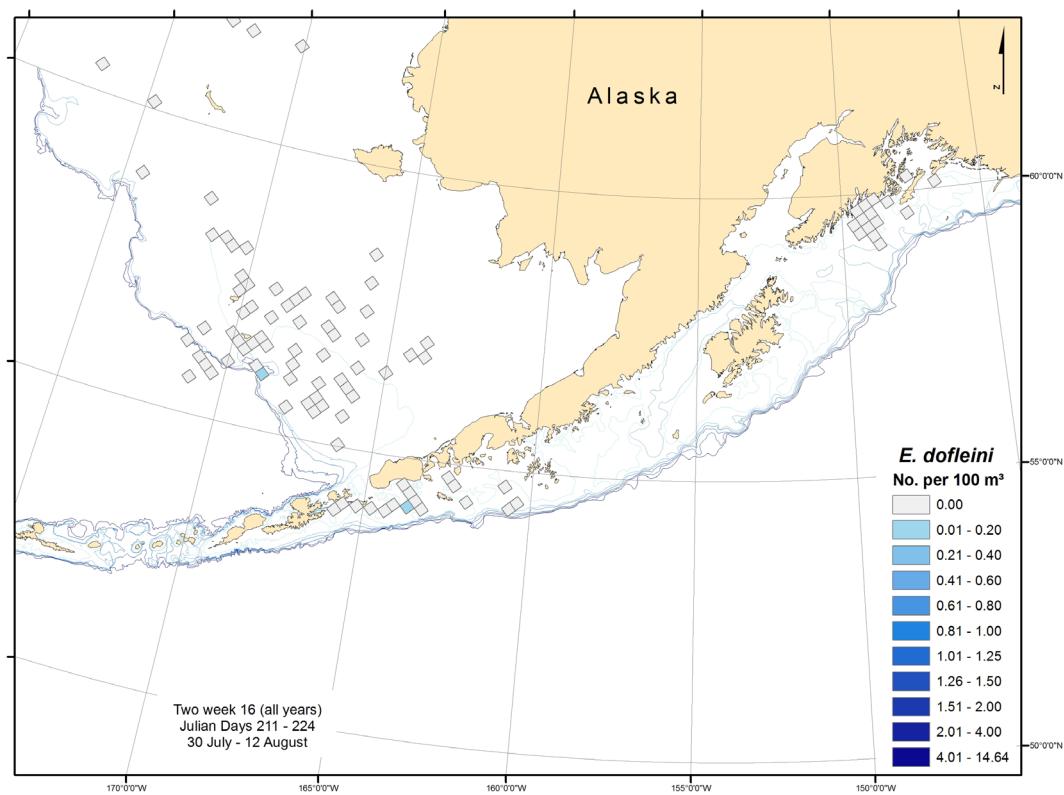


M

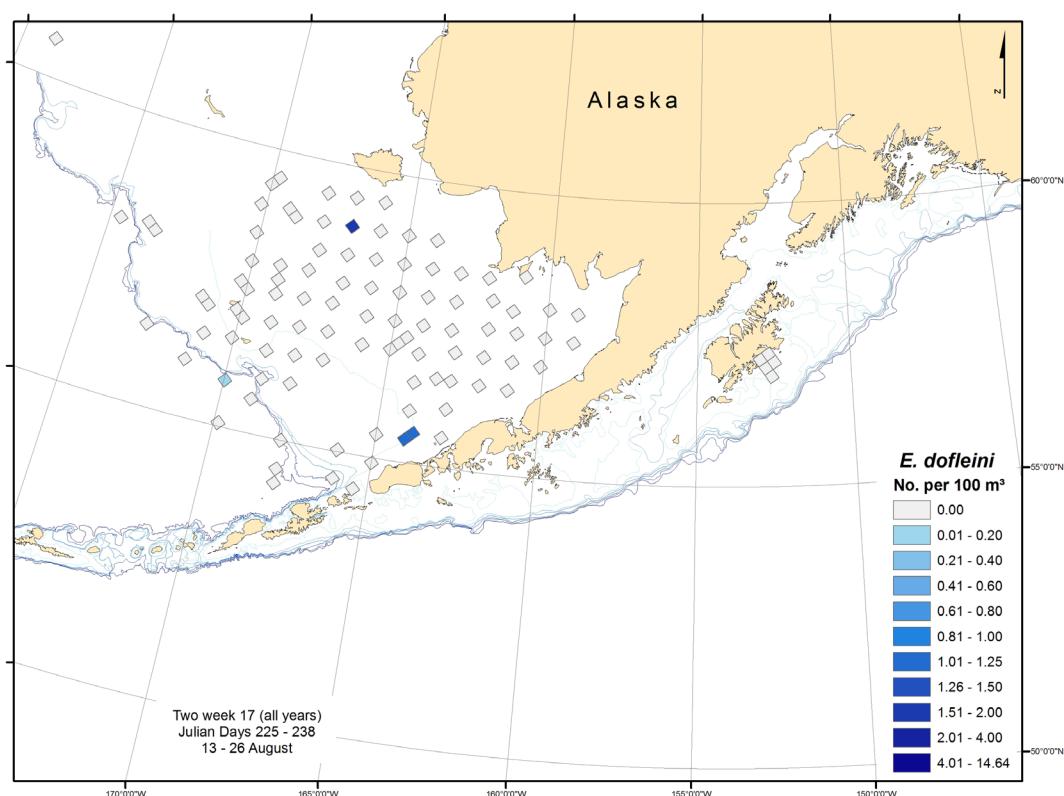


Figures 3.2A-S continued.

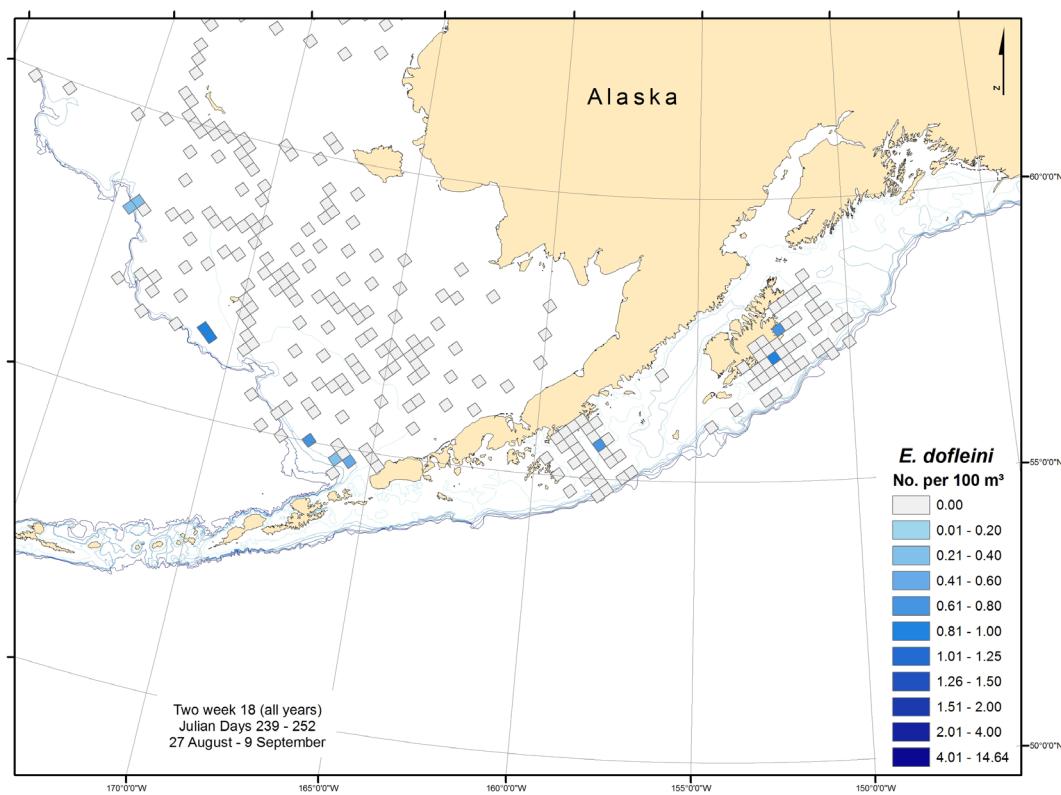
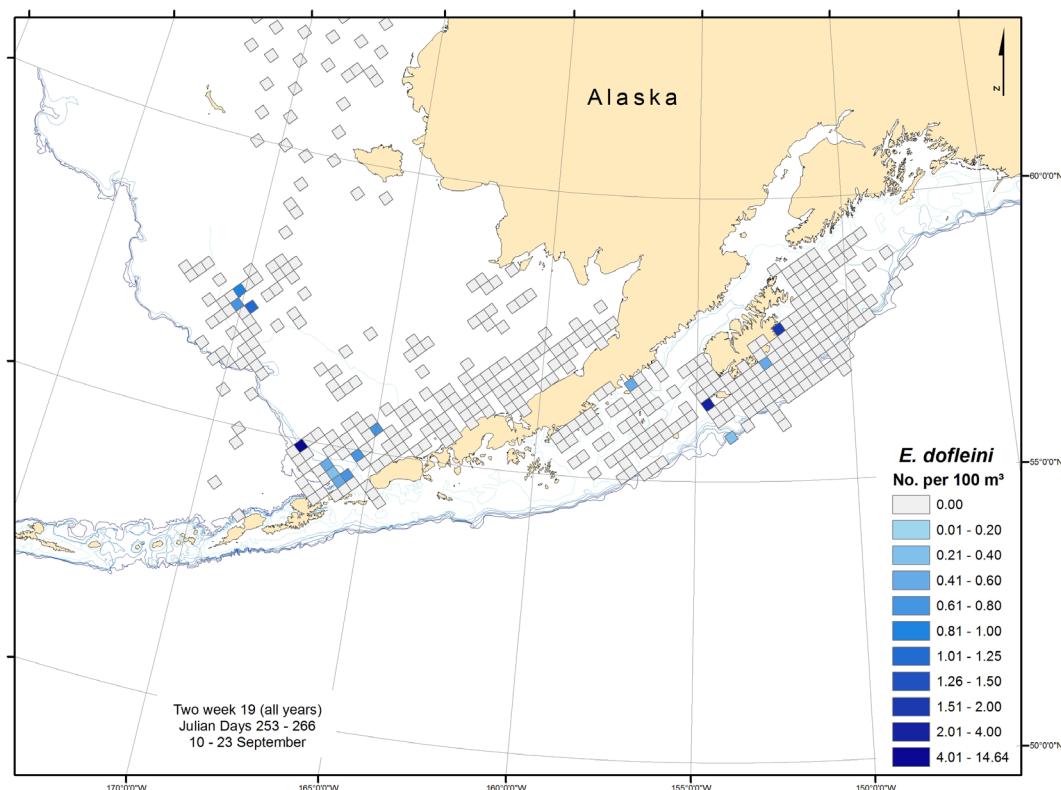
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O

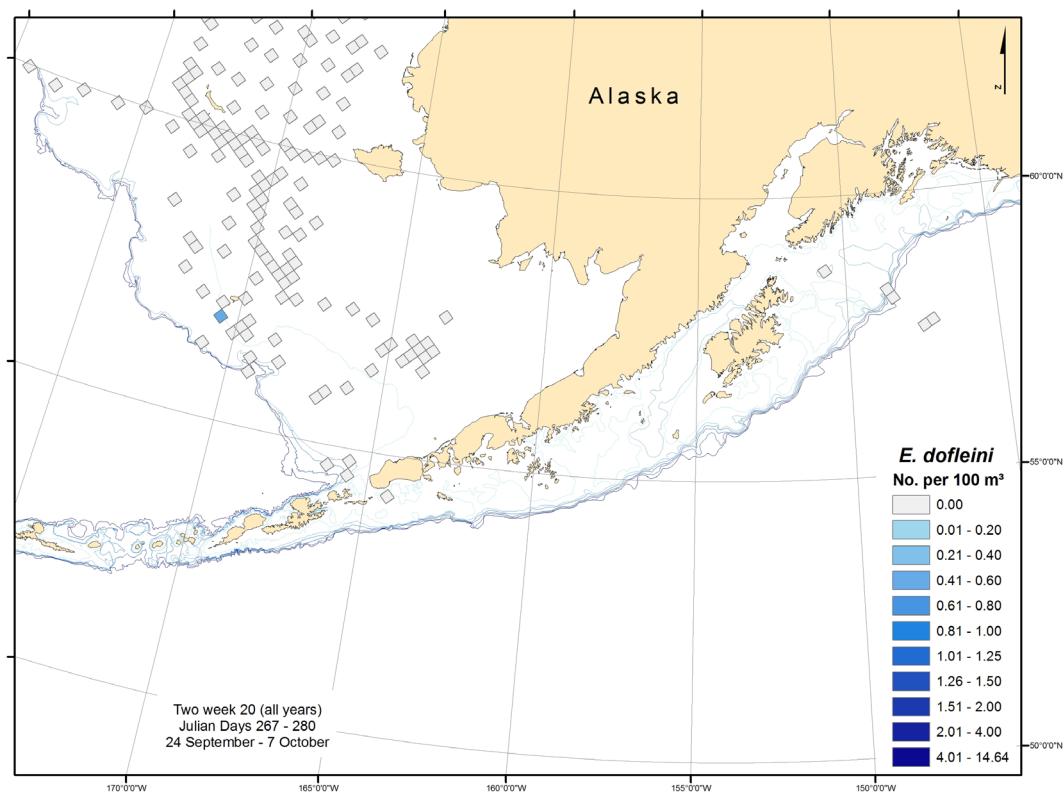


Figures 3.2A-S continued.

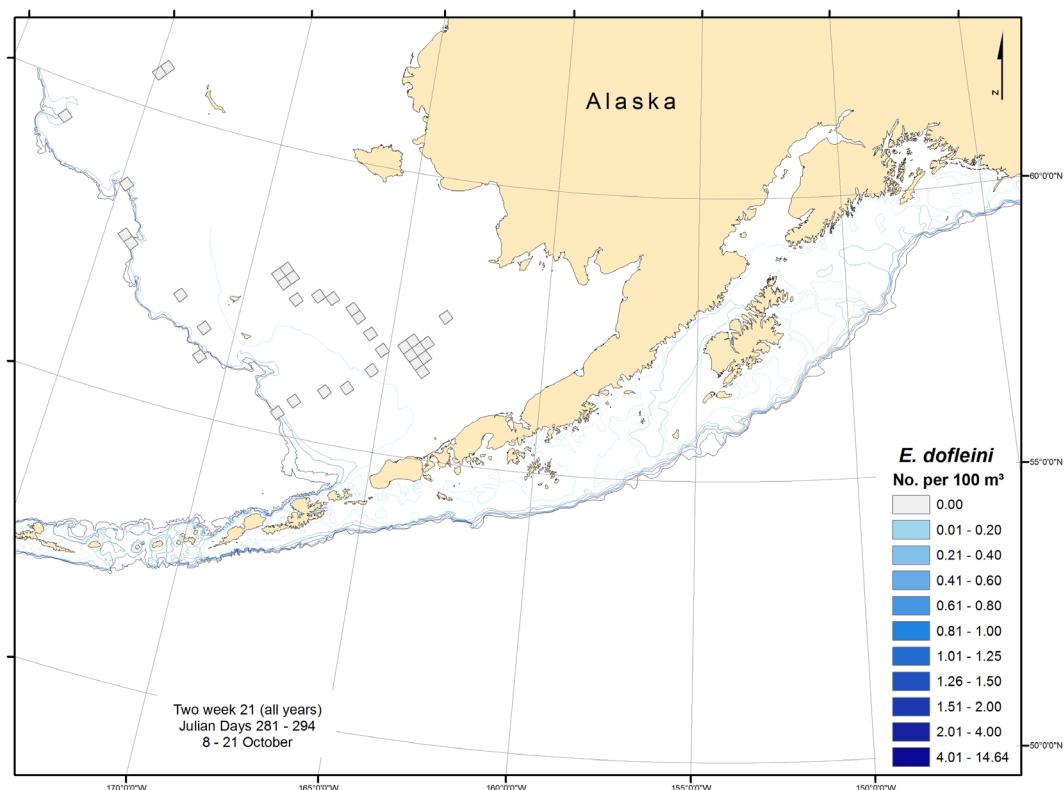
P**Q**

Figures 3.2A-S continued.

R



S



Figures 3.2A-S continued.

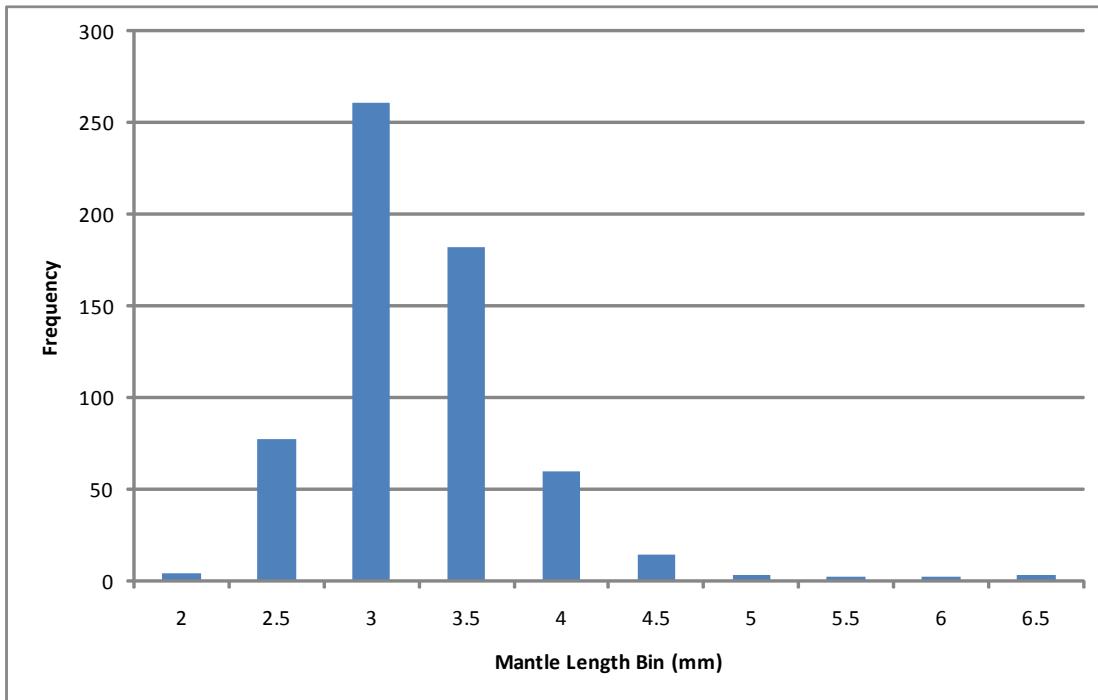


Figure 3.3. Binned length frequency for *Enteroctopus dofleini*. Frequency represents the total number of paralarvae collected in each size bin. Lengths are in mm.

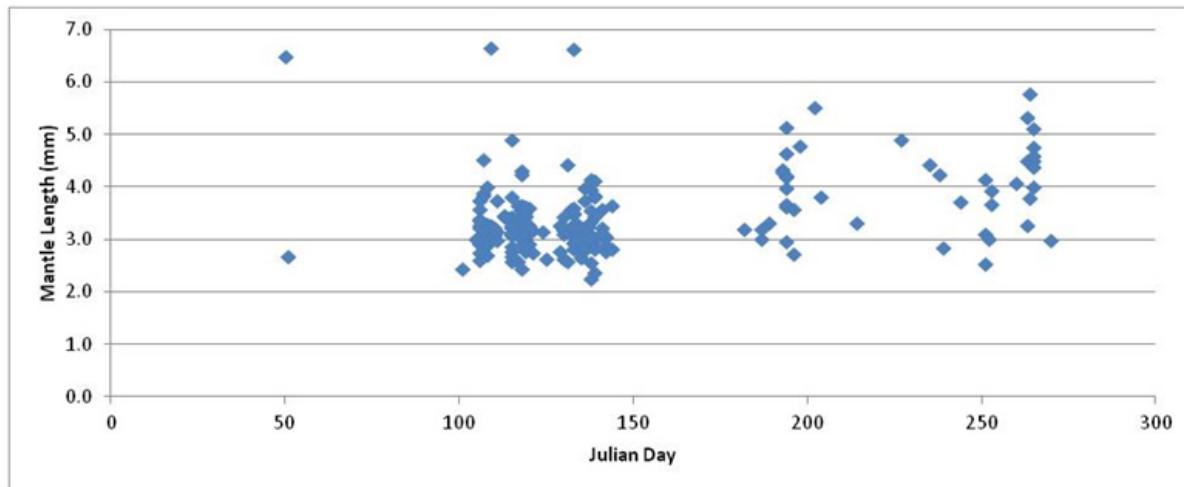


Figure 3.4. Scatter plot of all mantle length (mm) by Julian day for all Bering Sea *Enteroctopus dofleini* paralarvae specimens from 1991 - 2008.

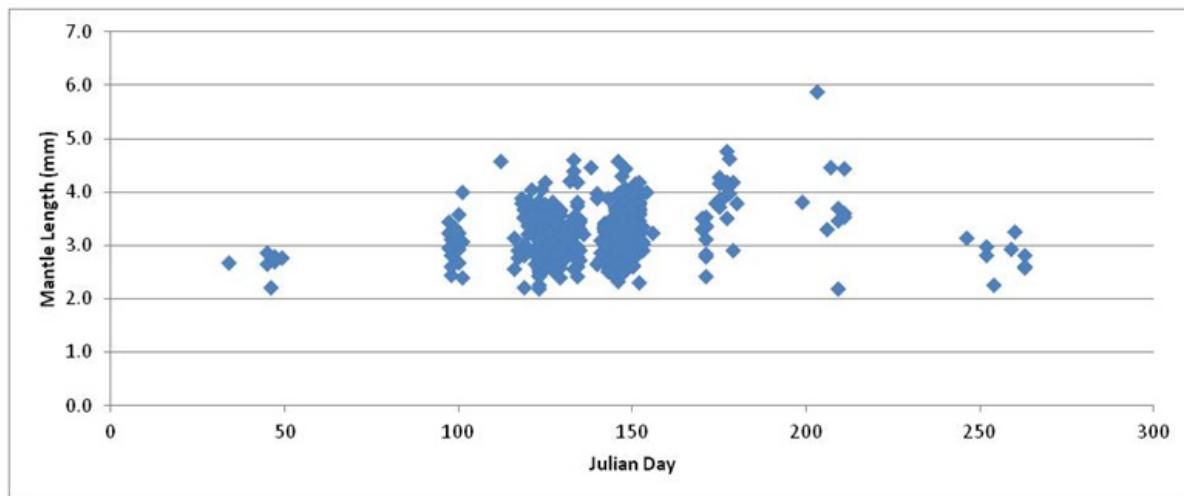


Figure 3.5. Scatter plot of all mantle length (mm) by Julian day for all Gulf of Alaska *Enteroctopus dofleini* paralarvae specimens from 1991 - 2008.

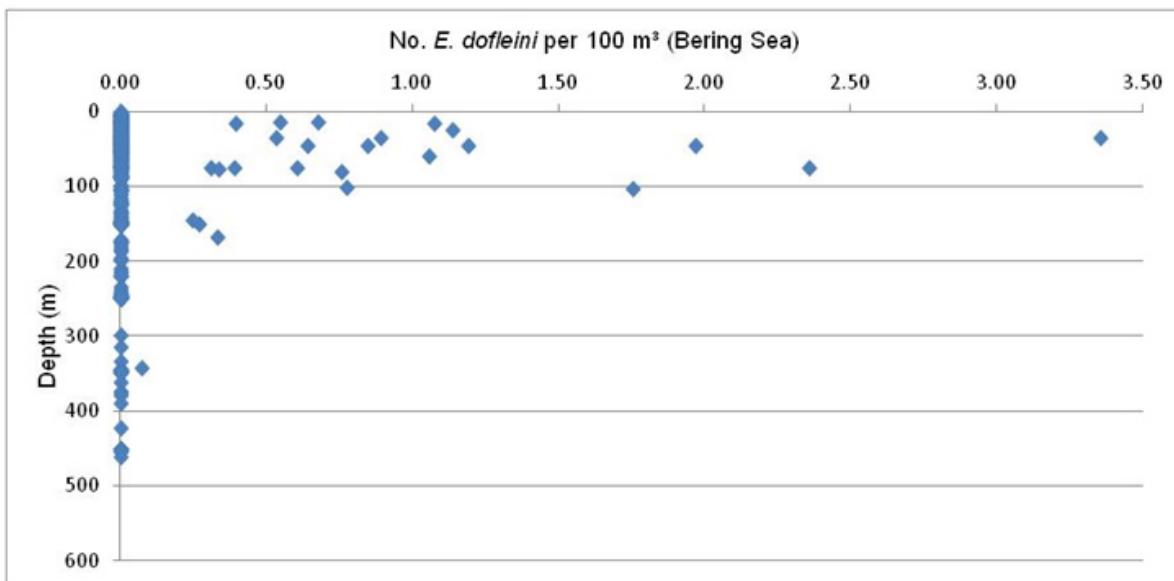


Figure 3.6A. Number of *Enteroctopus dofleini* per 100 m³ collected using the MOCNESS in the Bering Sea; includes all data from 1991 - 2008. Depth is the midpoint value between the minimum and maximum gear depths.

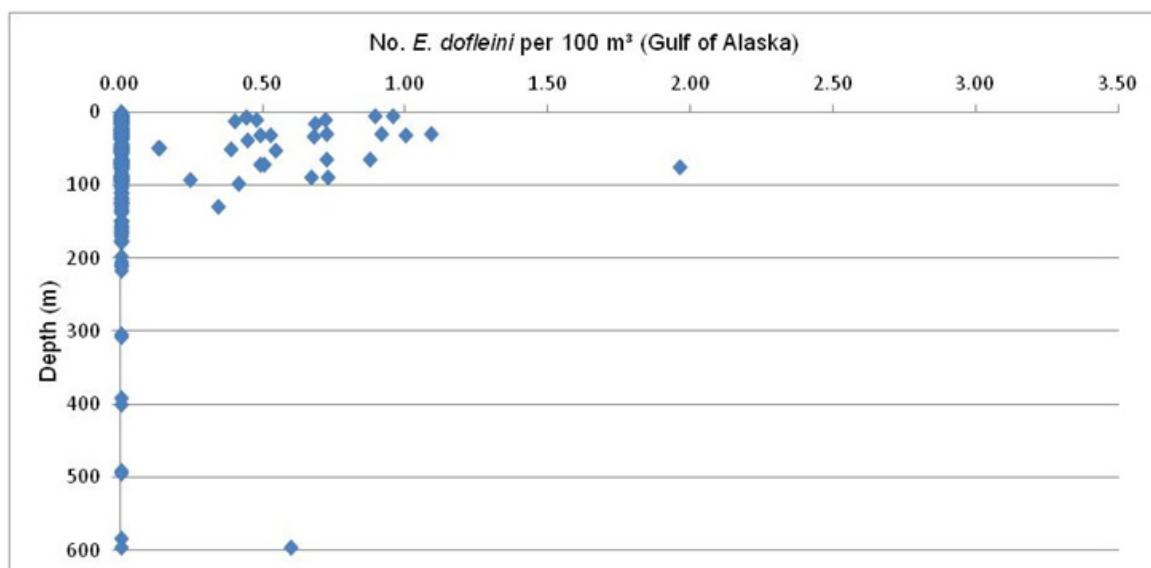


Figure 3.6B. Number of *Enteroctopus dofleini* per 100 m³ collected using the MOCNESS in the Gulf of Alaska; includes all data from 1991 - 2008. Depth is the midpoint value between the minimum and maximum gear depths.

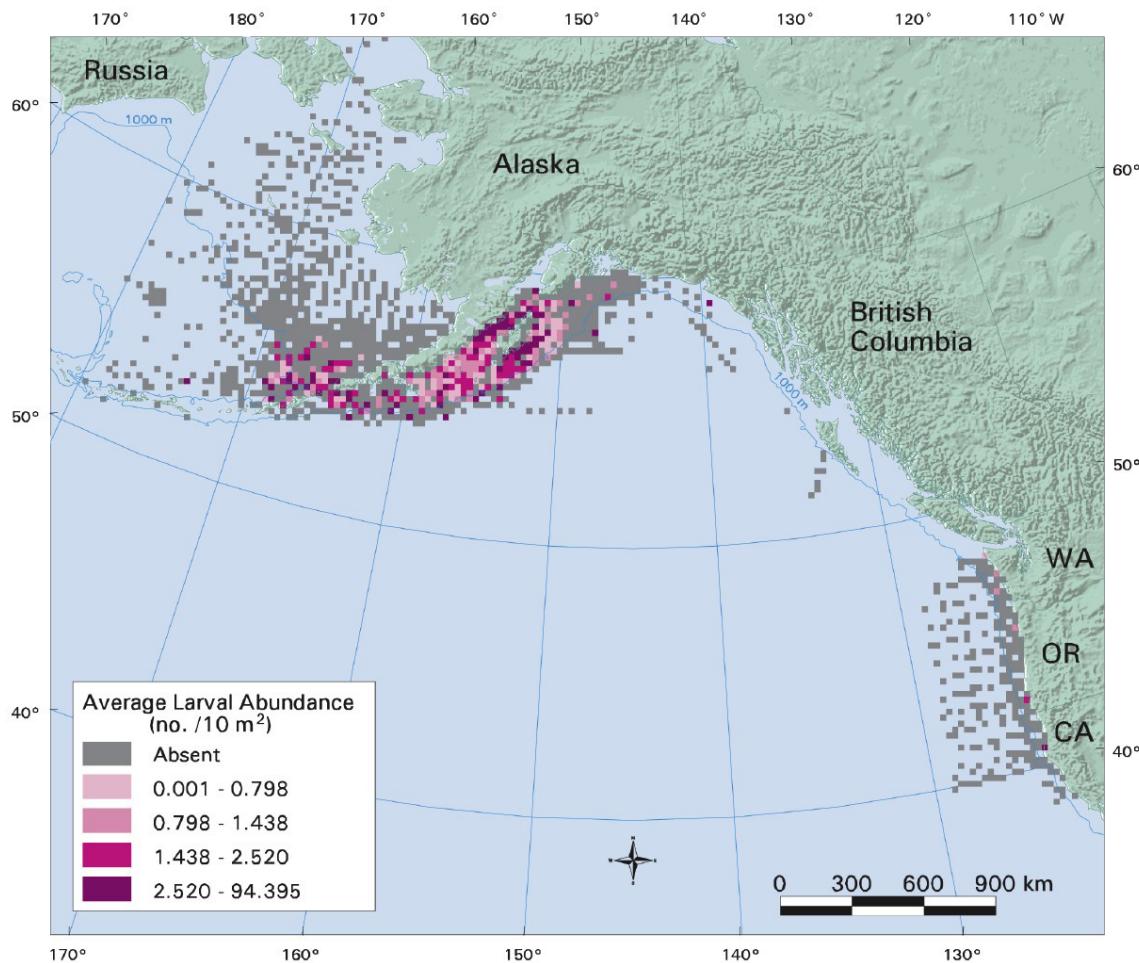


Figure 3.7. Larval kelp greenling (*Hexagrammos decagrammus*) distributions from 1979 - 2000. Units are number collected per 10 m². Reproduced with permission from Matarese et al. (2003).

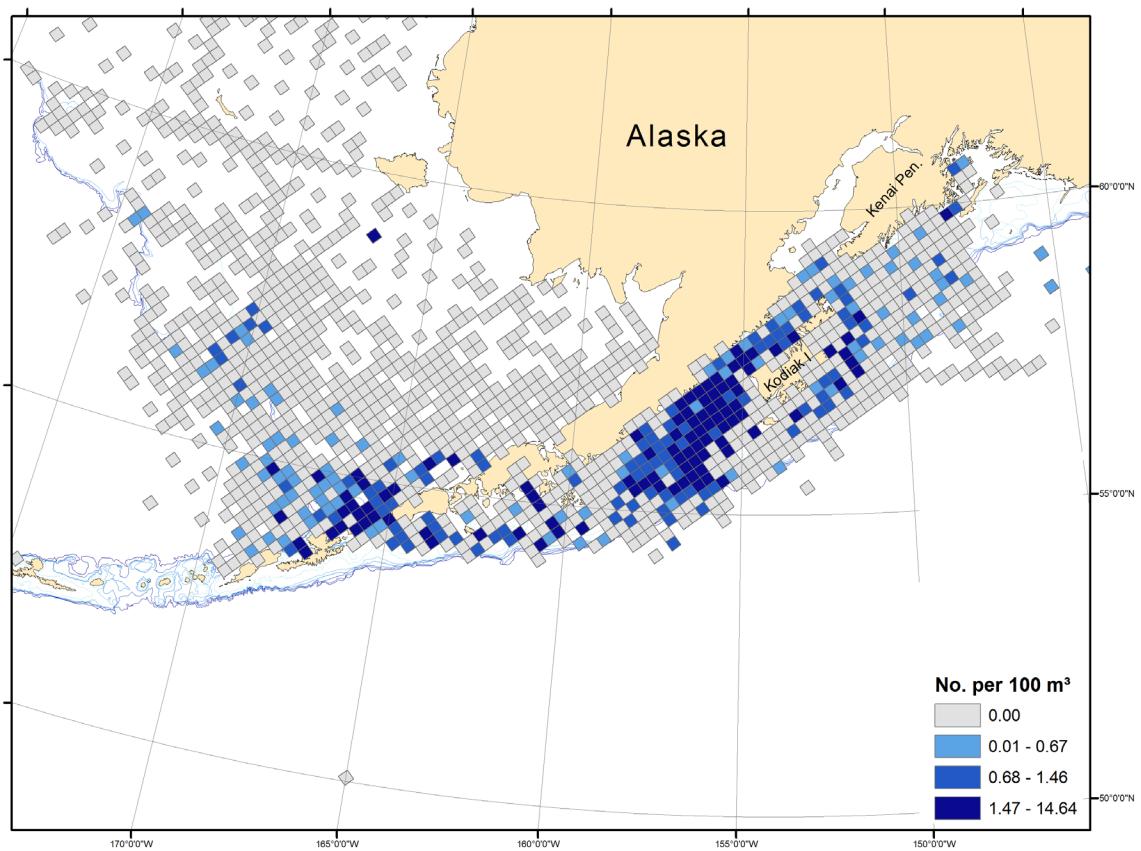


Figure 3.8. Paralarval *Enteroctopus dofleini* spatial distributions for 1991 - 2008. Units are number collected per 100 m³.

Chapter IV: Investigating the early life history of pelagic cephalopods from the Bering Sea and Gulf of Alaska, 1991 - 2009

Abstract

Early life history data on 11 species of pelagic cephalopods from the Gulf of Alaska and Bering Sea was analyzed. The most abundant species were *Berryteuthis anonymus*, *Gonatus onyx*, *Berryteuthis magister*, and *Gonatopsis borealis*. Their spatial and vertical distributions were determined as well as paralarval duration and hatching timing and locations. The data presented here provide a useful framework for design research targeted at understanding cephalopods in the region by elucidating these early life history traits.

Introduction

The Gulf of Alaska and Bering Sea are highly productive ecosystems and are home to one of the world's largest fisheries, walleye pollock (*Theragra chalcogramma*). These regions are similar in that both are dominated by episodic events but the Bering Sea and Gulf of Alaska are very different structurally - the Bering Sea is dominated by a broad, shallow shelf while the shelf in the Gulf of Alaska is relatively narrow (Figure 4.1). The shelf in the Gulf of Alaska has valleys and troughs that facilitate the movement of deep-water organisms onto the shelf. An annual large eddy produced in early spring also helps to entrain deep-sea organisms and transport them to the shelf, as well as transport shelf organisms offshore. High winds generated by the surrounding mountainous landmass mix the shelf water and produce episodic upwelling. The current in the Bering Sea is dominated by the portion of the Alaska coastal current that flows through Unimak Pass. Winds in the Bering Sea also mix the shelf water there. A result of these differences is two

distinct ecosystems that can accommodate a diverse assemblage of cephalopods.

The cephalopods of the region include five orders (Myopsida, Oegopsida, Octopoda, Sepioidea, and Vampyromorpha), two of which (Myopsida and Vampyromorpha) were only published from Alaskan waters two years ago (Jorgensen, 2009) (Table 4.1). Of the 29 species that occur in Alaskan waters, the life history of only two of them is known (*Enteroctopus dofleini* (Wölker, 1910) and *Doryteuthis opalescens* (Berry, 1911)), and the information of which is based on more temperate populations. Very little is known about the other 27 species.

Cephalopods are important members of the Bering Sea and Gulf of Alaska ecosystems (Nesis, 1997; Okutani et al., 1988; Radchenko, 1992). Vecchione (1987) concluded the best way to study populations of cephalopods was via the paralarval stage. Of the 29 species of cephalopod that occur in the Bering Sea and Gulf of Alaska, 11 are represented in the paralarval collections (Table 4.2). Cephalopod paralarvae have been collected as bycatch during ichthyoplankton surveys in the Gulf of Alaska and Bering Sea since 1981. This represents the largest contiguous data set of cephalopod paralarvae from the region.

The primary objective of this study was to investigate the variations in the early life history strategies of the planktonic paralarval stages of cephalopods in the Bering Sea and Gulf of Alaska.

Methods

Cephalopods were collected during ongoing ichthyoplankton surveys, conducted since 1981. Surveys were conducted from February to October with the majority of samples taken in April and May. Sampling was done using MOCNESS, Tucker, Methot, and neuston samplers but the 60 cm bongo was used most often. Net mesh sizes were typically either 333 or 505 µm except the Methot which has a 1000 µm. Net contents were fixed with 5% formalin buffered seawater solution and

sorted for ichthyoplankton and cephalopod paralarvae. Specimens were identified to species using Jorgensen (2007) and mantle length (ML) was recorded. Cephalopod catch per unit effort (CPUE) was calculated using volume filtered data recorded for each sample from calibrated flowmeters mounted at the net opening. Values of CPUE are presented at number per 100 m³.

For ease of data visualization, all catch data from all years was summed spatially in 20 x 20 km cells and temporally into two week bins beginning at the earliest Julian day sampled. Mantle length data were condensed into half millimeter bins using standard rounding rules (e.g. 2.251 - 2.75 mm mantle was represented by 2.5 mm bin value). Samples obtained with the MOCNESS (Multiple Opening Closing Net Environmental Sampling System) are displayed as CPUE (number per 100 m³) for each species at the midpoint of each haul. For example, a tow that sampled from 100 m to 50 m is represented as 75 m.

Results

Eleven species of Decapodiformes in the Order Oegopsida were collected and identified (Table 4.2) (a twelfth species was collected by the plankton samplers, *Belonella borealis*, however, it was a juvenile, not paralarvae so will not be presented here). The four most abundant species were examined in detail and presented in sections I - IV. The remaining nine rare species are presented in section V.

I. *Berryteuthis anonychus*

Berryteuthis anonychus was collected primarily in the Gulf of Alaska beginning in mid-April. Sampling in February to early April was limited to an area south, southwest, and northeast of Kodiak Island (Figures 4.2A-C). Mid-April samples yielded patches of *B. anonychus* at the shelfbreak in the region south of the Kenai Peninsula at the shelfbreak, near the mouth of Amatuli Trough (Figure

2D). Extensive sampling in the Bering Sea began in mid-April, which yielded only a single location with this species, at the shelfbreak near Bering Canyon. Sampling during late April to early May was more extensive in both regions. *Berryteuthis anonymus* had highest values at the shelfbreak near Amatuli Trough in the Gulf of Alaska. There were a few positive cells on the shelf, primarily in the region northeast of Kodiak Island but also near the shelfbreak southwest of Kodiak Island. Shelikof Straight was devoid of specimens. Despite more extensive sampling on the Bering Sea shelf, no specimens were collected. A single location at the shelfbreak north of Umnak Island was the only positive location in the Bering Sea (Figure 4.2E).

Spatial coverage of sampling was greater during 7 - 20 May, extending southwest to the Shumagin Islands (southwest of Kodiak Island) and filling in, somewhat, a gap in sampling between Amatuli Trough and Kodiak Island. *Berryteuthis anonymus* abundances were highest at the shelfbreak and on the shelf near Amatuli Trough and at the shelfbreak southwest of Kodiak Island. Positive cells in the Bering Sea were randomly distributed in the region north of Unimak and Unalaska Islands over the canyon, shelfbreak, and shelf (Figure 4.2F).

The period of 21 May - 3 June was the most intensively sampled period during the year in the Gulf of Alaska with relatively few samples in the Bering Sea; sampling was primarily on the Gulf of Alaska shelf with some samples at the shelfbreak and very few over the abyss. The region northeast of Kodiak Island had high abundances on the shelf, shelfbreak, and over the abyss however the highest abundances were on the shelf and shelfbreak southwest of Kodiak Island between Chirikof Island and the Shumagin Islands as well as a region south of Unimak Island. In addition to these hot spots, there were many positive cells randomly distributed on the shelf, including in Shelikof Strait (Figure 4.2G).

Sampling effort during the period of 4 - 17 June was much less extensive and intensive. Only 14 cells were sampled in the Bering Sea; of them, the two just north

of Unimak Pass were positive for *B. anonychus*. In the Gulf of Alaska, sampling was primarily on the shelf and shelfbreak south of Umnak, Unalaska, and Unimak Islands and northeast of Kodiak Island with a few samples southwest of Kodiak Island. Highest abundances were at the shelfbreak south of Umnak, Unalaska, and Unimak Islands followed by the region northeast of Kodiak Island (Figure 4.2H).

Sampling during 18 June - 1 July was only conducted in the Bering Sea, primarily on the shelf. *Berryteuthis anonychus* was not present in any of the samples (Figure 4.2I). The period of 2 - 15 July had few samples in both the Bering Sea and Gulf of Alaska with the only positive cells over the shelfbreak southeast of Kodiak Island (Figure 4.2J). The period of 16 - 29 July had samples from the Bering Sea shelf and the area south and east of Kodiak Island. The cell at the mouth of Amatuli Trough in the Gulf of Alaska had the highest abundance; other locations were randomly distributed in the Bering Sea samples and Gulf of Alaska samples (Figure 4.2K).

Few samples were taken over the Bering Sea shelf and shelfbreak and the shelf south of the Kenai Peninsula and Prince Williams Sound in the Gulf of Alaska during the period of 30 July - 12 August. Only a single cell south of the Kenai Peninsula was positive for *B. anonychus* (Figure 4.2L). No sampling was conducted during 13 - 26 August. Sampling during 27 August - 9 September was limited to a relatively small region east of Kodiak Island as well as a small area east of the Shumagin Islands; no *B. anonychus* were collected (Figure 4.2M).

Sampling extent and intensity was greater during the period of 10 - 23 September, however only a single cell at the shelfbreak south of Kodiak Island was positive for *B. anonychus* (Figure 4.2N). The period of 24 September - 7 October was the last temporal bin with samples and had just four cells; no *B. anonychus* were collected (Figure 4.2O).

In all, 3224 *B. anonychus* were collected. Of these, 1891 individuals were

measured and their mantle length (ML) recorded. Mantle lengths ranged from 2.5 to 8.5 mm, with a single individual at 13.5 mm; peak ML bin was 4.5 mm (Figure 4.3).

Of the 1892 measured specimens, 23 were collected from the Bering Sea and 1869 were collected from the Gulf of Alaska. *Berryteuthis anonymus* was collected as early as Julian day 107 and late as 204 with a peak between Julian days 124 and 141 in the Bering Sea (Figure 4.4A). It was collected between Julian day 100 and 212 in the Gulf of Alaska with a peak between Julian days 116 and 158 (Figure 4.4B).

MOCNESS was used to obtain discrete depth distribution information. In the 705 MOCNESS samples, 172 *B. anonymus* were collected. Sampling was conducted between the surface and 650 m; however the majority of sampling occurred in the upper 100 m. *Berryteuthis anonymus* was collected from the surface to 110 m; maximum abundances were found at a midpoint depth of 6 m (Figure 4.5).

II. *Gonatus onyx*

Gonatus onyx was collected primarily in the Gulf of Alaska throughout the majority of time bins. During 12 February - 11 March, it was found in only three cells at the shelfbreak south and southwest of Kodiak Island (Figures 4.6A & B). It was collected in all six cells sampled during 26 March - 8 April; all located at the shelfbreak south of Kenai Peninsula (Figure 4.6C). It was collected from the majority of cells sampled during 9 - 22 April in the same area; however, it was only found in six cells along the shelfbreak in the Bering Sea (Figure 4.6D).

Sampling intensity and extent increased in each of the next three two-week bins, 23 April - 3 June. During 23 April - 6 May, *Gonatus onyx* was found only in six cells in the Bering Sea, all at the shelfbreak; in the Gulf of Alaska, it was found at the shelfbreak and on the shelf, including in Shelikof Strait (Figure 4.6E). During 7 - 20

May, Bering Sea specimens were limited to a region north of Umnak, Unalaska, and Unimak Islands. Highest concentrations during this time were in the Gulf of Alaska south of the Kenai Peninsula. The remaining samples were found over the outer shelf, at the shelfbreak, and over the abyss in the northern Gulf of Alaska (Figure 4.6F).

Sampling during 21 May - 3 June was focused on the shelf in the Gulf of Alaska. In the few cells sampled in the Bering Sea, only three cells were positive for *G. onyx*, all were at the shelfbreak near Unalaska Island or in Unimak Pass. Highest concentrations in the Gulf of Alaska were in the region between Kodiak and the Shumagin Islands, near the shelfbreak. Remaining samples were found throughout the shelf region, including Shelikof Strait (Figure 4.6G).

Sampling was relatively reduced during 4 - 17 June and specimens were most abundant at or near the shelfbreak in the Gulf of Alaska in the regions south of the Kenai Peninsula, south of Unalaska and Umnak Islands and south of Unimak Island (Figure 4.6H). Sampling during 18 June - 1 July was limited to the Bering Sea; *G. onyx* was not collected (Figure 4.6I). Sampling during 2 - 15 July was also reduced but included the Gulf of Alaska. Only four cells in the Gulf of Alaska were positive for *G. onyx* (Figure 4.6J). During 19 - 29 July, sampling was limited to the shelf in the Bering Sea and Gulf of Alaska; highest concentrations were at the shelfbreak in the Gulf of Alaska. In the Bering Sea, three of the four positive cells were on the shelf, the fourth was at the shelfbreak (Figure 4.6K).

Sampling was limited during 30 July - 12 August; *G. onyx* was found in only five cells in the Bering Sea over the shelfbreak and abyss (Figure 4.6L). Sampling during 27 August - 9 September was limited to the Gulf of Alaska; *G. onyx* was not collected (Figure 4.6M). Sampling during 10 - 23 September was extensive but only over the shelf in the Gulf of Alaska; only four cells were positive for *G. onyx* (Figure 4.6N). Sampling during 24 September - 7 October was the least extensive (4 cells)

and *G. onyx* was not collected there (Figure 4.6O).

In all 676 *G. onyx* were collected, of these the mantle length of 533 was measured. Mantle lengths ranged from 3.5 - 20.5 mm, with a single 27 mm ML specimen. A length frequency graph shows an increase in frequency of specimens between 5 and 11.5 mm ML with no clear peak (Figure 4.7).

Of the 533 specimens measured, 52 were collected from the Bering Sea, 482 from the Gulf of Alaska. *Gonatus onyx* was collected from Julian day 107 to 221 in the Bering Sea (Figure 4.8A). It was collected from Julian day 96 to 256 in the Gulf of Alaska with a peak corresponding to peak spring-time sampling (Figure 4.8B).

In the 705 MOCNESS samples, 97 *G. onyx* were collected. *Gonatus onyx* was collected throughout the upper 100 m with a peak abundance at the 16 m midpoint (Figure 4.9). A single specimen was collected in a tow that sampled 140 - 190 m.

III. *Berryteuthis magister*

Although *Berryteuthis magister* abundances were not high, it was collected throughout most of months sampled in both the Bering Sea and Gulf of Alaska. From 12 February to 8 April, it was found in five cells, three of which were at the shelfbreak, one over the abyss, and one on the shelf near southern Kodiak Island (Figures 4.10A-C). Sampling during 9-22 April had increased in the Bering Sea; sampling in the Gulf of Alaska was reduced and limited to an area south of the Kenai Peninsula. *Berryteuthis magister* was abundant in cells over the shelfbreak and abyss in both the Bering Sea and Gulf of Alaska (Figure 4.10D).

Sampling on the shelf in both the Bering Sea and Gulf of Alaska increased during 23 April - 6 May, however *B. magister* abundance decreased. It was found primarily at the shelfbreak in the Bering Sea. Highest abundances were at the shelfbreak in the Gulf of Alaska; other positive cells were located on the shelf and

shelfbreak (Figure 4.10E).

Sampling during 7 - 20 May was extensive in the Bering Sea and Gulf of Alaska. *Berryteuthis magister* was most abundant in the region north of Unimak, Unalaska, and Umnak Islands and in Unimak Pass in the Bering Sea. In the Gulf of Alaska, highest abundances were in the region south of the Kenai Peninsula (Figure 4.10F). Sampling during 21 May - 3 June was primarily in the Gulf of Alaska, over the shelf. Highest abundances were in the region between Kodiak and the Shumagin Islands, near the shelfbreak. High abundances were also found at the shelfbreak and over the abyss south of the Kenai Peninsula and on the shelf south of Unimak Island.

Few samples were taken in the Bering Sea, one cell over the shelfbreak north of Unalaska was positive for *Berryteuthis magister* (Figure 4.10G). Sampling during 4 - 17 June was relatively reduced. *Berryteuthis magister* was collected at two cells in Unimak Pass in the Bering Sea and in the Gulf of Alaska over the shelf and shelfbreak (Figure 4.10H). Sampling during 18 June - 1 July was limited to the Bering Sea; *B. magister* was not collected (Figure 4.10I). Sampling during 2 - 15 July included both the Gulf of Alaska and Bering Sea but was not extensive in either area. *Berryteuthis magister* was found only in the Gulf of Alaska samples; highest abundances were over the abyss however several cells over the shelf also had high abundances (Figure 4.10J).

Sampling during 16 - 29 July and 30 July - 12 August included both the Bering Sea and Gulf of Alaska but was not extensive; *B. magister* was found in both areas. During 16 - 29 July, it was found on the shelf in the Bering Sea but highest abundances were at the shelfbreak in the Gulf of Alaska (Figure 4.10K). During 30 July - 12 August, it was found at the shelfbreak and over the abyss in the Bering Sea and on the shelf in the Gulf of Alaska (Figure 4.10L). Sampling did not occur during 13 - 26 August.

Sampling was limited to the Gulf of Alaska in the three remaining temporal bins: 27 August - 9 September, 10 - 23 September, and 24 September - 7 October. Sampling during 27 August - 9 September revealed only a single positive cell at the shelfbreak (Figure 4.10M). Sampling during 10 - 23 September had three positive cells, all at the shelfbreak (Figure 4.10N). And sampling during 24 September - 7 October had one positive cell, over the abyss (Figure 4.10O).

In all, 629 *B. magister* were collected, of which the mantle length of 465 was measured. Mantle lengths ranged from 3.0 - 14.0 mm, with single specimens at 18, 20, 21.5, and 23.5 mm and a peak in frequency 6.5 mm ML (Figure 4.11).

Of the 465 measured specimens, 228 were collected from the Bering Sea and 238 were collected from the Gulf of Alaska. *Berryteuthis magister* was collected from Julian day 106 - 221 in the Bering Sea (Figure 4.12A). It was collected from Julian day 97 to 269 in the Gulf of Alaska (Figure 4.12B).

In the 705 MOCNESS samples, 70 *B. magister* were collected. It was found throughout the upper 56 m with a few specimens collected at 94 m; the midpoint depth with the highest abundance was 16 m (Figure 4.13).

IV. *Gonatopsis borealis*

Gonatopsis borealis was the least abundant of the numerically dominant squids. During 12 - 25 February, sampling was limited to southeast and northeast of Kodiak Island; *G. borealis* was found in only two cells at the shelfbreak (Figure 4.14A). Sampling was limited to south and west of Kodiak Island during 26 February - 11 March; *G. borealis* was found at three cells along the shelfbreak (Figure 4.14B). Sampling was not conducted during 12 - 25 March. Sampling during 26 March - 8 April was limited to six cells at the shelfbreak and over the abyss in the Gulf of Alaska; one cell was positive for *G. borealis* (Figure 4.14C). During 9 - 22 April, sampling was extensive in the Bering Sea while limited to south of the Kenai in the

Gulf of Alaska. *Gonatopsis borealis* was limited to a few cells at the shelfbreak and over the abyss in both the Bering Sea and Gulf of Alaska (Figure 4.14D).

Sampling was more extensive in the Bering Sea and Gulf of Alaska during 23 April - 6 May. *Gonatopsis borealis* was collected in only two cells at the shelfbreak and one over the abyss in the Bering Sea and at the shelfbreak and over the shelf in the Gulf of Alaska (Figure 4.14E). Despite more extensive sampling on the shelf in both the Bering Sea and Gulf of Alaska during 7 - 20 May, *G. borealis* was primarily limited to just a few areas. In the Bering Sea, it was clustered in the area north of Unimak, Unalaska, and Umnak Islands. In the Gulf of Alaska, it showed the highest abundances over the abyss and shelfbreak south of the Kenai and over the shelfbreak in the area between Kodiak Islands and the Shumagin Islands (Figure 4.14F).

Sampling during 21 May - 3 June was limited in the Bering Sea but extensive over the shelf in the Gulf of Alaska. Highest abundances were over the abyss and at the shelfbreak south of the Kenai Peninsula, near the shelfbreak between Kodiak Island and the Shumagin Islands, and over the shelf south of Unimak Island (Figure 4.14G).

Sampling during 4 - 17 June was reduced in both the Bering Sea and Gulf of Alaska. Highest abundances were at the shelfbreak south of the Kenai Peninsula, south of Unalaska Island, Unimak Pass, and over the shelfbreak south of Unimak Island (Figure 4.14H). Sampling was limited to the Bering Sea during 18 June - 1 July; *G. borealis* was not collected (Figure 4.14I). Sampling was limited in both the Bering Sea and Gulf of Alaska during 2 - 15 July; *G. borealis* was collected only over the abyss, south of Kenai Peninsula (Figure 4.14J). During 16 - 29 July, it was collected over the shelf in the Bering Sea and at a single cell at the shelfbreak south of the Kenai (Figure 4.14K). Sampling during 30 July - 12 August was limited. Highest abundances were south of the Kenai Peninsula in the Gulf of Alaska; it was

collected at one cell over the shelf and two cells over the abyss in the Bering Sea (Figure 4.14L). Sampling was not conducted during 13 - 26 August.

Sampling during 27 August - 9 September was limited to the Gulf of Alaska. *Gonatopsis borealis* was collected at a single cell over the shelfbreak in the area between Kodiak Island and the Shumagin Islands (Figure 4.14M). Sampling was limited to the Gulf of Alaska during 10 - 23 September. Highest abundances were over the shelf, south of the Kenai Peninsula; five other positive cells were found at the shelfbreak south of the Kenai Peninsula, south of Kodiak Island, and between Kodiak Island and the Shumagin Islands (Figure 4.14N). Sampling during 24 September - 7 October was limited to four cells over the shelfbreak and abyss south of the Kenai Peninsula; *G. borealis* was not collected (Figure 4.14O).

In all, 500 *G. borealis* were collected. Mantle lengths of 367 were measured. Mantle lengths ranged from 3.5 - 8.0 mm, with a single individual at 13.0 mm; frequency peaked at 4.5 mm (Figure 4.15).

Of the 367 measured specimens, 70 were collected from the Bering Sea and 297 were collected from the Gulf of Alaska. *Gonatopsis borealis* was collected from Julian day 107 to 221 in the Bering Sea (Figure 4.16A). It was collected from Julian day 97 to 262 in the Gulf of Alaska (Figure 4.16B).

In the 705 MOCNESS samples, 50 *G. borealis* were collected. It was collected throughout the upper 100 m with highest abundance found at a midpoint depth of 69 m (Figure 4.17).

V. Rare species

In addition to the four abundant species listed above, eight species of squid and one species of octopod were collected (total number collected in parenthesis): *Gonatus madokai* (69), gonatid sp. A (45), *G. middendorffi* (13), *G. berryi* (4), and *G. pyros* (3) (Family Gonatidae), *Galiteuthis phyllura* (46) (Family Cranchiidae),

Chiroteuthis calyx (7) (Family Chiroteuthidae), and *Japetella diaphana* (9) (Family Bolitaenidae).

Among species in the Family Gonatidae, 69 *Gonatus madokai* were collected from the Bering Sea (14) and Gulf of Alaska (55). The average mantle length for the 44 measured specimens was 10.9 mm. Gonatid sp. A was collected from the Bering Sea (11) and Gulf of Alaska (34). The average mantle length for the 33 measured specimens was 7.6 mm. *Gonatus middendorffii* was collected only from the Gulf of Alaska. Of the 13 specimens, eight were measured; the average mantle length was 17 mm. *Gonatus berryi* was collected from the Bering Sea. Of the four specimens collected, only one of 23.6 mm was measurable. *Gonatus pyros* was collected from the Gulf of Alaska. The only measurable specimen of the three collected was 8.9 mm ML.

Two species from the Family Cranchiidae were collected during the study. Of the 46 *Galiteuthis phyllura* collected, 7 were from the Bering Sea and 39 from the Gulf of Alaska. The average mantle length for the 25 specimens measured was 10.4 mm. A single juvenile *Belonella borealis* was collected from the Gulf of Alaska. It was not measured since the study was primarily interested in paralarval specimens.

A single species of the Family Chiroteuthidae, *Chiroteuthis calyx*, was collected only from the Gulf of Alaska. Of the seven specimens collected, three were measured; with average mantle length of 32.4 mm. One species of the Family Bolitaenidae, *Japetella diaphana*, was collected from both the Bering Sea (5) and Gulf of Alaska (4). The average mantle length of the five measured specimens was 6.3 mm.

Discussion

The paralarval stage of several species of cephalopod were collected from the Gulf of Alaska and Bering Sea. Compared to the fish larvae collected at

the same time, which were the basis for the sampling, even the most abundant cephalopod paralarvae are relatively rare. The discussion will be limited to the four most abundant species since the remaining seven species are poorly represented in the data. Because the species are so rare, the data presented is for all time combined which provides important contributions to our understanding of these organisms but limits interpretation.

Berryteuthis anonychus did not appear in the region until mid-April. It reached maximum abundances in May (Figures 4.2F, 4.2G) and was mostly gone by mid-June (Figure 4.2H). Hatching may begin as early as mid-April however the peak abundance is in May. There are two main areas of high abundance, at the shelfbreak south of the Kenai Peninsula and the shelfbreak between Kodiak Island and the Shumagin Islands; there is a third smaller area of high abundance on the shelf, south of Unimak Pass. The paralarvae appear first at the shelfbreak south of the Kenai Peninsula (Figure 4.2F), then become abundant at the shelfbreak south of Kodiak Island and fill in on the shelf (Figure 4.2G), then have highest abundances at the shelfbreak south of Unimak Island (Figure 4.2H). No eggs have been collected. The trend of high abundances moving eastward along the shelfbreak, in the direction of the prevailing ocean current, Alaska Stream, could indicate that the paralarvae are hatching at the shelfbreak from south of the Kenai Peninsula to south of Unimak Island, minimally, and swept onto the shelf via the troughs, canyons, and sea valleys.

It has a very narrow range of mantle lengths (Figure 4.3), indicating that it has a short paralarval duration, is not in the region for very long, or is very efficient at avoiding plankton samplers at a very small size. *Berryteuthis anonychus* paralarvae are the most muscular of the species collected so it is possible that it has the capability to avoid sampling at a small size. The shape of the length frequency graph (Figure 4.3) suggests that the population is well sampled. Based on regions

of highest abundance in the Gulf of Alaska and a relatively low abundances from the Bering Sea, spawning likely occurs in the Gulf of Alaska. Specimens in the Bering Sea were likely swept into the Bering Sea through Unimak Pass by the Alaska Coastal Current.

The pattern of distribution of all available data of *B. anonychus* (Figure 4.18) is very similar to that of arrowtooth flounder (*Atheresthes stomias* (Jordan and Gilbert, 1880)) (Figure 4.19). The eggs and larvae of arrowtooth flounder are highest near the shelfbreak at Amatuli Trough and the Shelikof Sea Valley (Matarese et al., 2003). Arrowtooth flounder is a deep-water spawner in the Gulf of Alaska (Blood et al., 2007). Eggs of *B. anonychus* have not been recorded from the study area so spawning behavior remains unknown however, it can be concluded, based on the similarity in larval distributions between *B. anonychus* and arrowtooth flounder, that *B. anonychus* is also hatching at great depths (400 - 600 m) at the shelfbreak in the Gulf of Alaska, near Amatuli Trough and the Shelikof Sea Valley.

Interpretation of *B. anonychus* mantle length by Julian day data are limited because all years of samples were combined however, based on the presence of very small specimens (approximately 3 mm ML) from Julian day 100 to 212, it can be concluded that *B. anonychus* is spawning from April through July in the Gulf of Alaska. Vertical distribution data also consist of all years combined which limits interpretation however, similar vertical distributions for this species was found by Bower and Takagi (2004). Also, for the purposes of this research, the absolute depth distribution is not as important as the ability to make informed hypotheses about the relative effects of different environmental conditions e.g. winds, sea surface temperature, and eddy activity. Of the four most abundant squids in the study, *B. anonychus* had the shallowest maximum abundances (Figure 4.5).

Gonatus onyx was much less abundant than *B. anonychus* despite its longer duration in the region. It had relatively high abundances from early April through

July (Figures 4.6C - H), in both the Bering Sea and Gulf of Alaska. Given relatively high abundances as far north as 60°N in the Bering Sea, it can be concluded that it is spawning in the Bering Sea as well as the Gulf of Alaska. Grid cells with highest abundances were located at the shelfbreak in both regions, leading to the conclusion that this species is also hatching at the shelfbreak. Although much less abundant, the spatial distribution of paralarval *G. onyx* (Figure 4.20) is similar to that of arrowtooth flounder larvae (Figure 4.19), supporting the conclusion that it is spawning at the shelfbreak.

Gonatus onyx was collected in the plankton from 3.5 to 18 mm ML (Figure 4.7), giving it the longest planktonic duration of a species with planktonic paralarvae in the Gulf of Alaska. It is interesting to note that at the largest sizes, this species has developed hooks on its tentacular clubs and therefore is no longer considered a paralarva but was still collected by the plankton samplers. It appears that *Gonatus onyx* does not undergo an ontogenetic shift in habitat from the paralarval to juvenile stage, this is further evidenced by the strong correlation between Julian day and mantle length for this species (Figure 4.8). Unlike *B. anonychus*, *G. onyx* appears to hatch primarily in the springtime. These data represent the first published reports of the ecology of *G. onyx* paralarvae.

Similar to *G. onyx*, *B. magister* likely hatches at the shelfbreak in the Bering Sea and Gulf of Alaska; in the latter region, paralarvae are swept onto the shelf by prevailing currents via submarine canyons, troughs, and sea valleys. Hatching begins in early April, a month before *B. anonychus*. *Berryteuthis magister* had three main areas of high abundance: the Bering Canyon in the Bering Sea (Figures 4.10D, 4.10F) and the shelfbreak south of the Kenai Peninsula (Figure 4.10F) and between Kodiak Island and the Shumagin Islands in the Gulf of Alaska (Figure 4.10G). The map of *B. magister* distribution for all years combined (Figure 4.21) is similar to that of arrowtooth flounder (Figure 4.19) in the Gulf of Alaska, supporting the conclusion

that *B. magister* is hatching in the deep water off the shelfbreak.

Berryteuthis magister was collected from 3 - 13 mm ML. Like *G. onyx*, larger specimens collected in the plankton had developed tentacular clubs, so would be considered juveniles. The presence of juveniles in the plankton indicates that *B. magister* also does not undergo an ontogenetic shift from the paralarval to the juvenile stage. The paralarvae of *B. magister* and *G. onyx* are morphologically similar, both have large, loose mantles (Jorgensen, 2007). The mantle and head chromatophore patterns are very different but fin size, mantle shape, and arm and tentacle length are very similar throughout the paralarval stage. The morphological similarity of the two species at the paralarval stage may help to explain their persistence in the plankton. The adult stages of these two species are very different, *B. magister* is epibenthic, non-brooder while *G. onyx* is a pelagic, egg-brooder (Seibel and Robson, 2000). *Berryteuthis magister* is also a large squid (reaching over 34 cm ML) while *G. onyx* is relatively small (reaching only 13.5 cm ML). Unlike for *G. onyx*, the length frequency distributions indicate that the population of *B. magister* was well sampled which could indicate that the population of *B. magister* is local while that of *G. onyx* is being replenished by individuals spawned elsewhere. Kubodera (1982) and Okutani (1988) also noted the long paralarval duration of *B. magister*.

Gonatopsis borealis also had three main areas of high abundance: the Bering Canyon in the Bering Sea (Figure 4.14F) and Amatuli Trough and the shelfbreak near the Shelikof Sea Valley in the Gulf of Alaska (Figures 4.14F and G). This species appears in both the Bering Canyon and Amatuli Trough regions at the same time and reaches peak abundances at similar times (7 May - 3 June), supporting the conclusion that *G. borealis* is hatched in both the Bering Sea and Gulf of Alaska. High offshore abundances in the Gulf of Alaska support the idea that *G. borealis* is hatched offshore and swept onto the shelf by prevailing currents and eddies. Mantle length by Julian day scatter plot indicates that *G. borealis* may

have at least two hatching periods, a main hatch beginning in April and a secondary hatch in September; these hatching times roughly correspond to the spring and fall phytoplankton blooms. However, it is important to mention that sampling and identifications were focused on spring time so drawing conclusions about a second hatching period may be premature. Similar to *B. anonychus*, *G. borealis* length frequency distribution indicates a well-sampled population with a short paralarval duration in this region. Similar to *B. anonychus*, at the maximum size collected, *G. borealis* is still in the paralarval stage and therefore its absence in the collection is likely due to its absence in the area, not due to net avoidance. It is notable that *G. borealis* and *B. anonychus* paralarvae are similar morphologically; of the four most abundant species, *G. borealis* and *B. anonychus* have compact, muscular mantles while *G. onyx* and *B. magister* have loose, thin mantles. As adults, *G. borealis* and *B. anonychus* have different ecological niches; *G. borealis* is an epibenthic squid while *B. anonychus* is a pelagic squid.

The cumulative length frequencies (a running total of all the individuals in each length bin summed with the total the individuals in all previous length bins) for the four most abundant species show the differences between the paralarval durations of the four species (Table 4.3; Figure 4.22). *Berryteuthis anonychus* and *G. borealis* have similar short and smooth curves, indicating that they have a short paralarval duration and are sampled well. *Gonatus onyx* and *B. magister* have more gradual, less smooth curves, indicating a longer paralarval duration and the population may not be sampled as well. It is interesting to note that *B. anonychus* and *G. borealis* have compact, muscular mantles while the species with the longer paralarval durations have loose, thin mantles. If growth rates are assumed to be equal, then *B. magister* and *G. onyx* spend at least twice as long in the plankton in this region than do *B. anonychus* and *G. borealis* (since *B. magister* and *G. onyx* reach a size that is twice as large as *B. anonychus* and *G. borealis*).

The rare species, by definition, were poorly sampled during the period of the study so few conclusions can be drawn. However, the regions where the rare species were found are the same regions where the highest abundances were found for the four common species so it would appear that all the species collected as plankton in these regions are hatched at the shelfbreak and not on the shelf. Their presence on the shelf is likely due to the action of currents, wind mixing, and local eddies.

Conclusion

This work makes significant contributions to our understanding of the early life histories of the pelagic cephalopods in the Bering Sea and Gulf of Alaska. All species collected are apparently hatched at the shelfbreak. *Berryteuthis anonychus* appears to be hatched in the Gulf of Alaska but not the Bering Sea while *G. onyx*, *B. magister*, and *G. borealis* are hatched at the shelfbreak in both regions. The Shelikof Sea Valley, Amatuli Trough, and the Bering Canyon are areas of high abundances. *Berryteuthis magister* and *G. onyx* hatch earliest, in April, while *B. anonychus* and *G. borealis* hatch in May. All four species are found throughout the upper 100 m. *Berryteuthis anonychus* and *G. onyx* exhibit highest abundances between 0 and 20 m; *B. magister* had highest abundances between 10 and 70 m; and *G. borealis* had highest abundances at 70 m. These subsurface maxima place the majority of *B. anonychus*, *G. onyx*, and *B. magister* in the surface waters where they will be influenced by varying sea surface temperatures and wind mixing. They have varying paralarval durations, with *B. anonychus* and *G. borealis* apparently leaving the area within a month of hatching while *B. magister* and *G. onyx* stay in the region for two to three months.

Early life history information of the four most abundant squids in the regions examined as well as data on rare species indicates that the Bering Canyon, in the

Bering Sea and Amatuli and Shelikof Sea Valley in the Gulf of Alaska area important regions in the life histories of cephalopods in the Gulf of Alaska and Bering Sea. At least for some of the species, these regions may act as conduits for the transport of hatchlings from the deep-sea into the productive waters of the shelf. This information provides valuable insight when considering possible effects of variations in climatic and oceanographic phenomena on the distribution and abundance of these species.

Table 4.1. Species represented in the paralarval sample collection.

Order	Family	Genus	Species
Oegopsida			
	Chiroteuthidae	<i>Chiroteuthis</i>	<i>calyx</i>
	Cranchiidae	<i>Galiteuthis</i>	<i>phyllura</i>
	Gonatidae	<i>Berryteuthis</i>	<i>anonychus</i>
			<i>magister</i>
		<i>Gonatopsis</i>	<i>borealis</i>
		<i>Gonatus</i>	<i>berryi</i>
			<i>madokai</i>
			<i>middendorffi</i>
			<i>onyx</i>
			<i>pyros</i>
	Unknown	A	

Table 4.2. Species with a planktonic paralarval stage and the number of each collected during the study period (1991 - 2009).

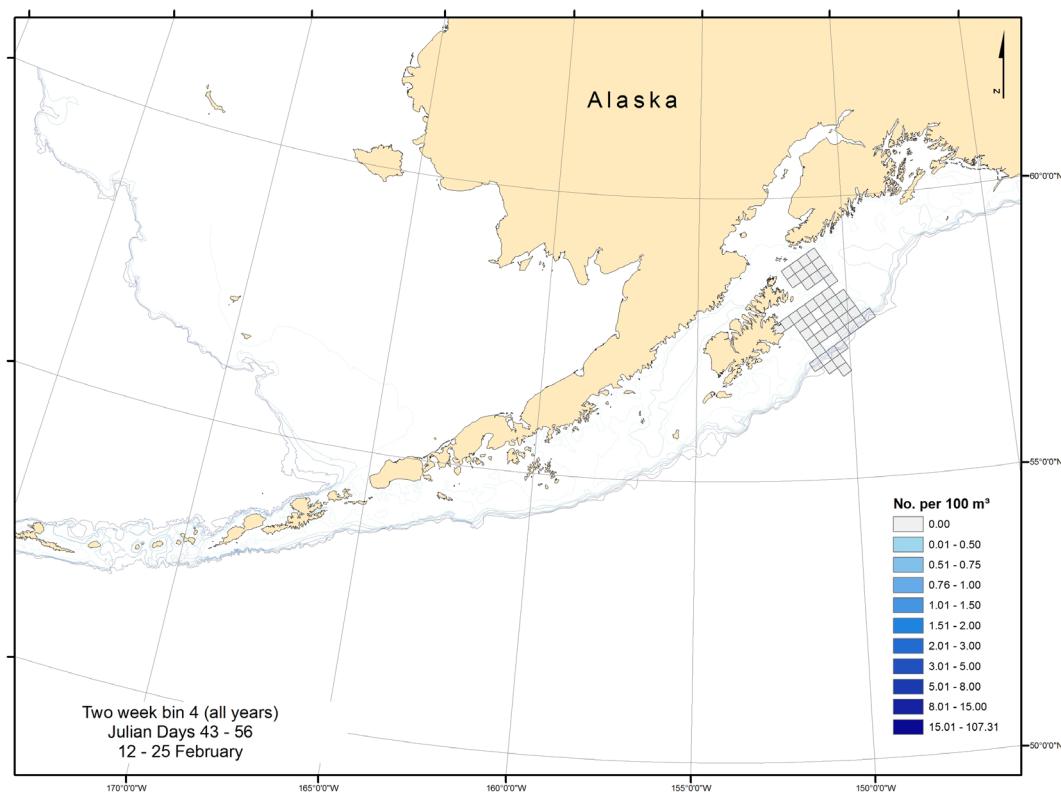
Order	Family	Genus	Species	No. collected
Oegopsida				
	Chiroteuthidae	<i>Chiroteuthis</i>	<i>calyx</i>	7
	Cranchiidae	<i>Galiteuthis</i>	<i>phyllura</i>	46
	Gonatidae	<i>Berryteuthis</i>	<i>anonychus</i>	3224
			<i>magister</i>	629
		<i>Gonatopsis</i>	<i>borealis</i>	500
		<i>Gonatus</i>	<i>berryi</i>	4
			<i>madokai</i>	69
			<i>middendorffi</i>	13
			<i>onyx</i>	676
			<i>pyros</i>	3
		Unknown	A	45
			unknown	337
Octopoda				
	Bolitaenidae	<i>Japetella</i>	<i>diaphana</i>	9

Mantle Length Bin	No. <i>B. anonychus</i>	Cumulative No. <i>B. anonychus</i>	No. <i>borealis</i>	Cumulative No. <i>borealis</i>	No. <i>G. borealis</i>	Cumulative No. <i>G. borealis</i>	No. <i>G. madokai</i>	Cumulative No. <i>G. madokai</i>	No. <i>B. magister</i>	Cumulative No. <i>B. magister</i>	No. <i>G. middendorffii</i>	Cumulative No. <i>G. middendorffii</i>	No. <i>G. onyx</i>	Cumulative No. <i>G. onyx</i>	No. Unknown A	Cumulative No. Unknown A	
2.5	1	1	2	2	9	9	0	0	5	5	0	0	0	0	0	0	
3	1	2	24	24	9	9	0	0	5	5	10	10	0	0	5	5	
3.5	22	24	102	126	38	47	0	0	9	9	19	21	0	0	6	11	
4	78	126	238	238	72	119	0	0	21	21	40	40	0	0	6	17	
4.5	136	238	316	316	34	153	0	0	19	19	59	59	0	0	15	32	
5	78	316	380	380	14	167	2	2	19	19	78	78	0	0	22	54	
5.5	64	380	411	411	8	175	2	4	29	29	107	107	0	0	13	67	
6	31	411	427	427	4	179	3	7	33	33	140	140	0	0	11	78	
6.5	16	427	434	434	1	180	7	7	27	27	167	167	0	0	20	98	
7	7	434	435	435	1	181	3	10	22	22	189	189	0	0	19	117	
7.5	1	435	441	441	1	182	1	11	15	15	204	204	0	0	19	136	
8	6	441	443	443	2	182	11	10	214	214	0	0	20	20	156	1	
8.5	2	443	443	443	9	182	2	13	5	5	219	219	0	0	17	173	
9	9	443	443	443	443	182	13	9	228	228	0	0	10	10	183	1	
9.5	9	443	443	443	443	182	4	17	6	234	234	1	1	12	195	24	24
10	10	443	443	443	443	182	1	18	3	237	237	1	1	23	218	3	24
10.5	10.5	443	443	443	443	182	2	20	5	242	242	1	2	12	230	1	24
11	11	443	443	443	443	182	2	22	2	244	244	2	2	11	241	1	24
11.5	11.5	443	443	443	443	182	3	25	1	245	245	2	2	10	251	29	29
12	12	443	443	443	443	182	2	27	2	247	247	2	2	6	257	29	29
12.5	12.5	443	443	443	443	182	1	29	2	249	249	2	2	8	265	29	29
13	13	443	443	443	443	183	2	29	2	249	249	1	2	12	230	1	28
13.5	1	444	444	444	444	183	29	29	249	249	2	2	10	275	29	29	
14	14	444	444	444	444	183	2	31	1	250	250	2	2	3	278	29	29
14.5	14.5	444	444	444	444	183	31	31	250	250	2	2	2	280	29	29	
15	15	444	444	444	444	183	1	32	32	250	250	1	3	3	283	29	29
15.5	15.5	444	444	444	444	183	1	33	33	250	250	1	4	2	285	29	29
16	16	444	444	444	444	183	33	33	250	250	4	4	1	286	29	29	
16.5	16.5	444	444	444	444	183	1	34	34	250	250	4	4	2	288	29	29
17	17	444	444	444	444	183	1	35	35	250	250	4	4	3	291	29	29
17.5	17.5	444	444	444	444	183	1	36	36	250	250	4	4	1	292	29	29
18	18	444	444	444	444	183	36	1	251	251	1	5	1	293	29	29	
18.5	18.5	444	444	444	444	183	1	37	37	251	251	5	5	1	293	29	29
19	19	444	444	444	444	183	1	38	38	251	251	5	5	1	295	29	29
19.5	19.5	444	444	444	444	183	38	38	251	251	1	6	1	294	29	29	
20	20	444	444	444	444	183	1	39	1	252	252	1	7	1	295	29	29
20.5	20.5	444	444	444	444	183	39	39	252	252	1	7	1	295	29	29	
21	21	444	444	444	444	183	39	39	252	252	1	7	1	295	29	29	
21.5	21.5	444	444	444	444	183	39	1	253	253	1	8	1	295	29	29	
22	22	444	444	444	444	183	39	39	253	253	1	8	1	295	29	29	
22.5	22.5	444	444	444	444	183	39	39	253	253	1	8	1	295	29	29	
23	23	444	444	444	444	183	39	39	253	253	1	9	1	295	29	29	
23.5	23.5	444	444	444	444	183	39	1	254	254	1	9	1	295	29	29	
24	24	444	444	444	444	183	39	39	254	254	1	9	1	295	29	29	
24.5	24.5	444	444	444	444	183	39	39	254	254	1	9	1	295	29	29	
25	25	444	444	444	444	183	39	39	254	254	1	9	1	295	29	29	
25.5	25.5	444	444	444	444	183	39	39	254	254	1	9	1	295	29	29	
26	26	444	444	444	444	183	39	39	254	254	1	9	1	295	29	29	
26.5	26.5	444	444	444	444	183	39	39	254	254	1	9	1	295	29	29	
27	27	444	444	444	444	183	39	39	254	254	1	9	1	296	29	29	

Table 4.3. Cumulative length frequency table. The 'cumulative' column is the running total of the 'No.' column.



Figure 4.1. Map of study area.

A

Figures 4.2A-O. Maps of *Berryteuthis anonychus* distribution and abundance. Each cell represents a 20 x 20 km region within which at least one station was occupied. Grey grid cells indicate that the cell was sampled but no *B. anonychus* were collected. Colors are according to legend and represent the summed number per 100 cubic meters at each station within each cell for the two-week period listed on the individual maps.

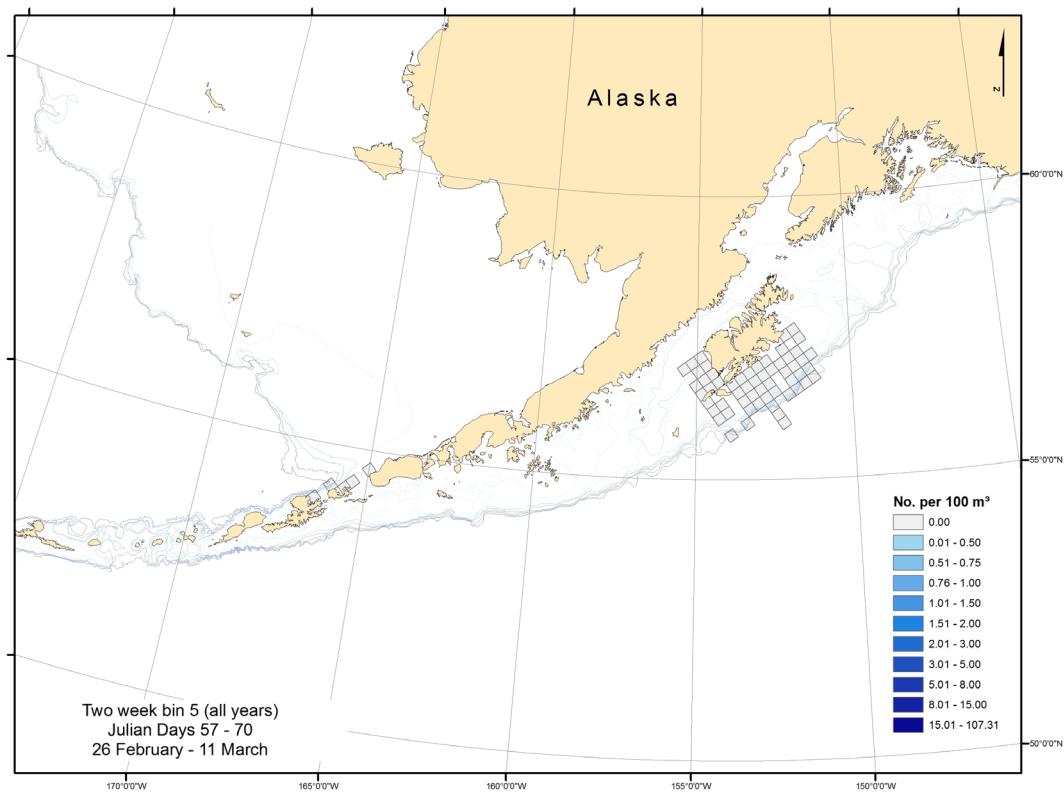
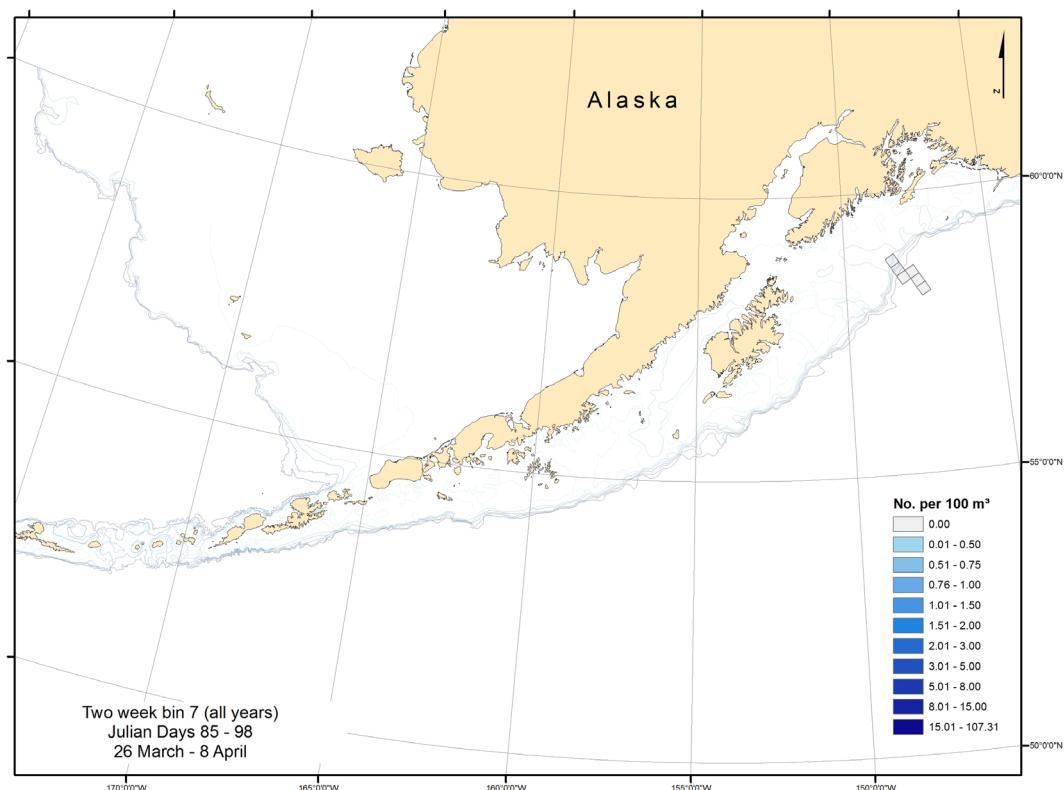
B**C**

Figure 4.2A-O continued.

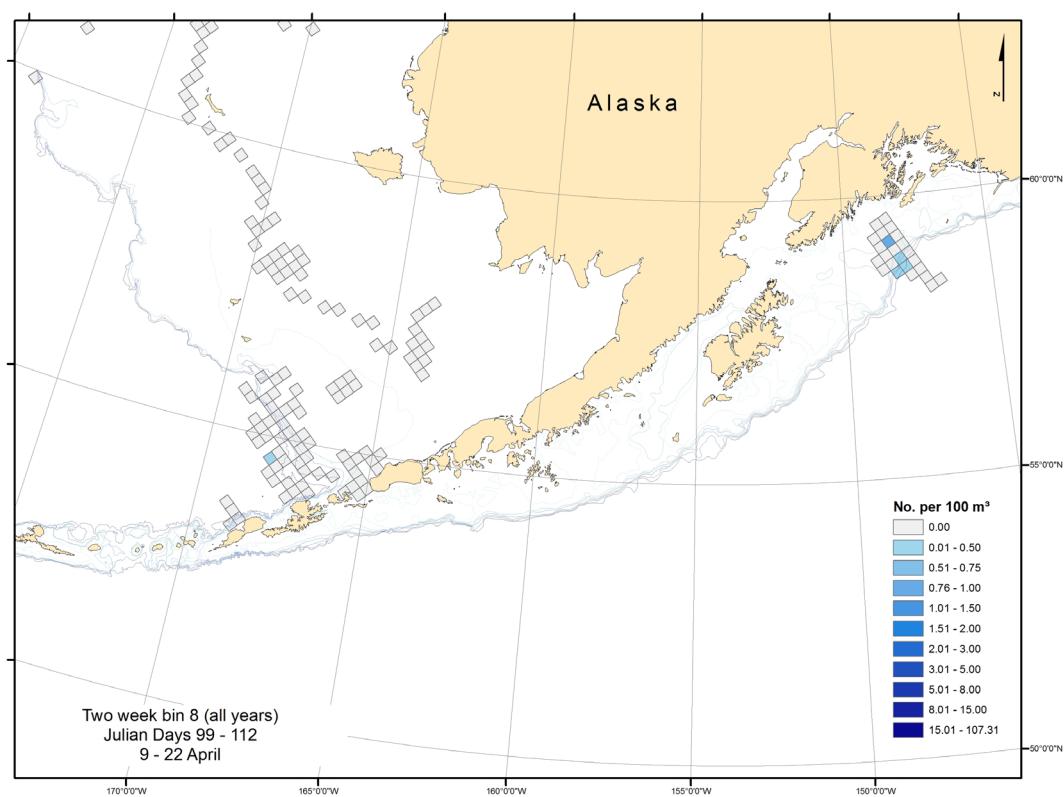
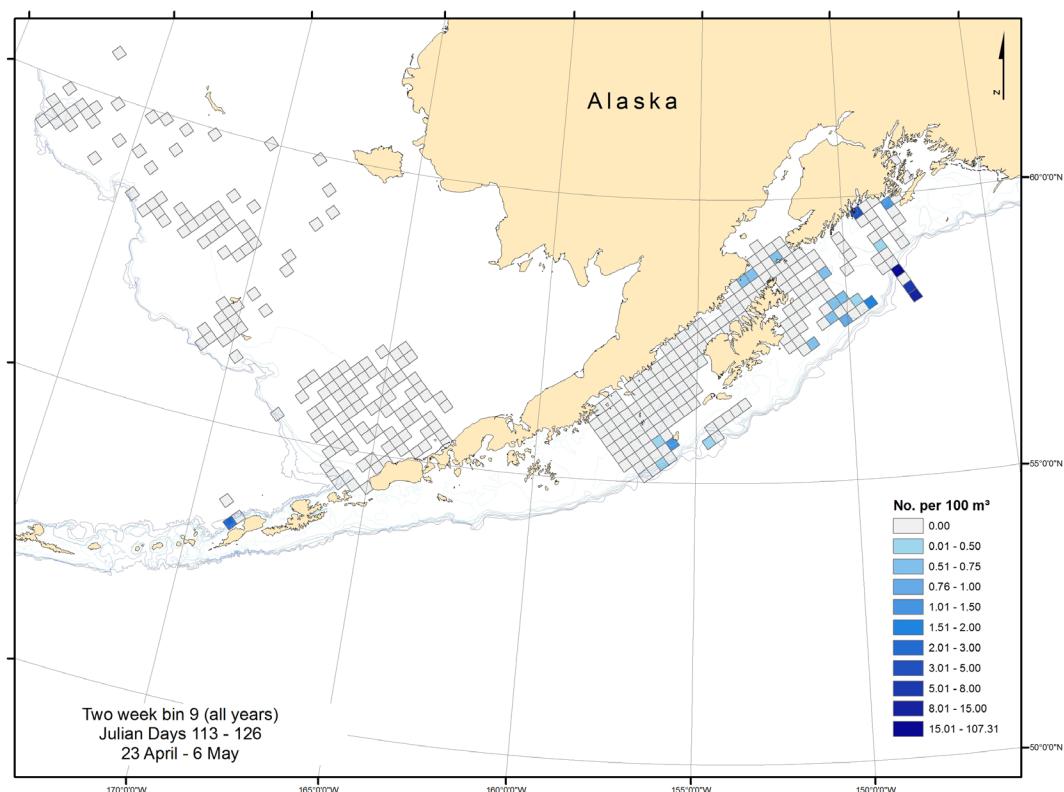
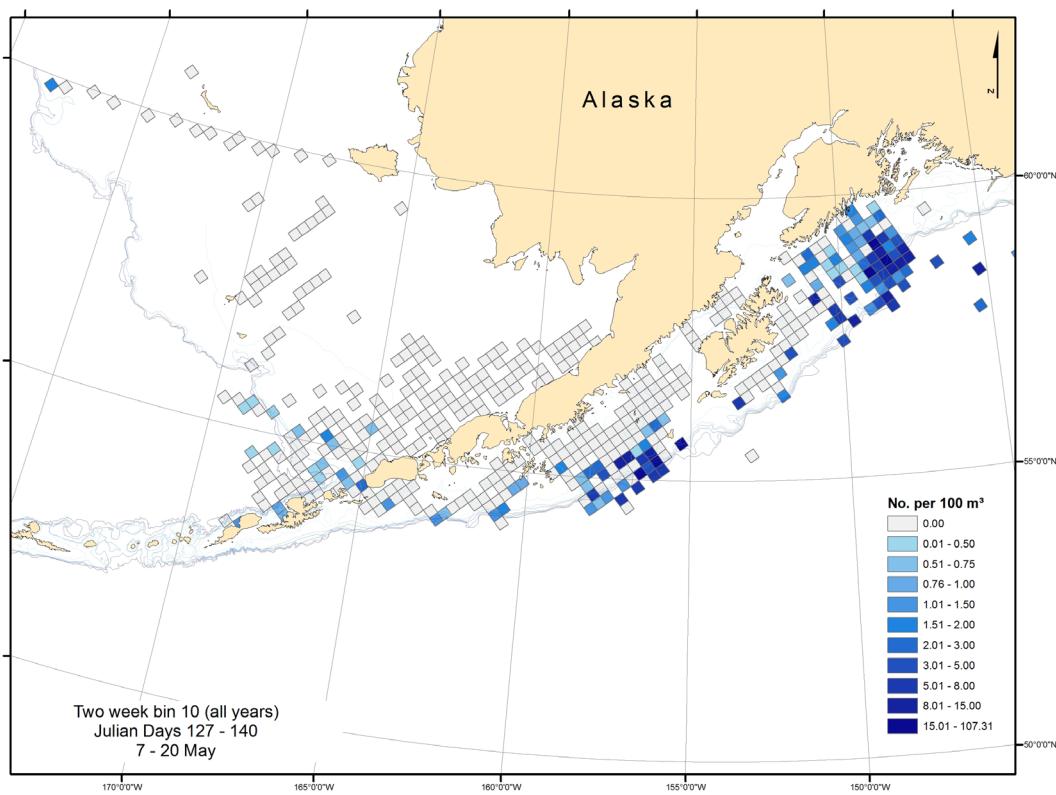
D**E**

Figure 4.2A-O continued.

F



G

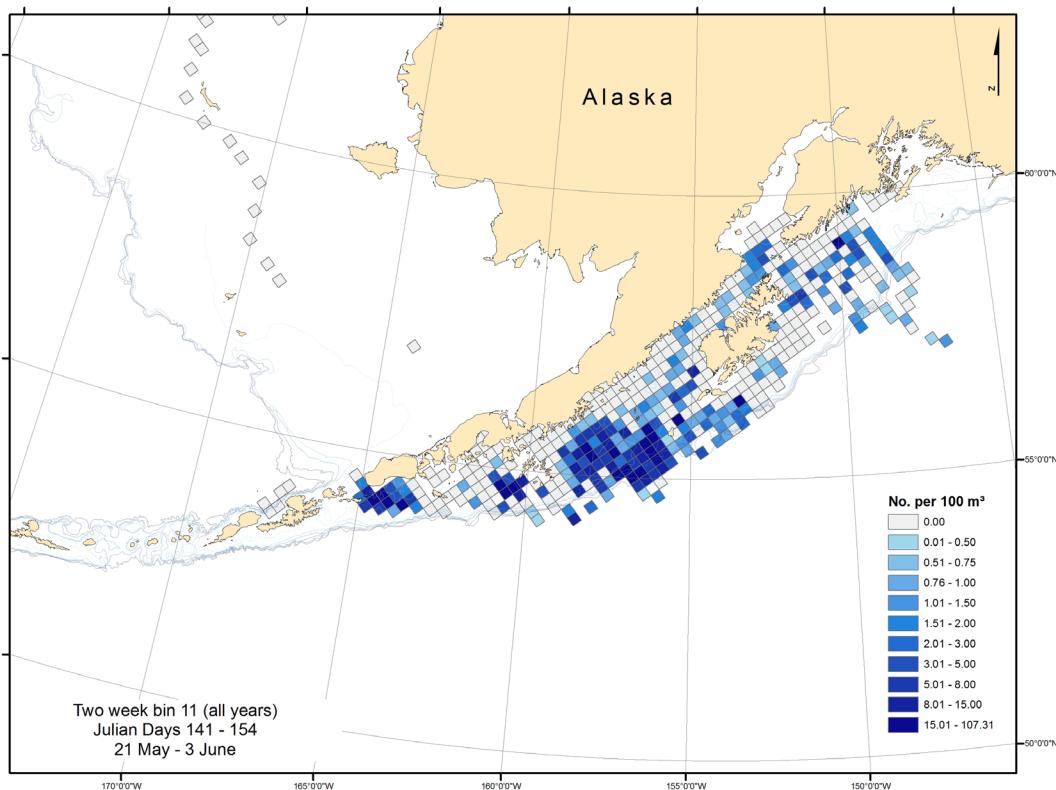
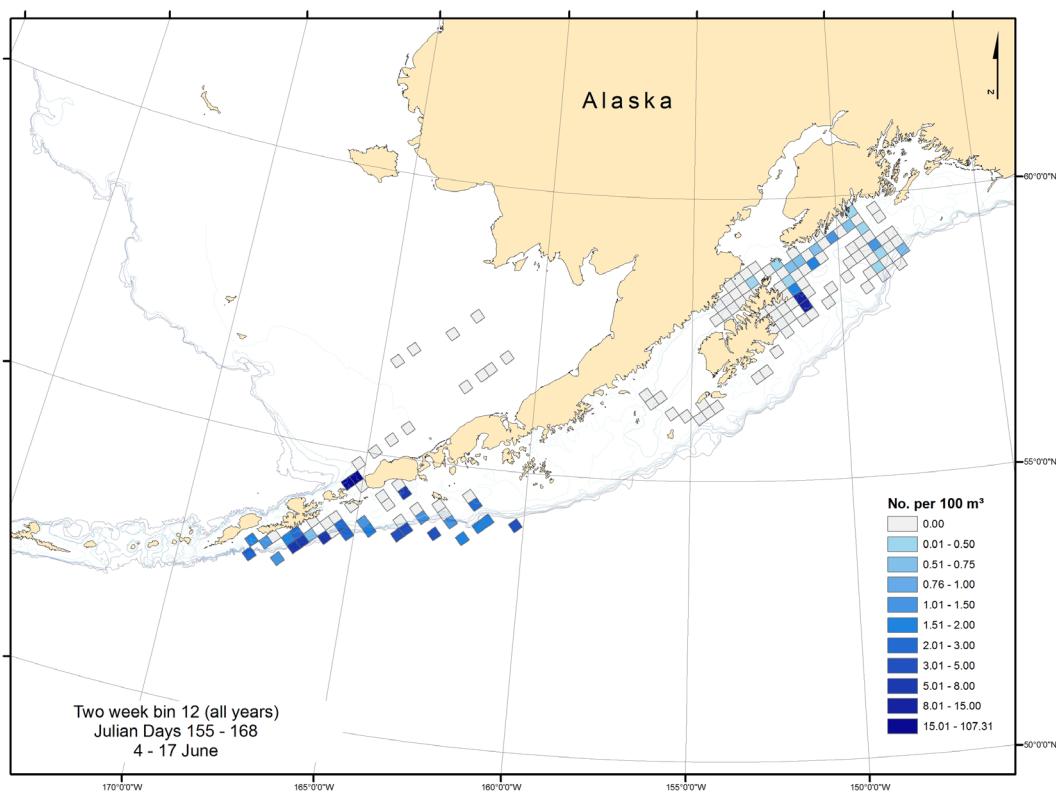


Figure 4.2A-O continued.

H



I

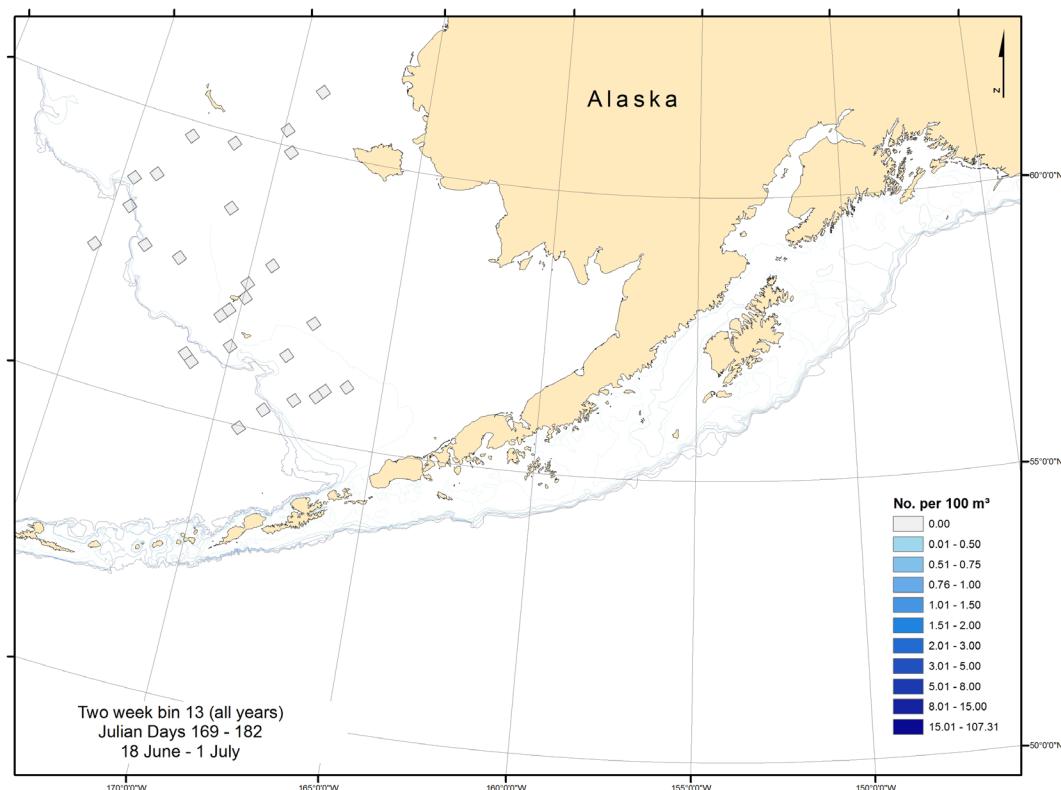


Figure 4.2A-O continued.

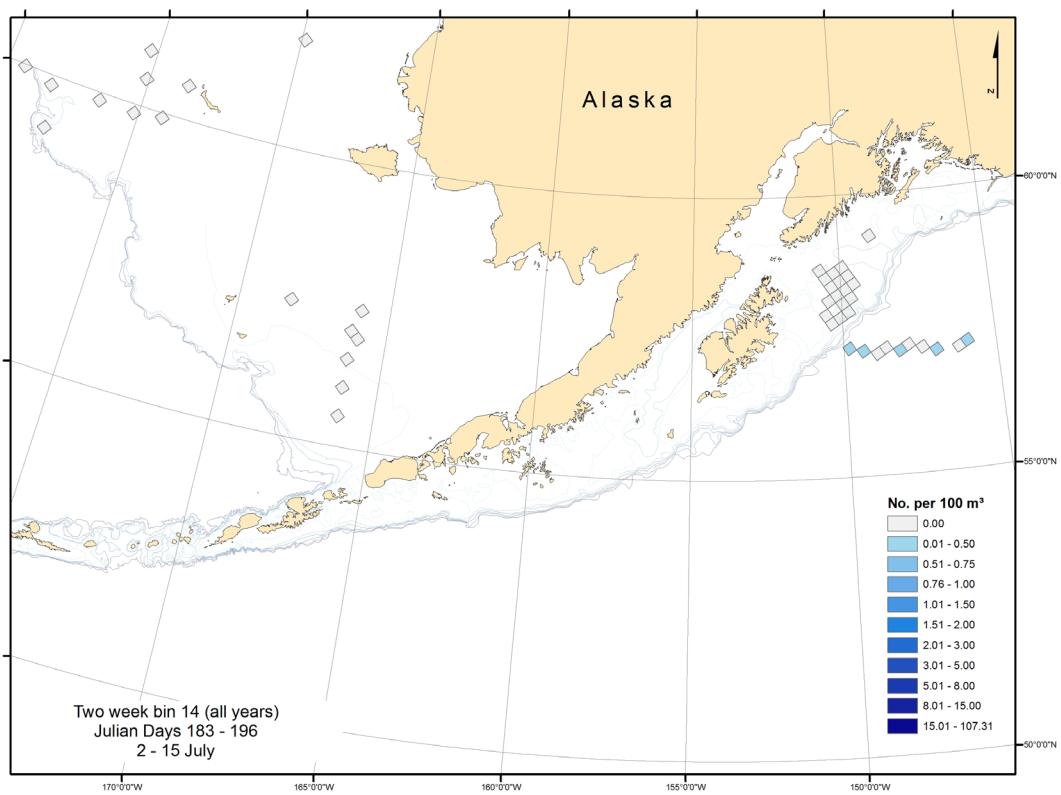
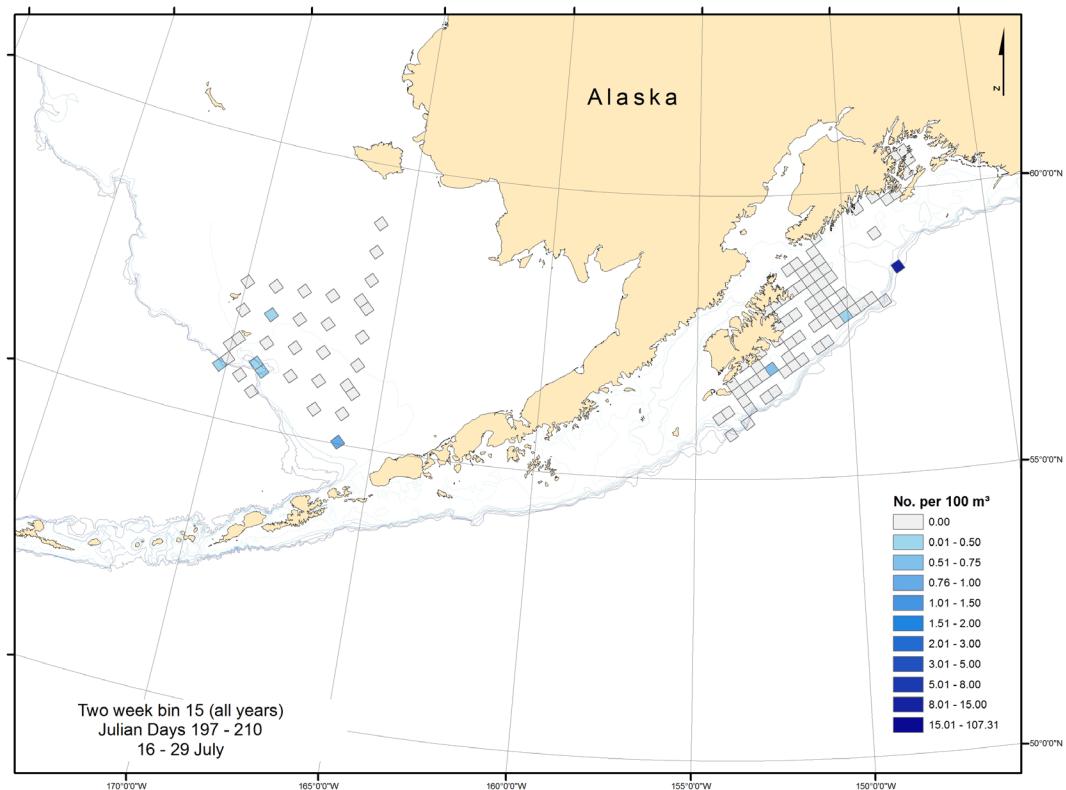
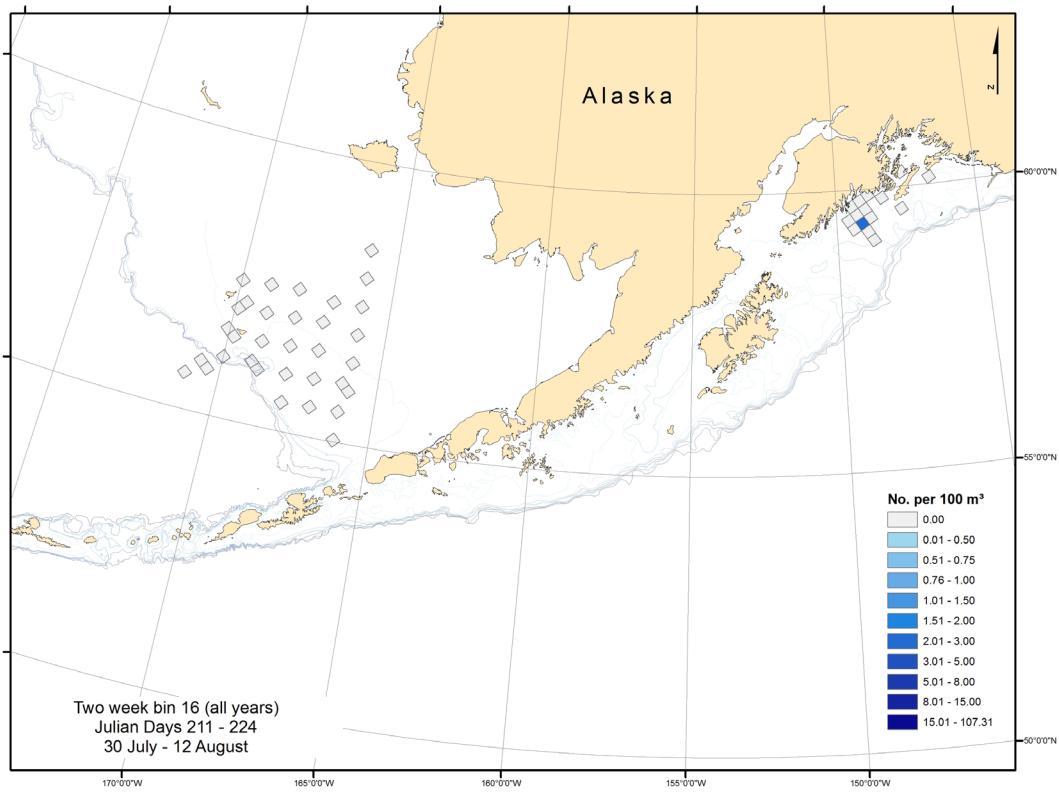
J**K**

Figure 4.2A-O continued.

L



M

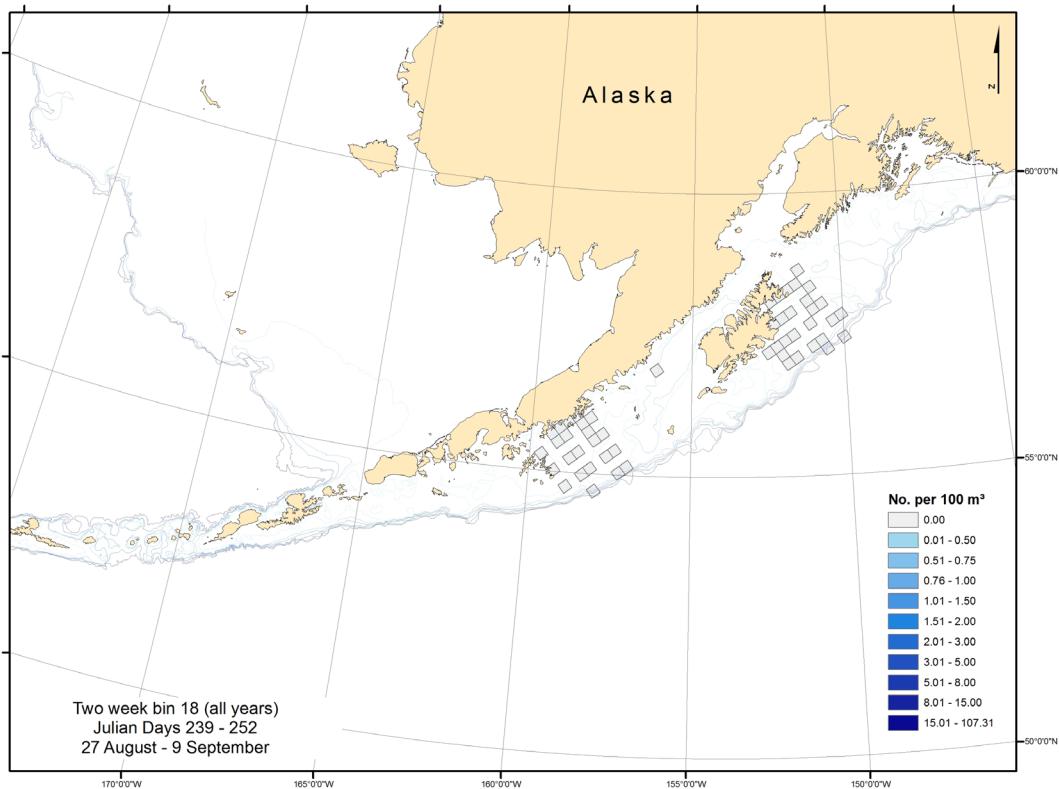
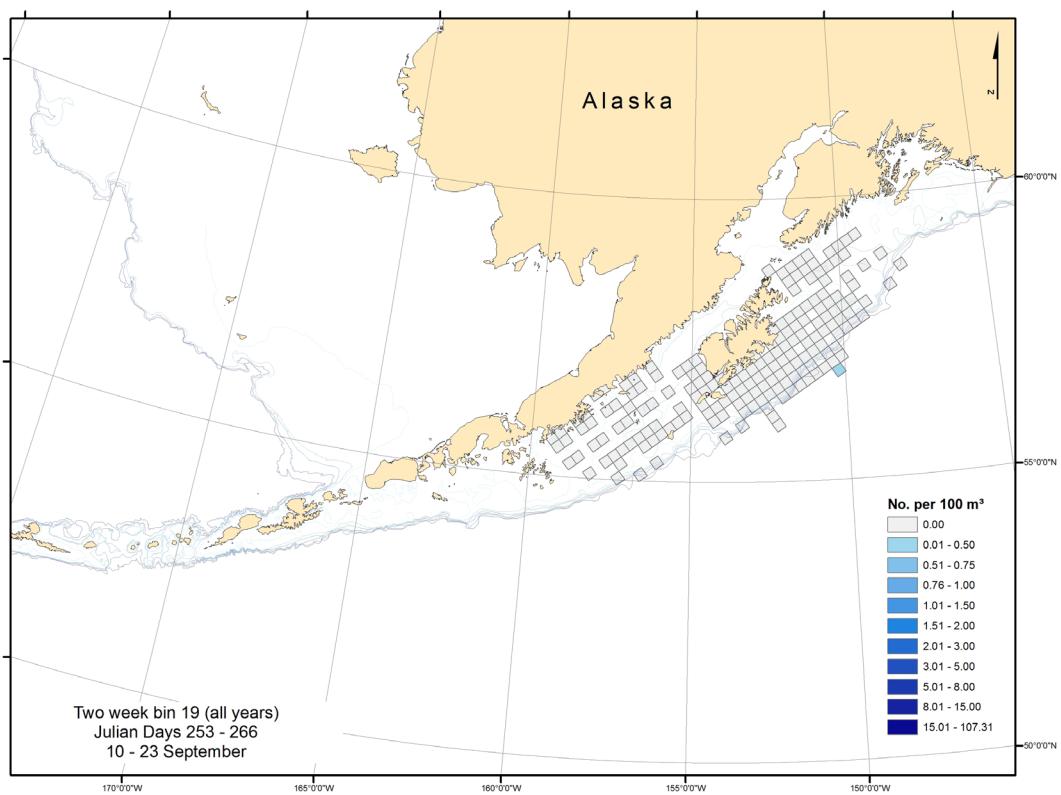


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N



O

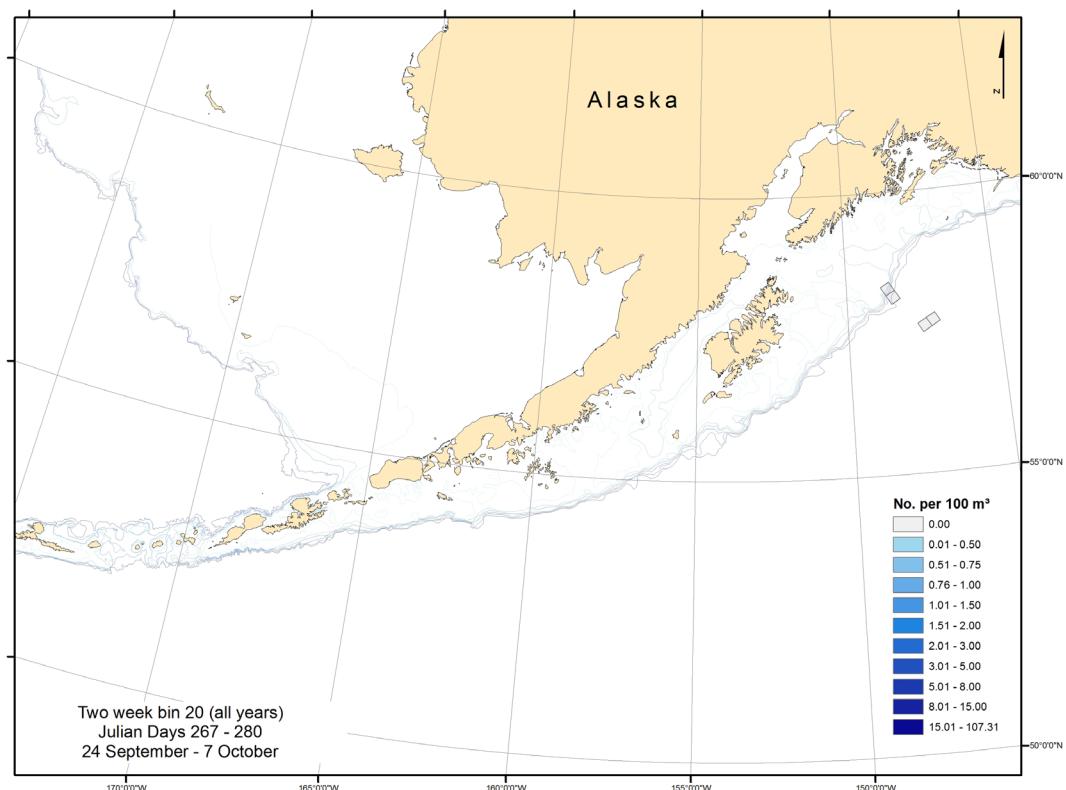


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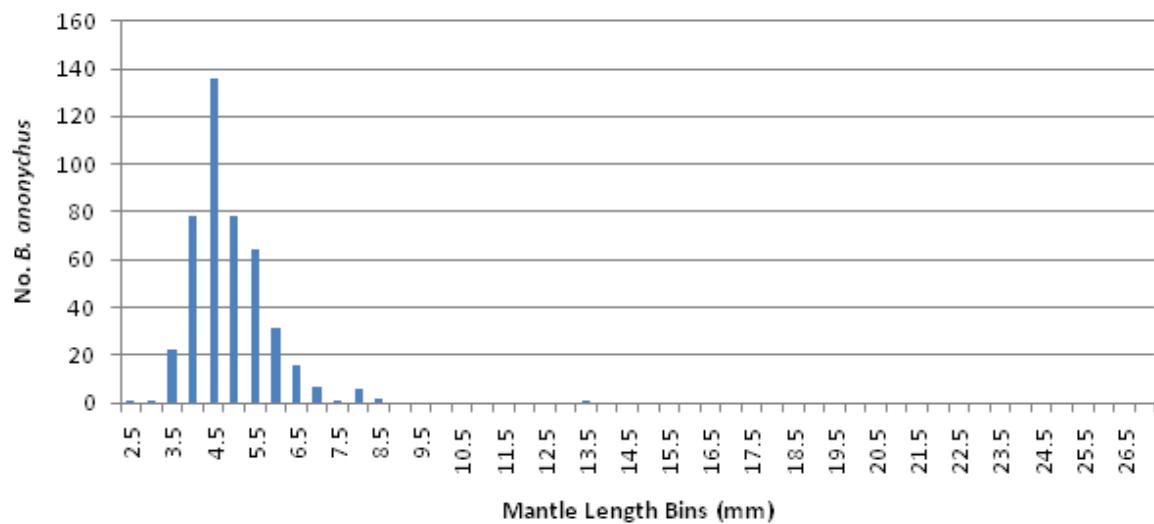


Figure 4.3. *Berryteuthis anonymus* mantle length frequency. Horizontal axis is mantle length bins (mm); vertical axis is the number of individuals in each bin.

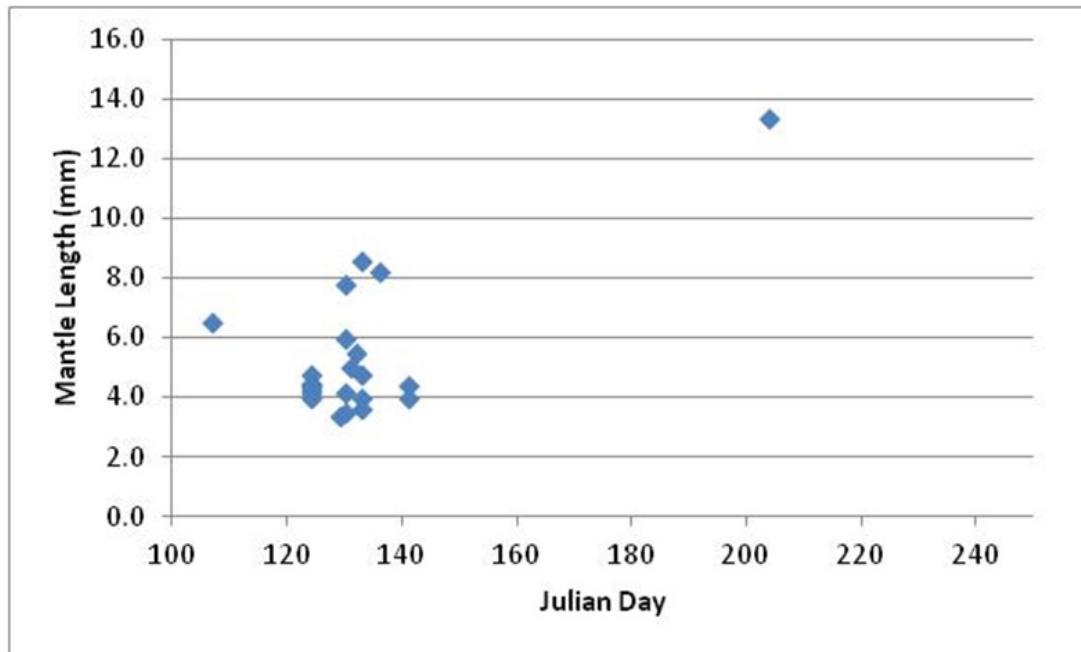


Figure 4.4A. All *Berryteuthis anonychus* mantle length (mm) data by Julian day for the Bering Sea.

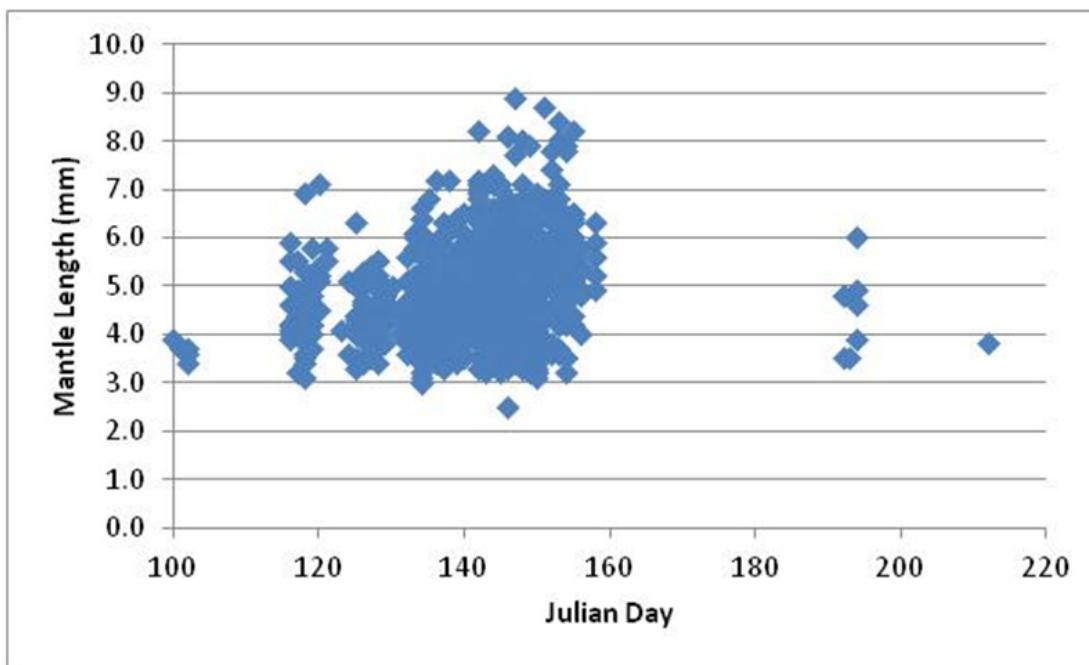


Figure 4.4B. All *Berryteuthis anonychus* mantle length (mm) data by Julian day for the Gulf of Alaska.

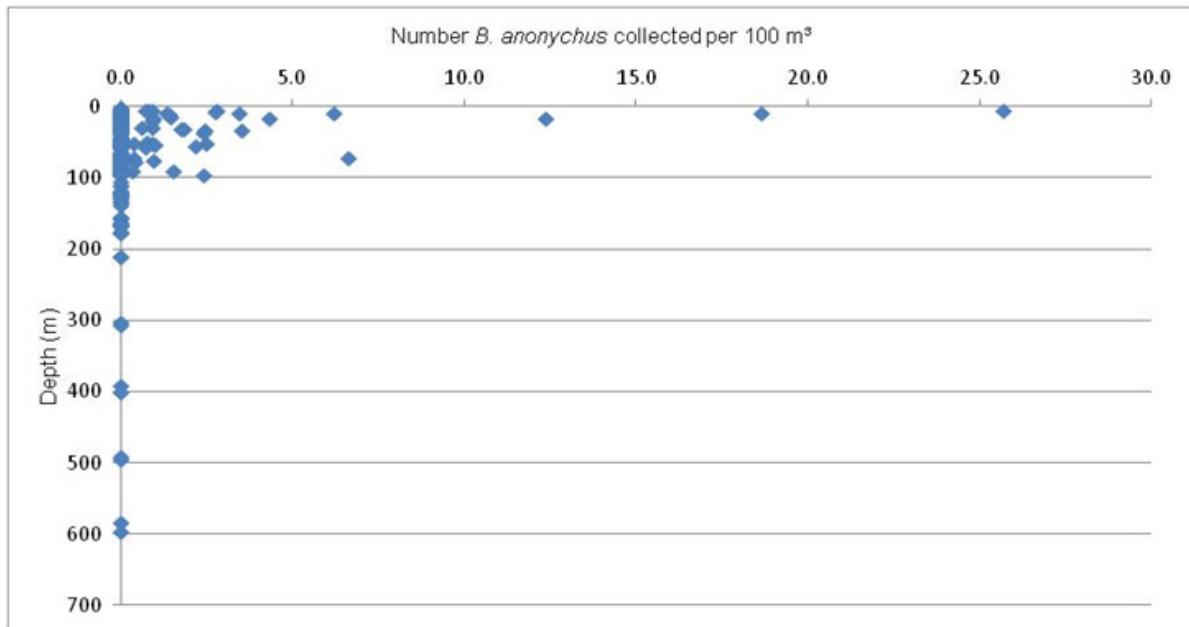
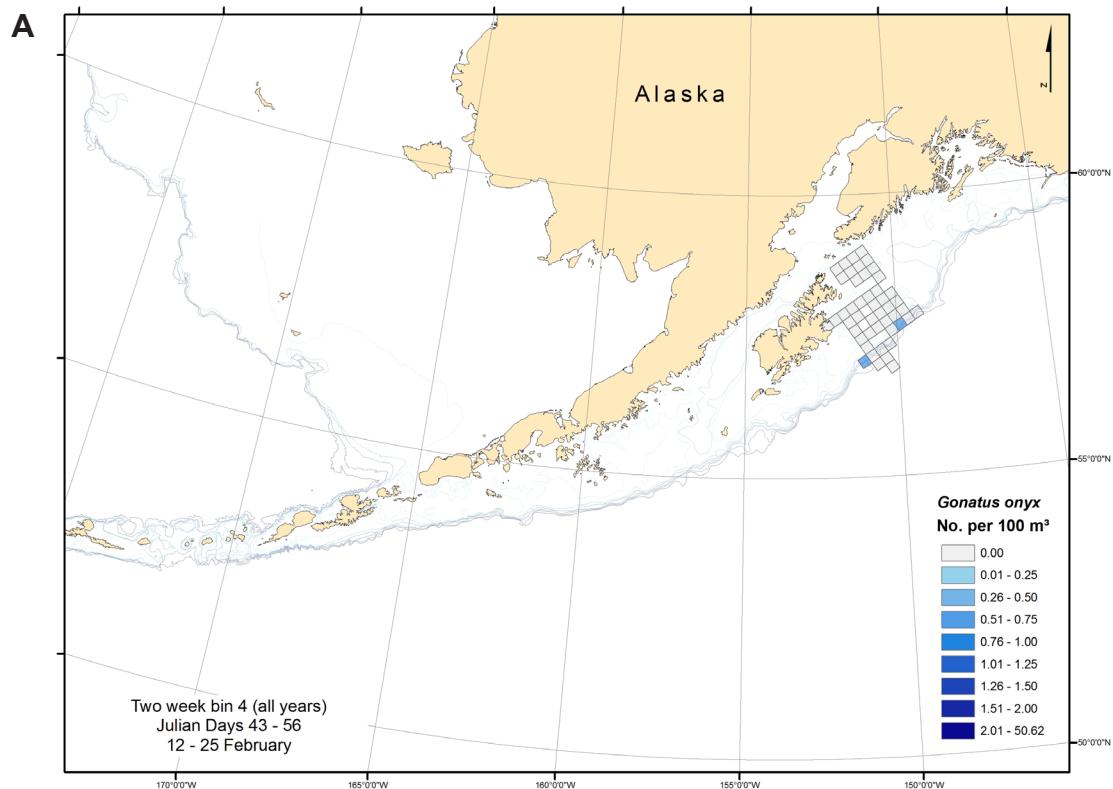
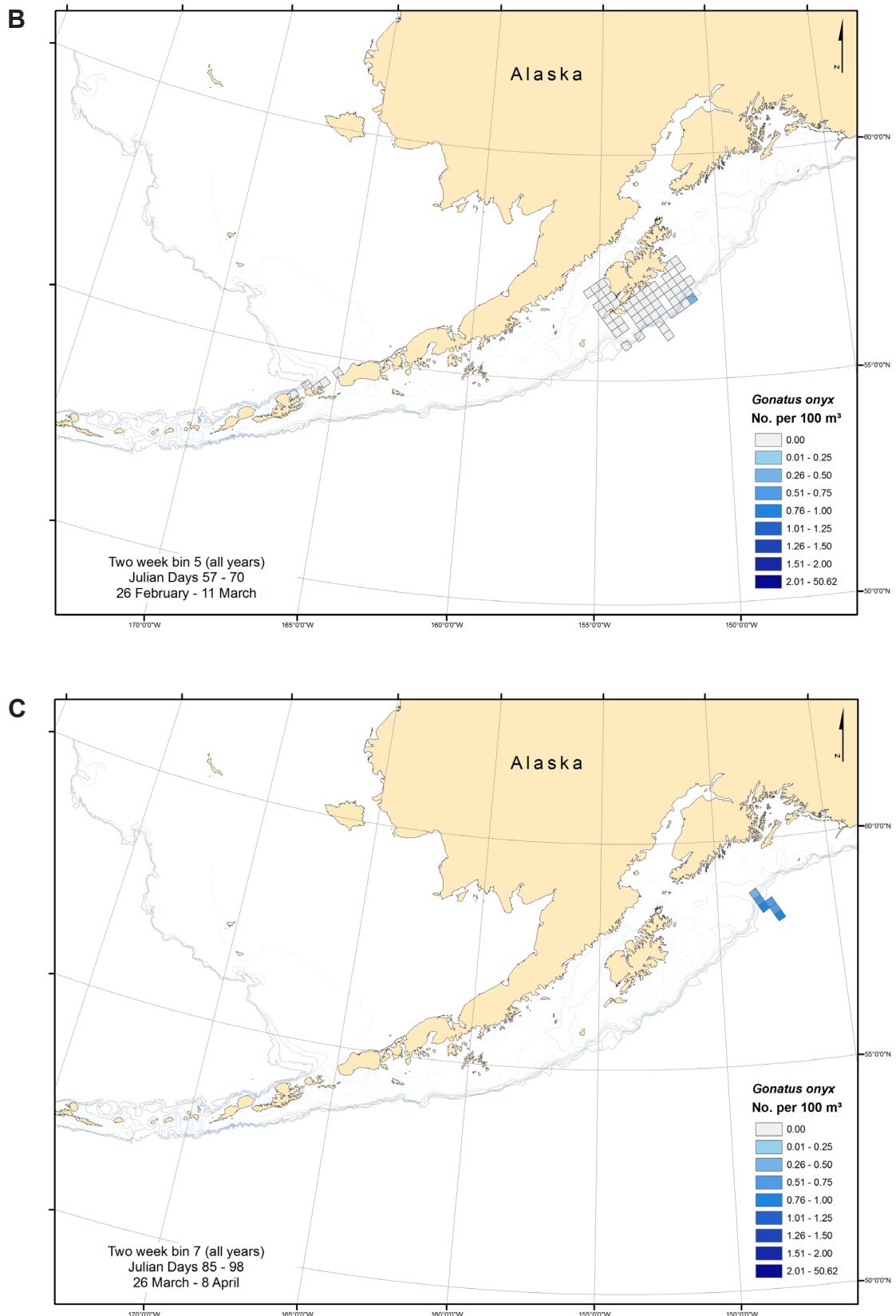


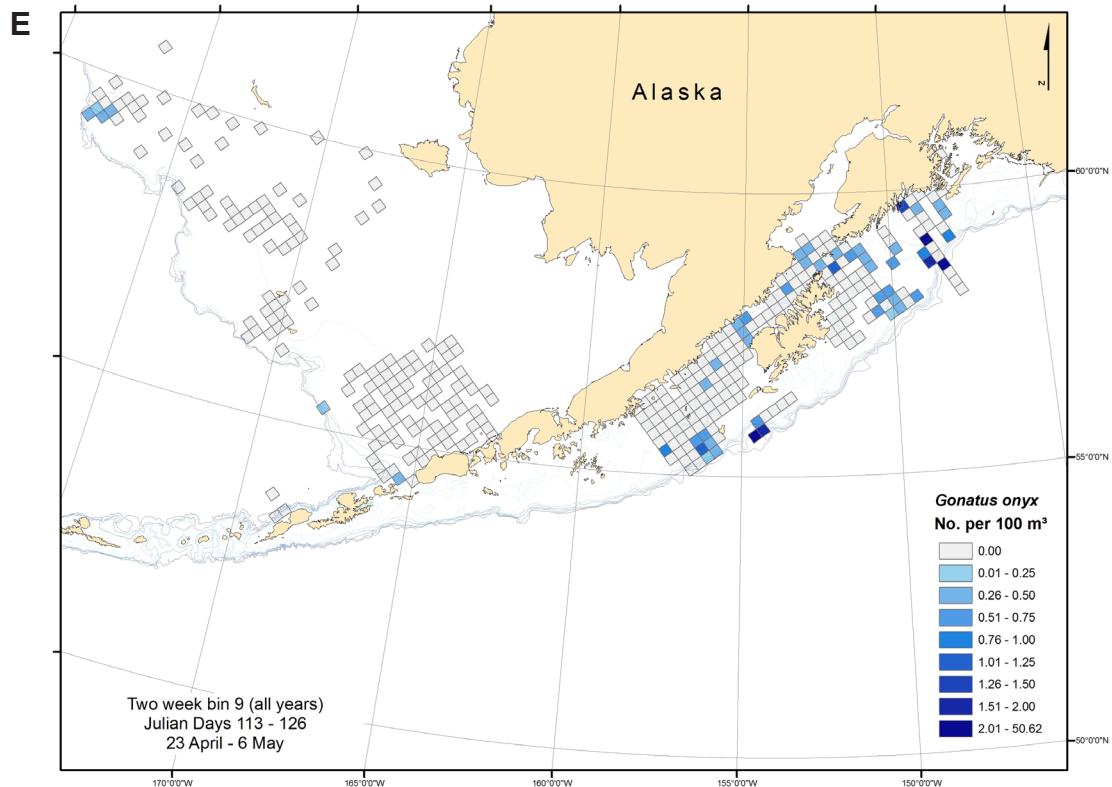
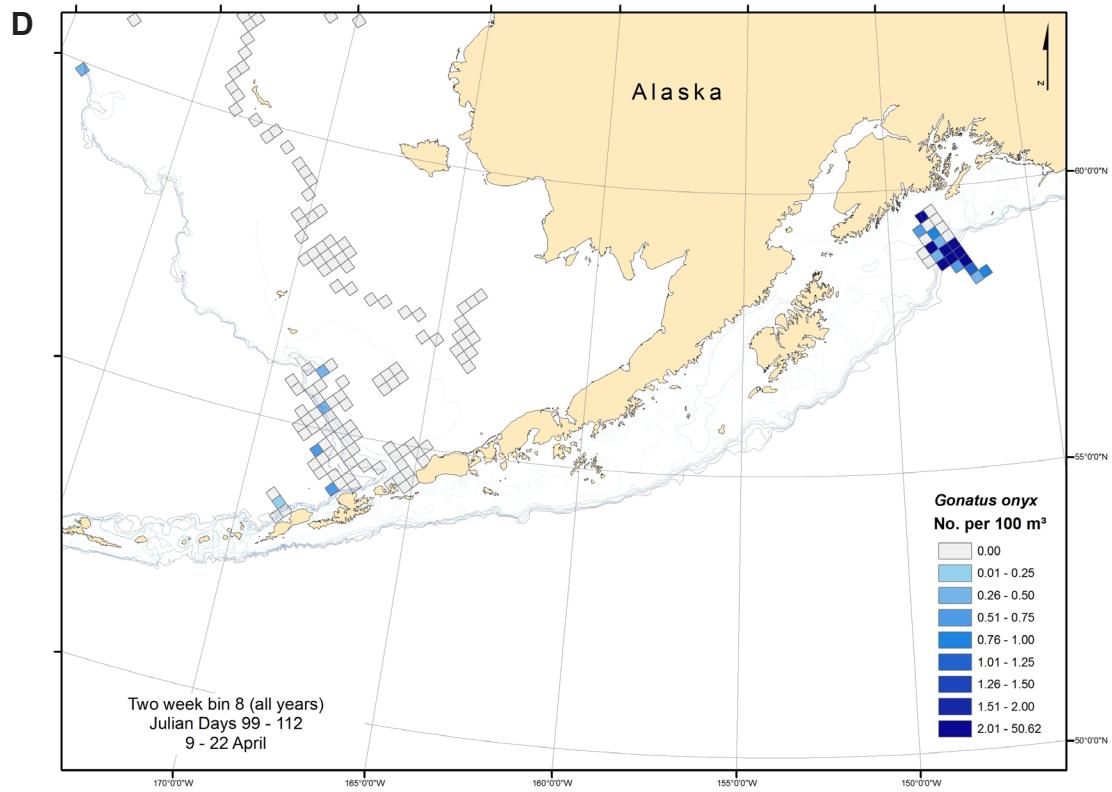
Figure 4.5. Vertical distribution of *Berryteuthis anonymus* (number collected per 100 m³). Includes all available data collected during the study. Depths represent the midpoint depth of each sample, e.g. a depth of 2 m represents a tow that sampled from 0 - 4 m.



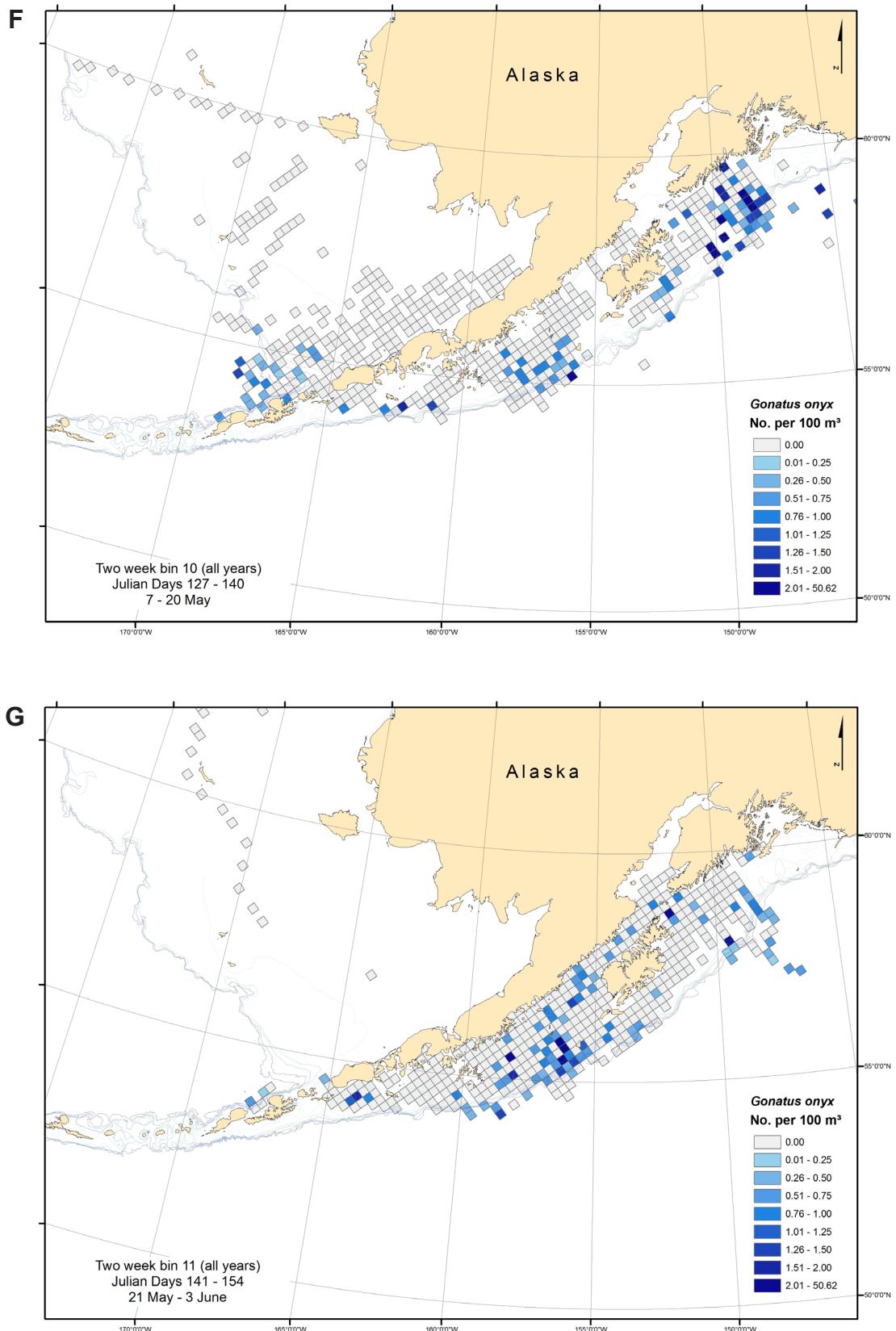
Figures 4.6A-O. Maps of *Gonatus onyx* distribution and abundance. Each cell represents a 20 x 20 km region within which at least one station was occupied. Grey grid cells indicate that the cell was sampled but no *G. onyx* were collected. Colors are according to legend and represent the summed number per 100 cubic meters at each station within each cell for the two-week period listed on the individual maps.



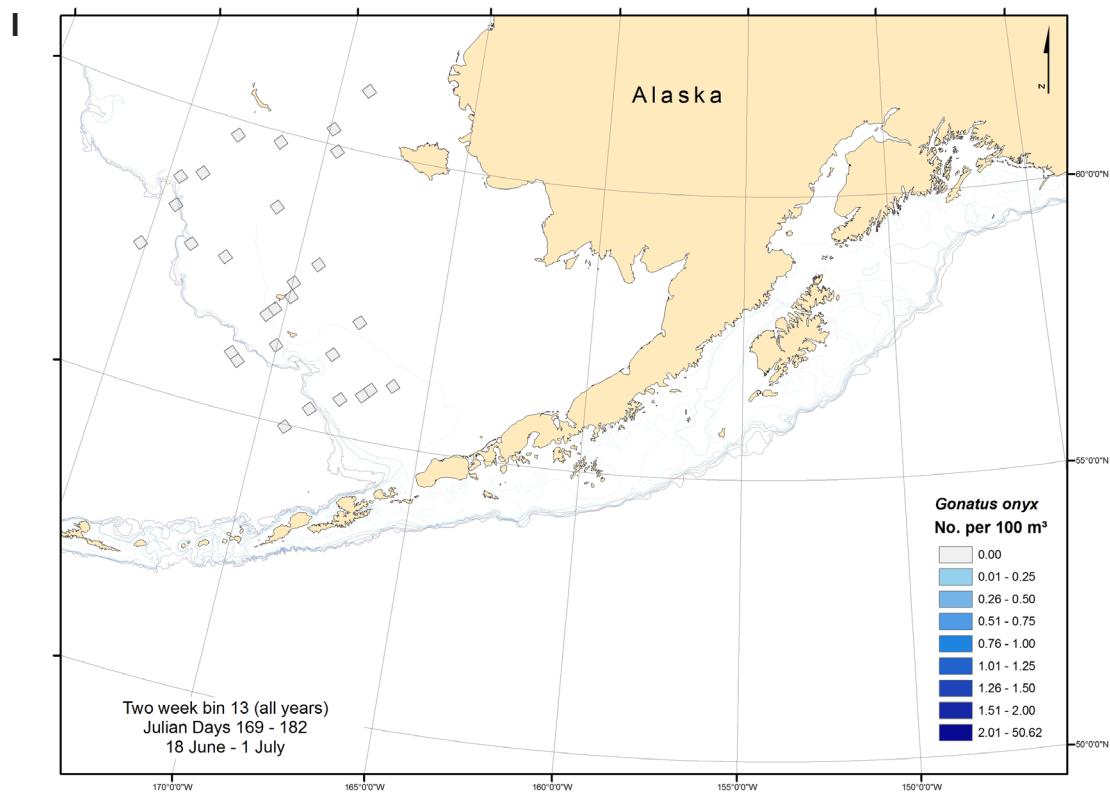
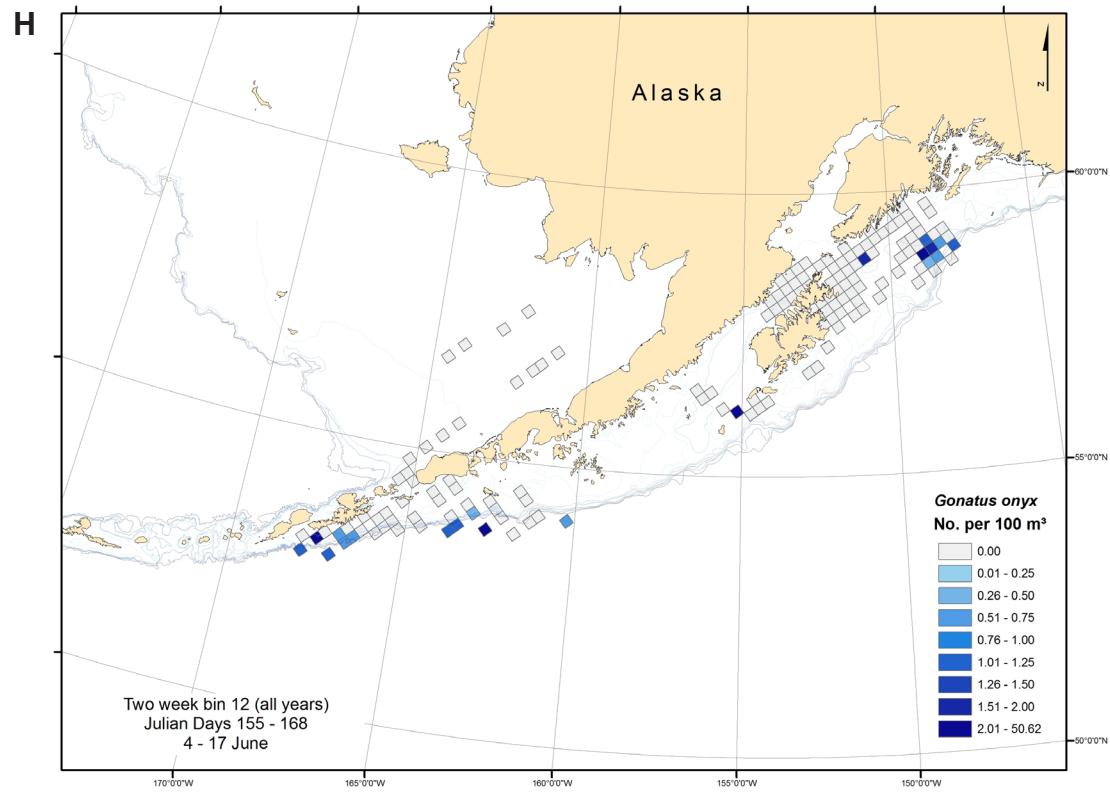
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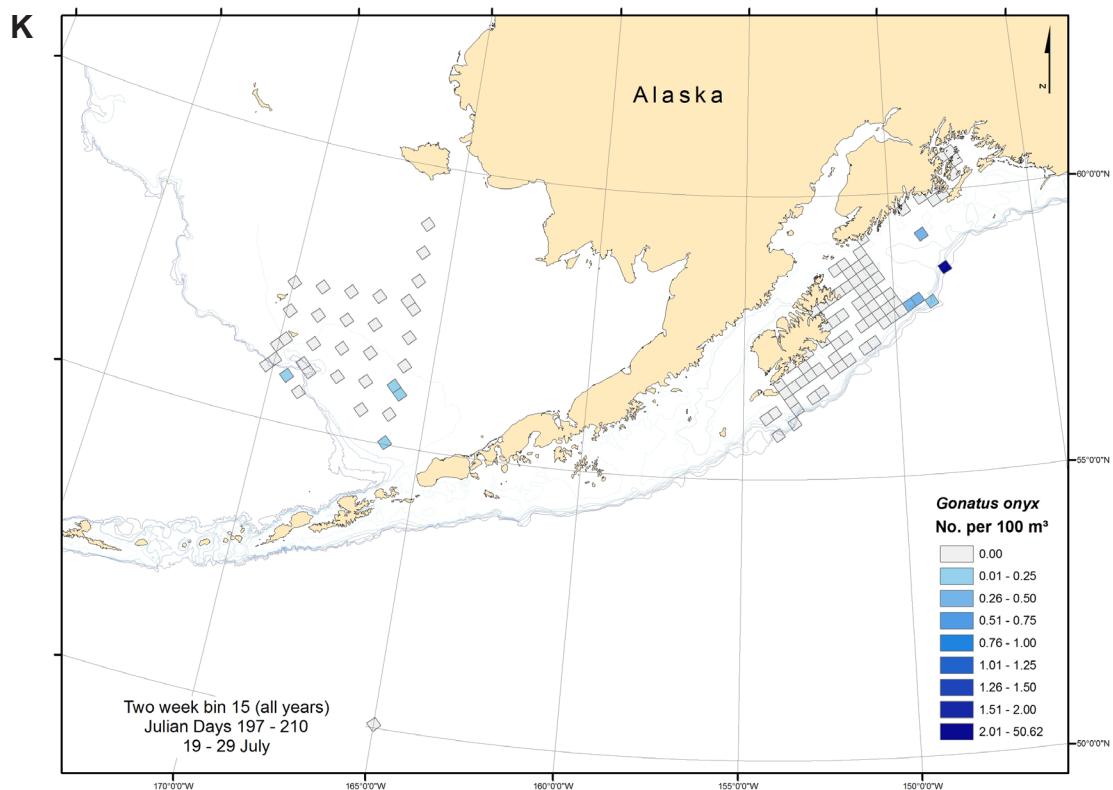
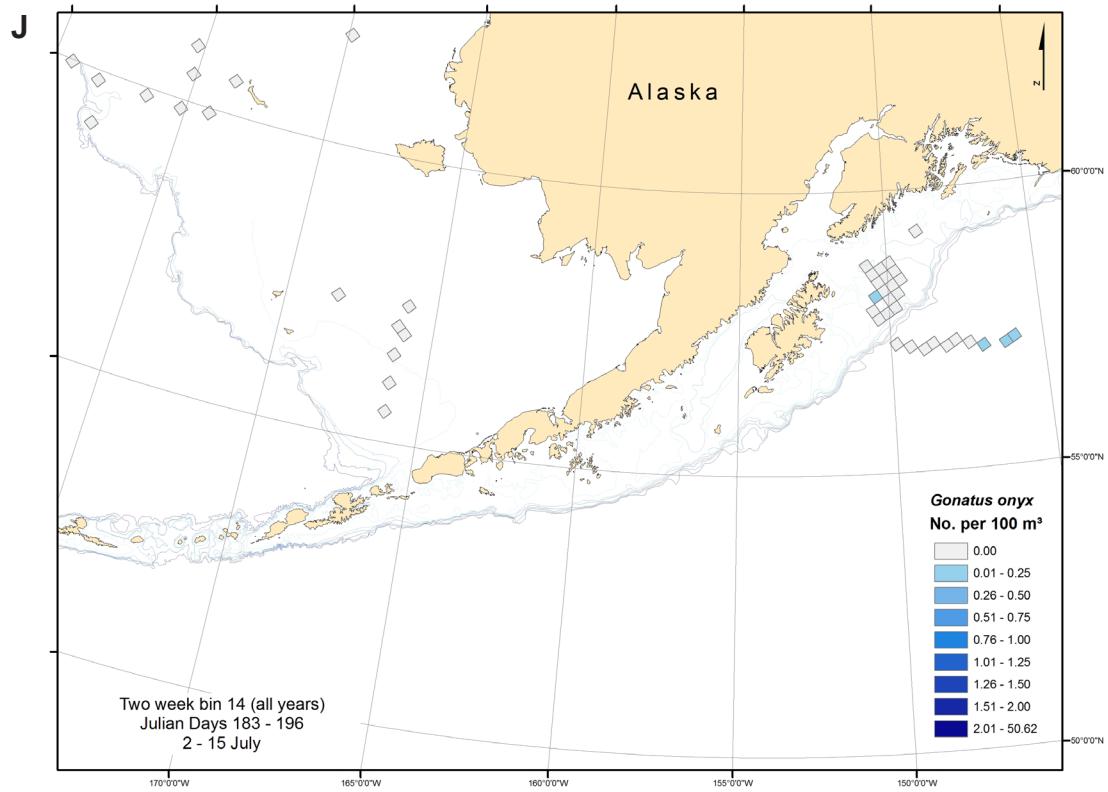
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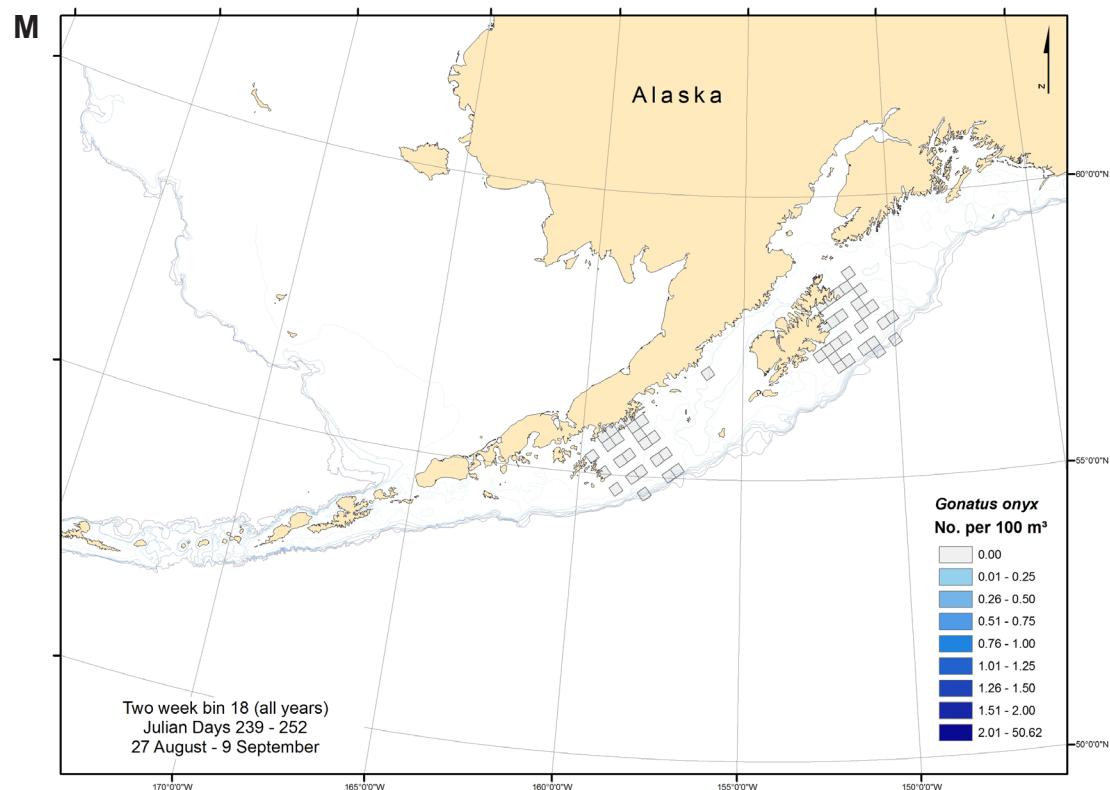
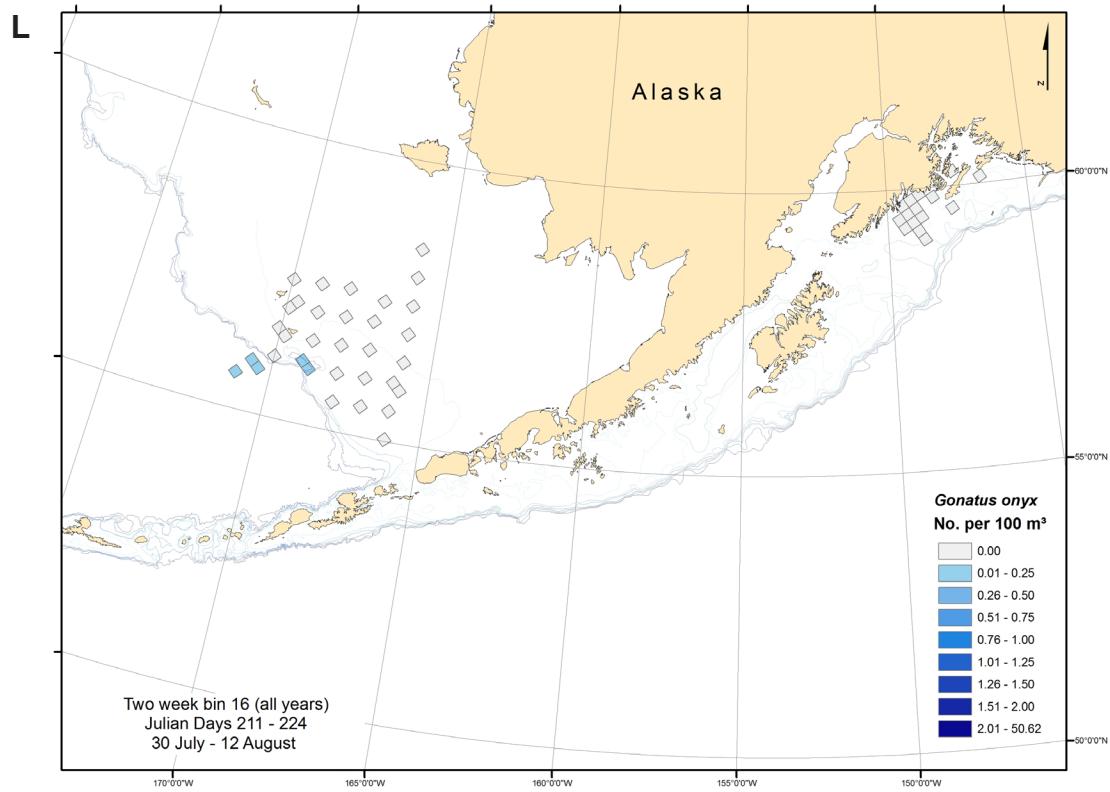
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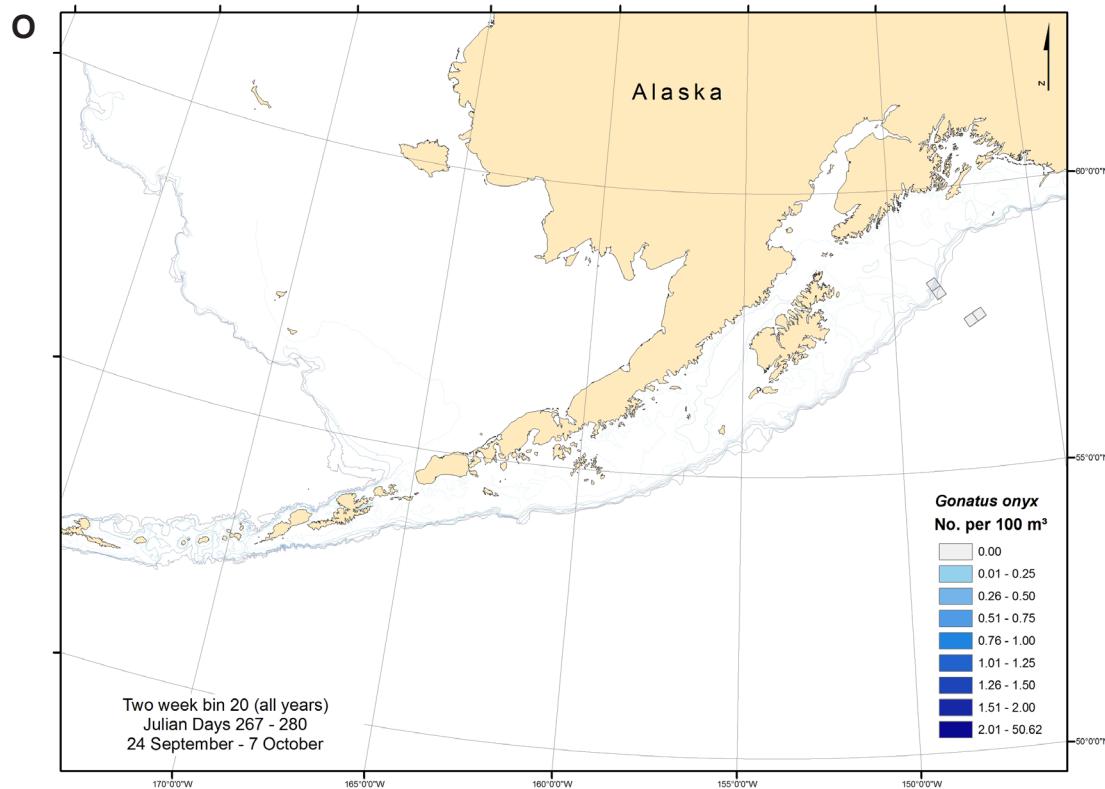
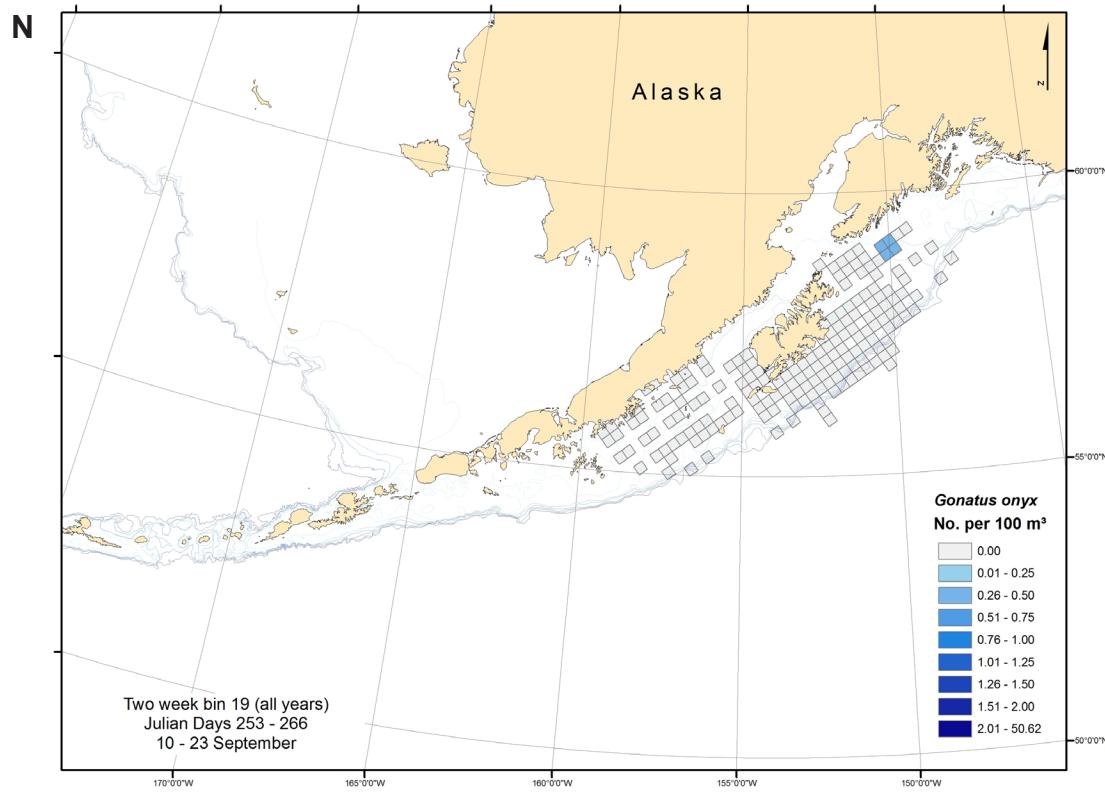
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Figures 4.6A-O continued.



Figures 4.6A-O continued.



Figures 4.6A-O continued.

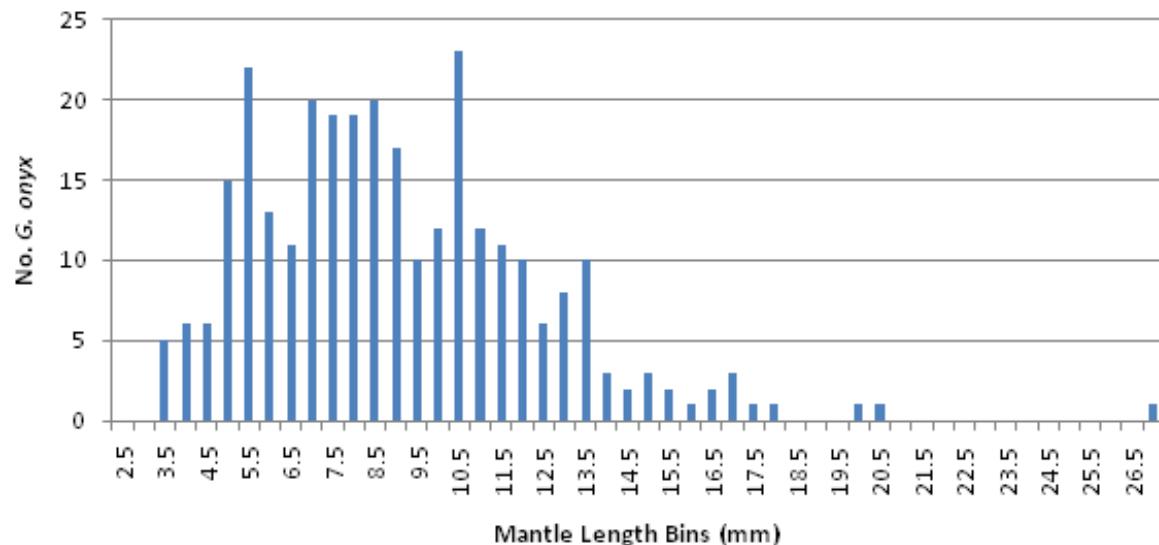


Figure 4.7. *Gonatus onyx* mantle length frequency. Horizontal axis is mantle length bins (mm); vertical axis is the number of individuals in each bin.

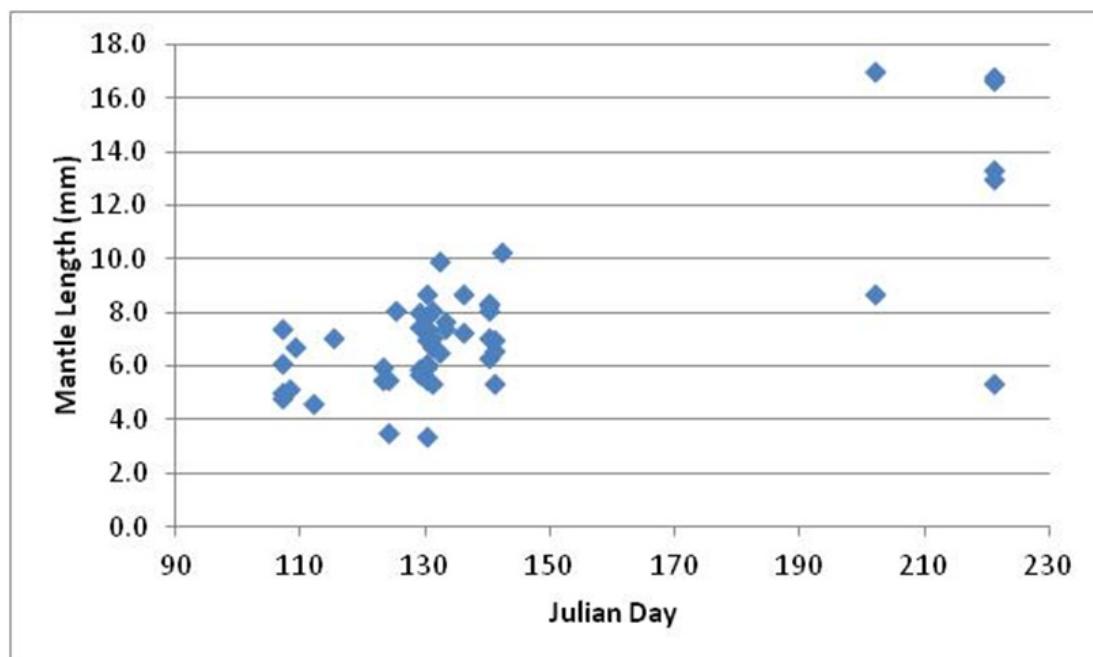


Figure 4.8A. All *Gonatus onyx* mantle length (mm) data by Julian day for the Bering Sea.

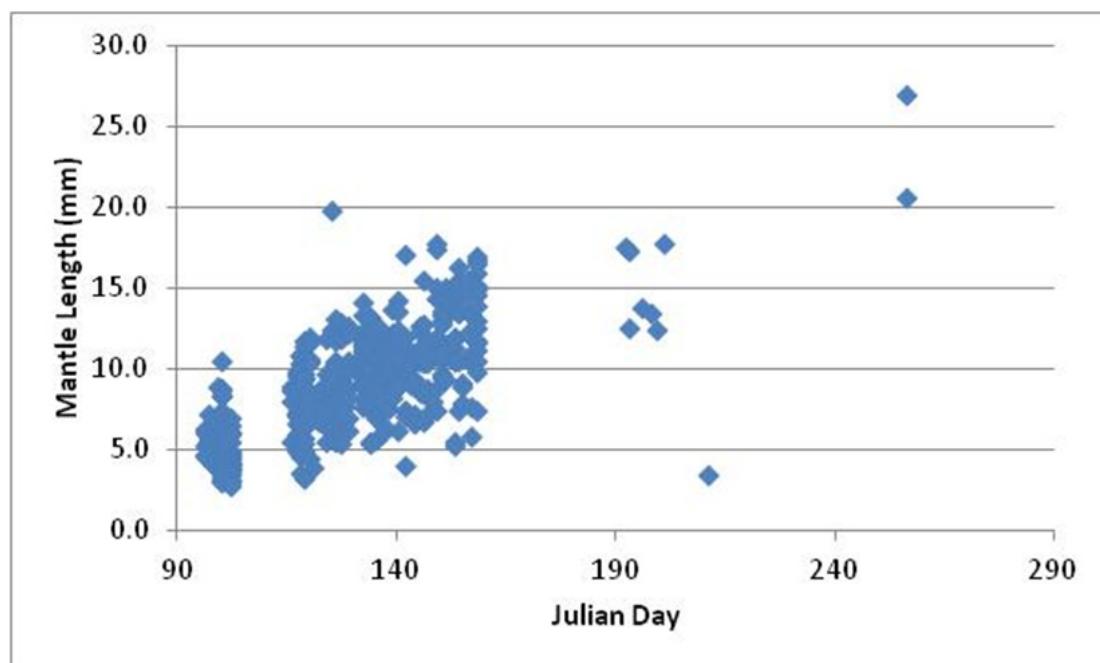


Figure 4.8B. All *Gonatus onyx* mantle length (mm) data by Julian day for the Gulf of Alaska.

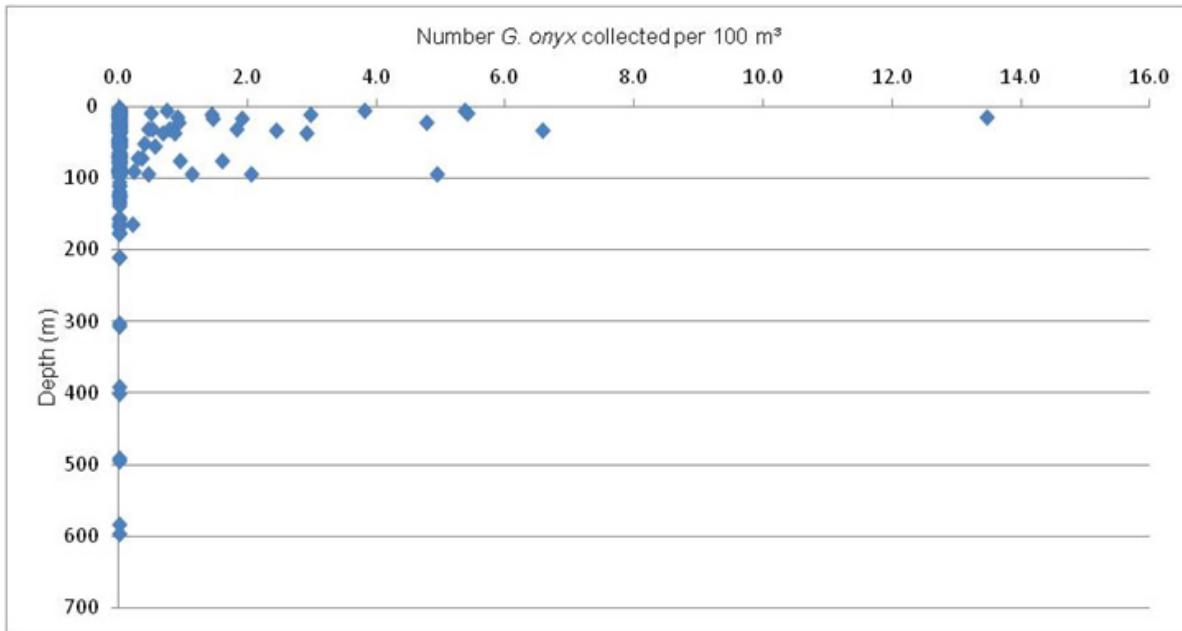
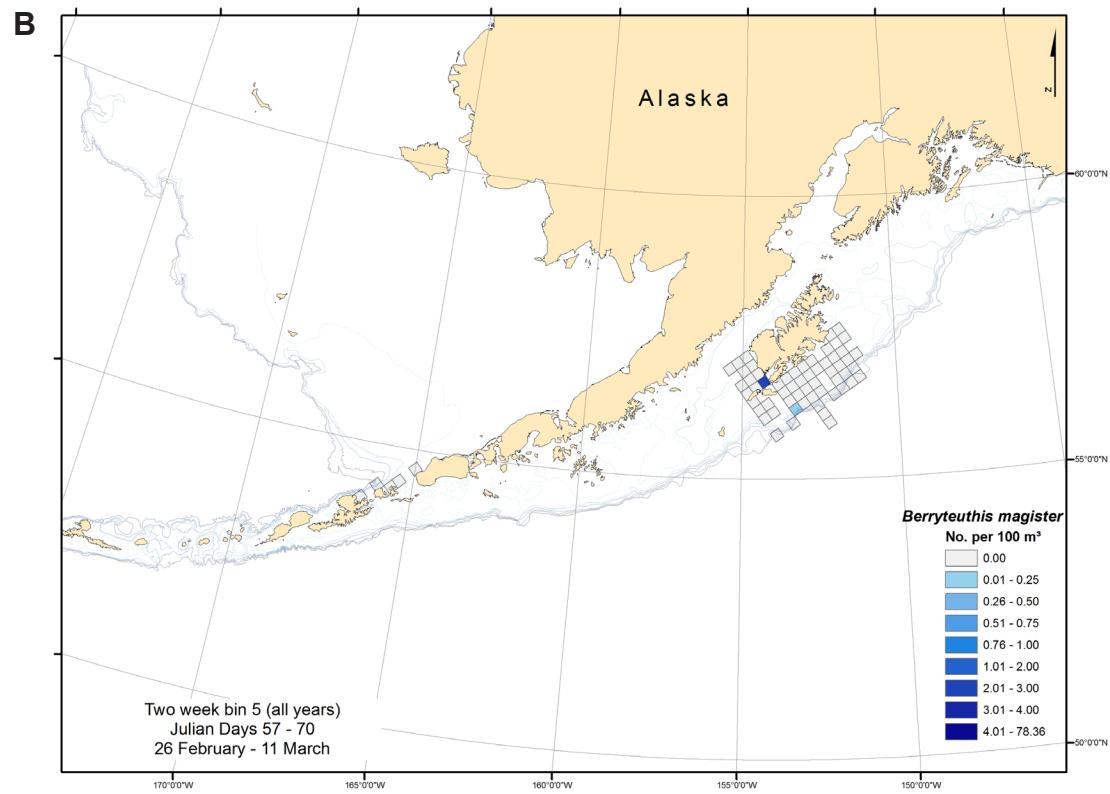


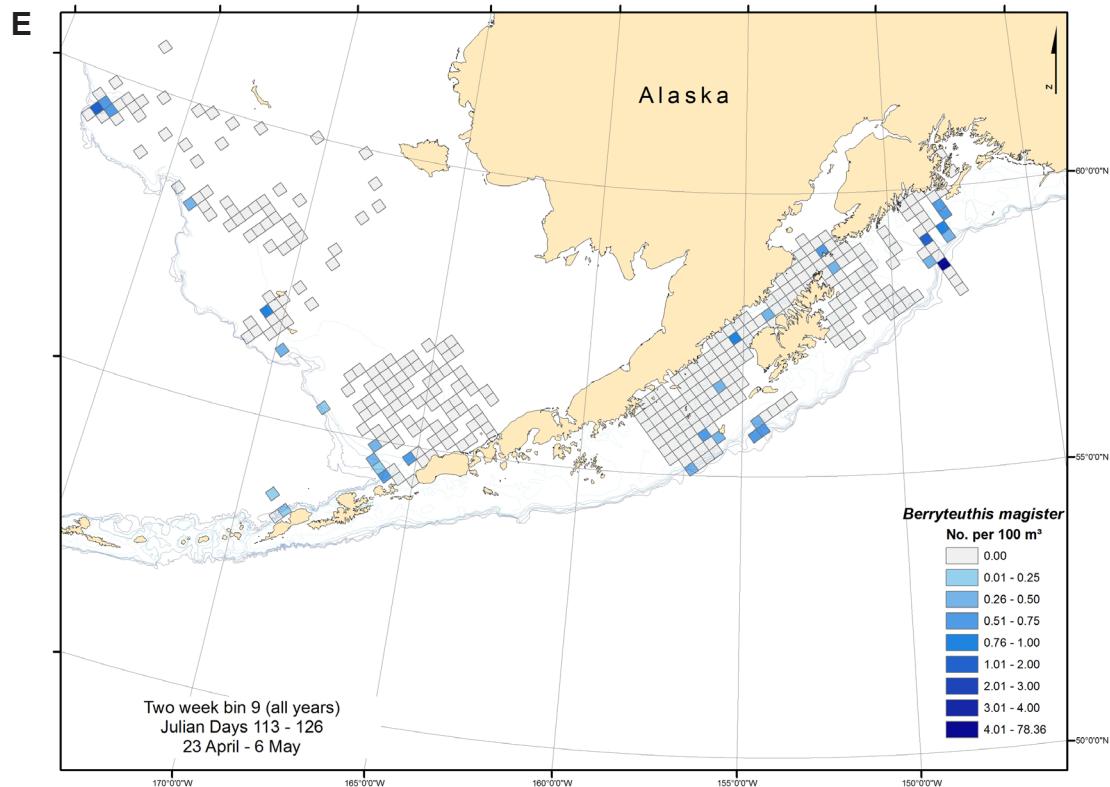
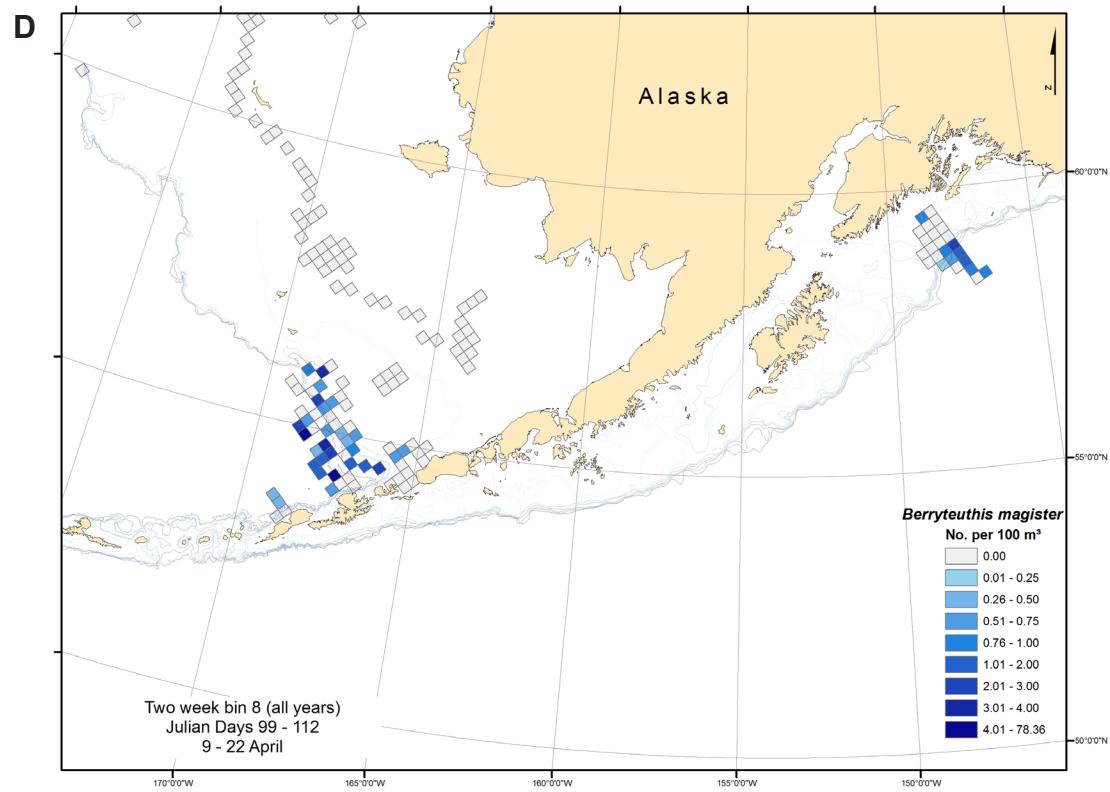
Figure 4.9. Vertical distribution of *Gonatus onyx* (number collected per 100 m³). Includes all available data collected during the study. Depths represent the midpoint depth of each sample, e.g. a depth of 2 m represents a tow that sampled from 0 - 4 m.



Figures 4.10A-O. Maps of *Berryteuthis magister* distribution and abundance. Each cell represents a 20 x 20 km region within which at least one station was occupied. Grey grid cells indicate that the cell was sampled but no *B. magister* were collected. Colors are according to legend and represent the summed number per 100 cubic meters at each station within each cell for the two-week period listed on the individual maps.

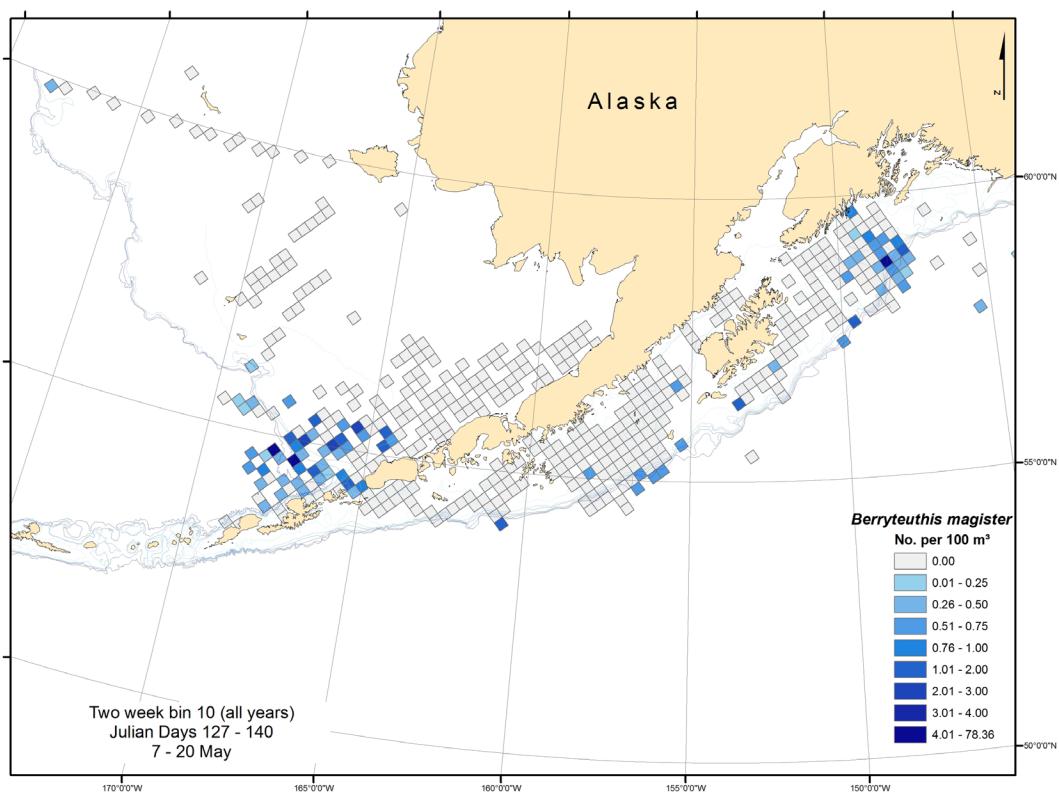


Figures 4.10A-O continued.

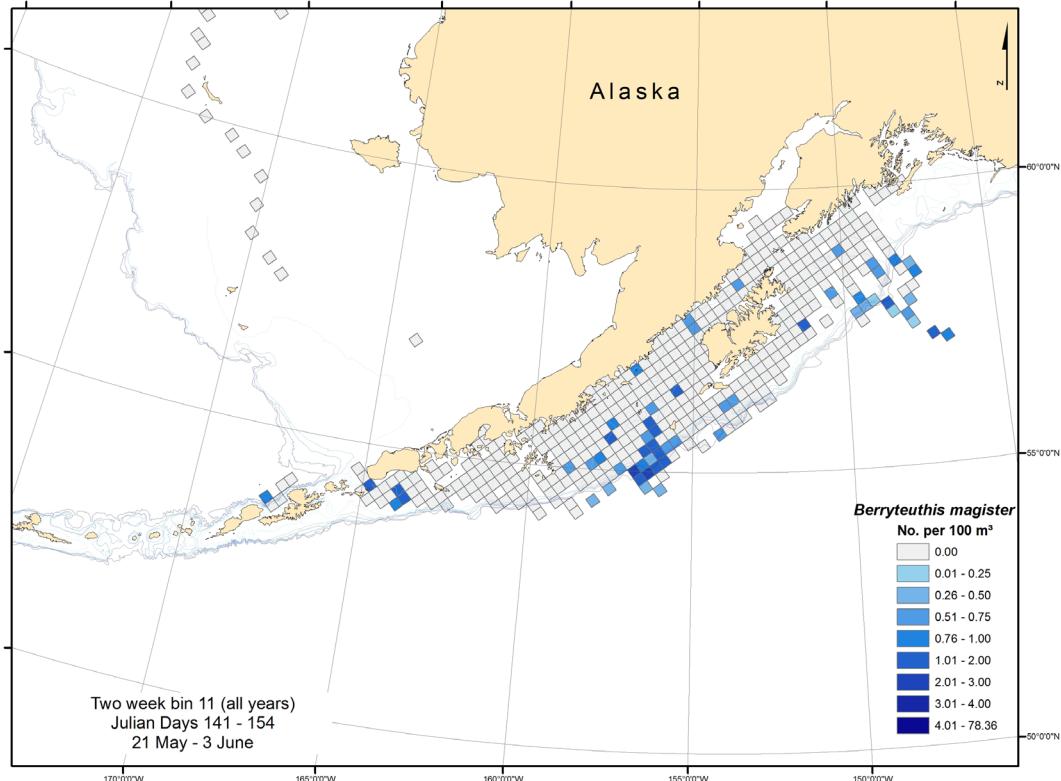


Figures 4.10A-O continued.

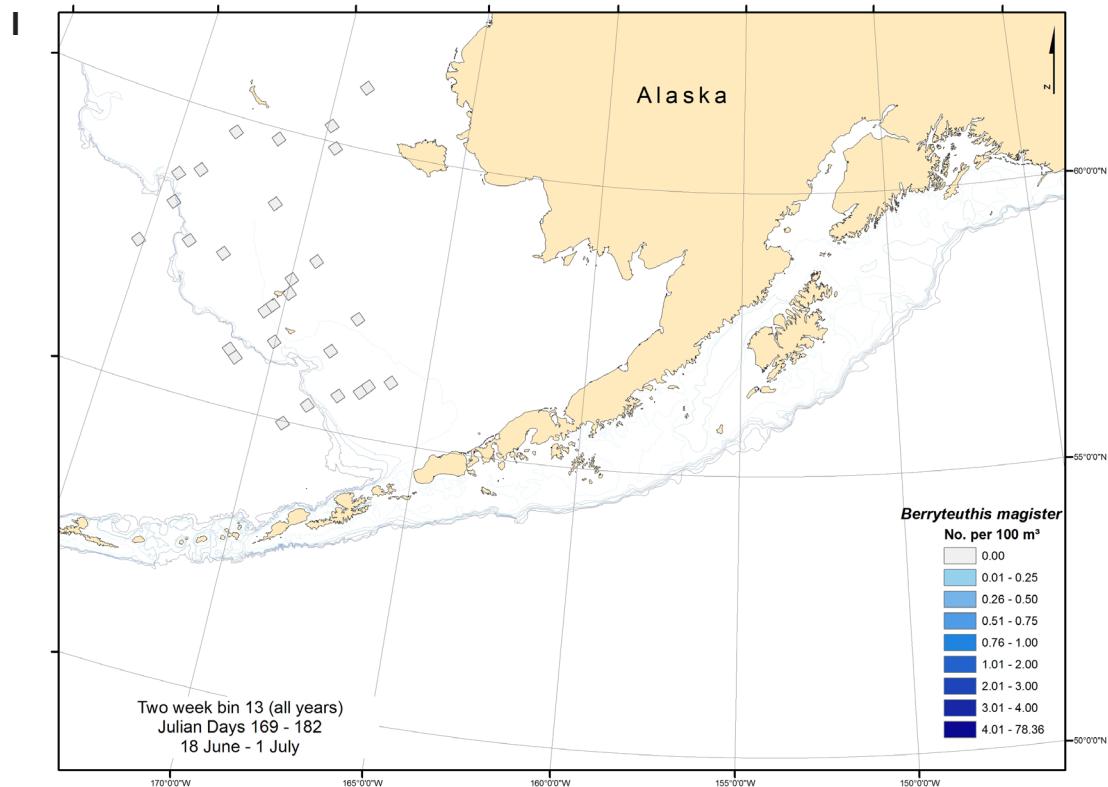
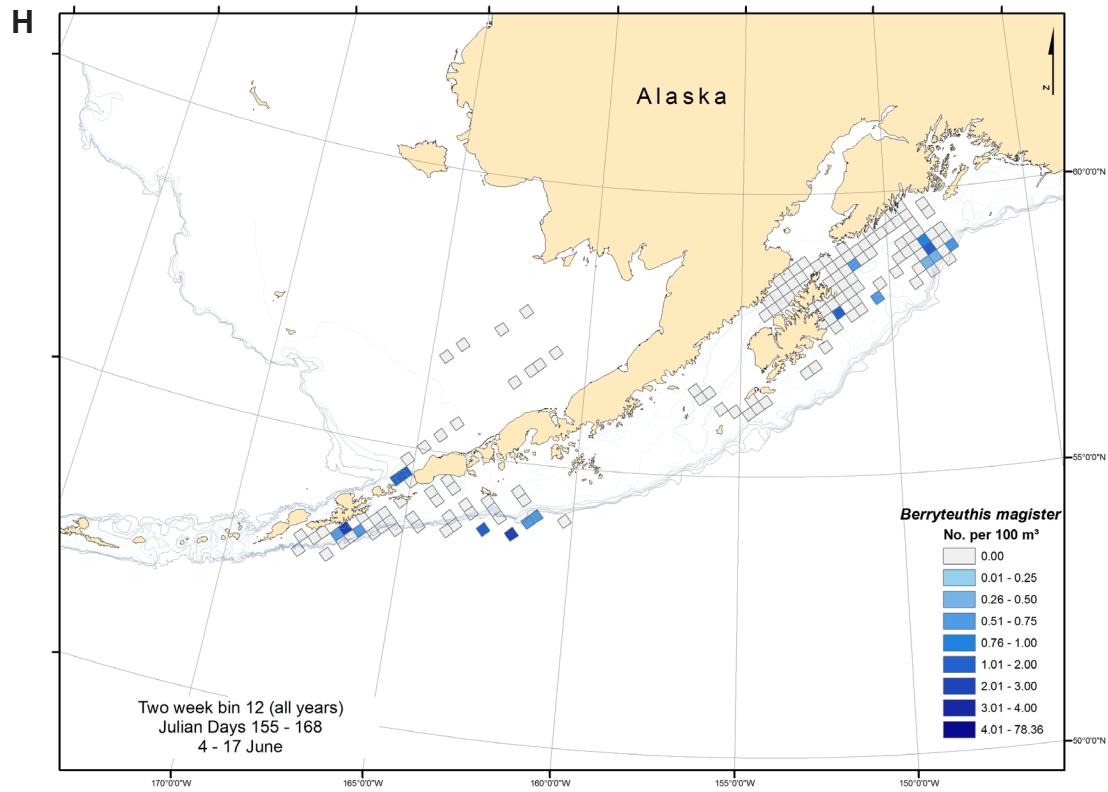
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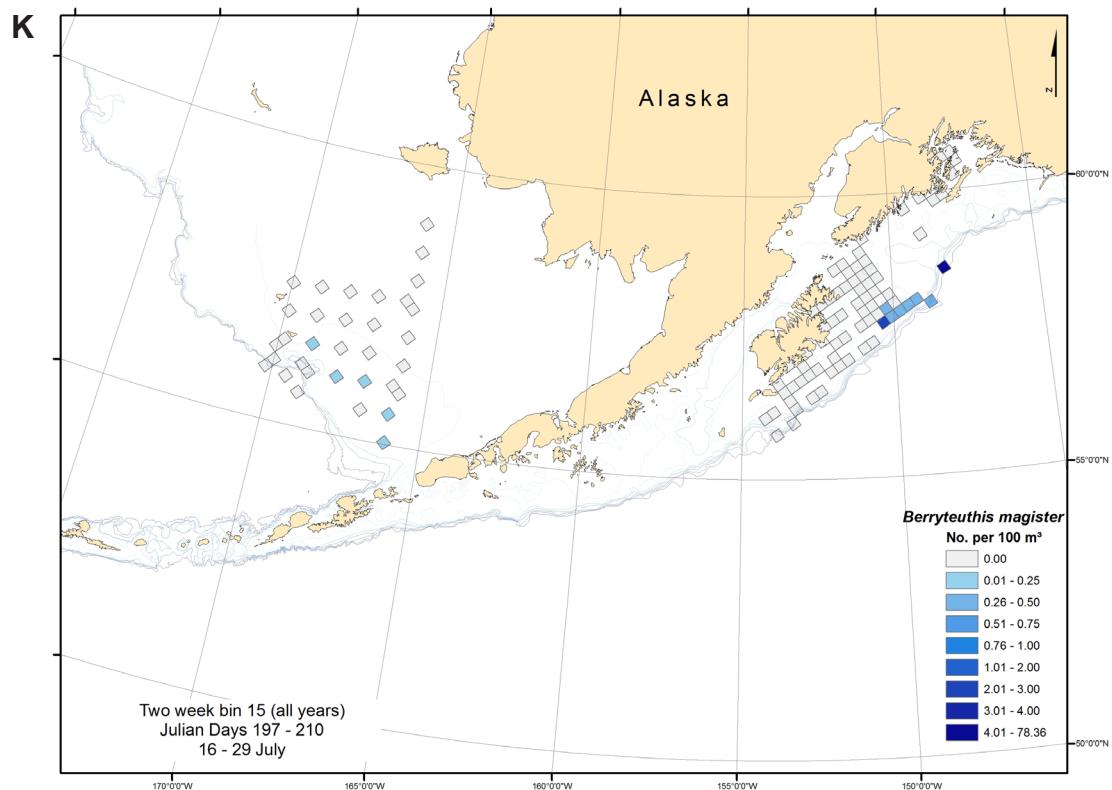
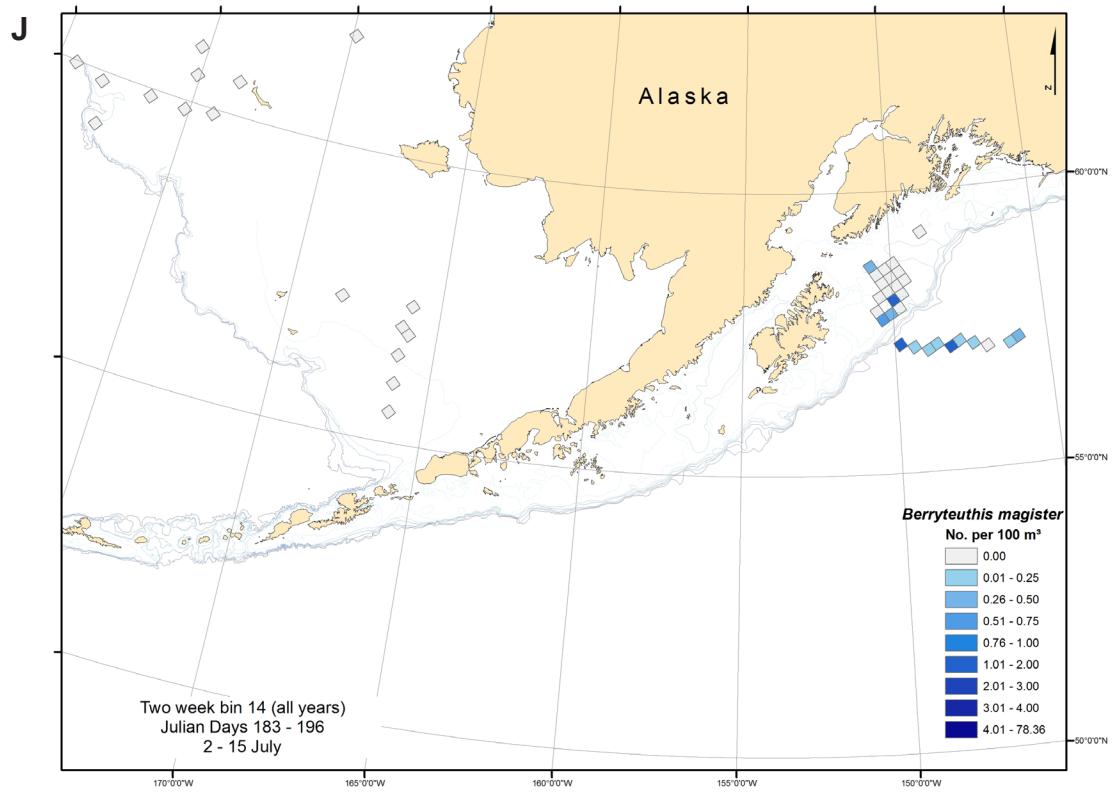
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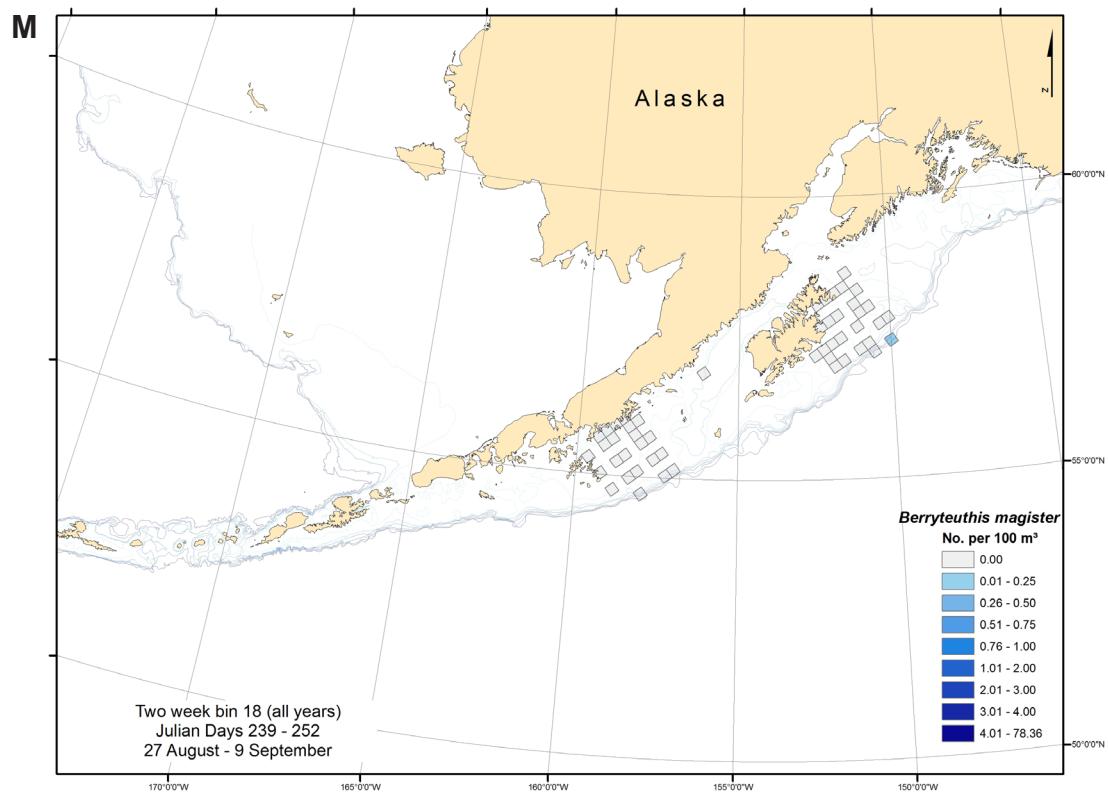
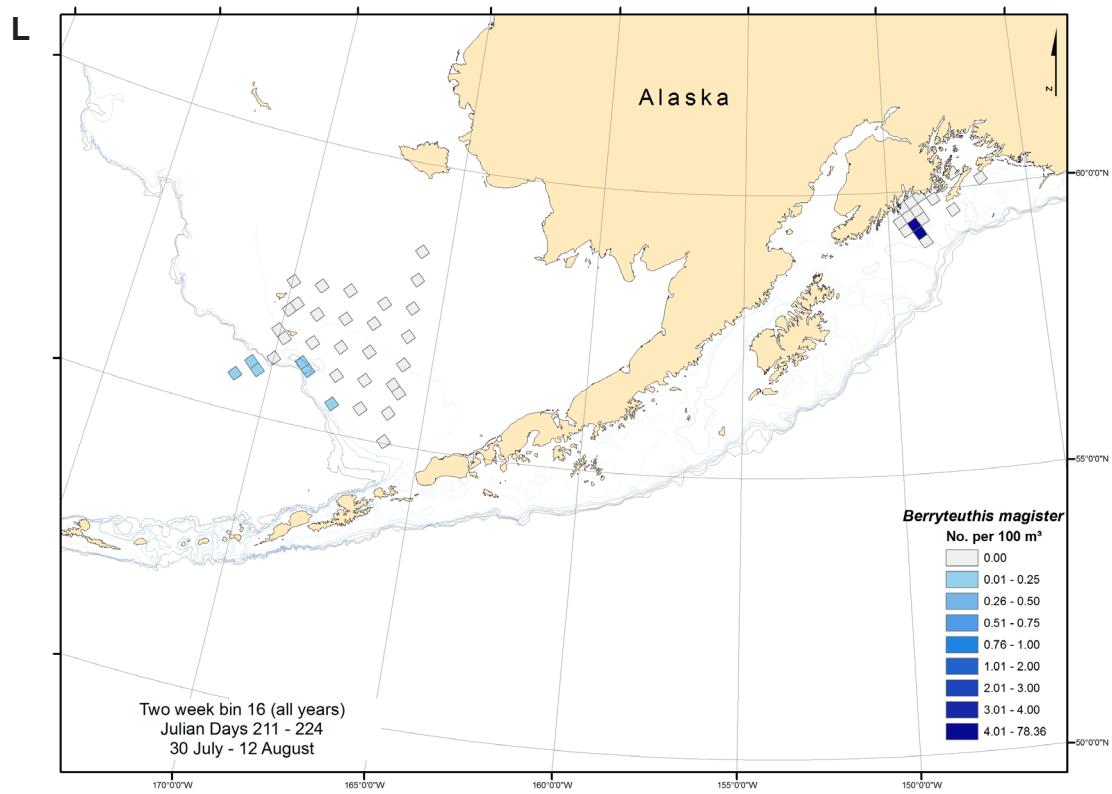
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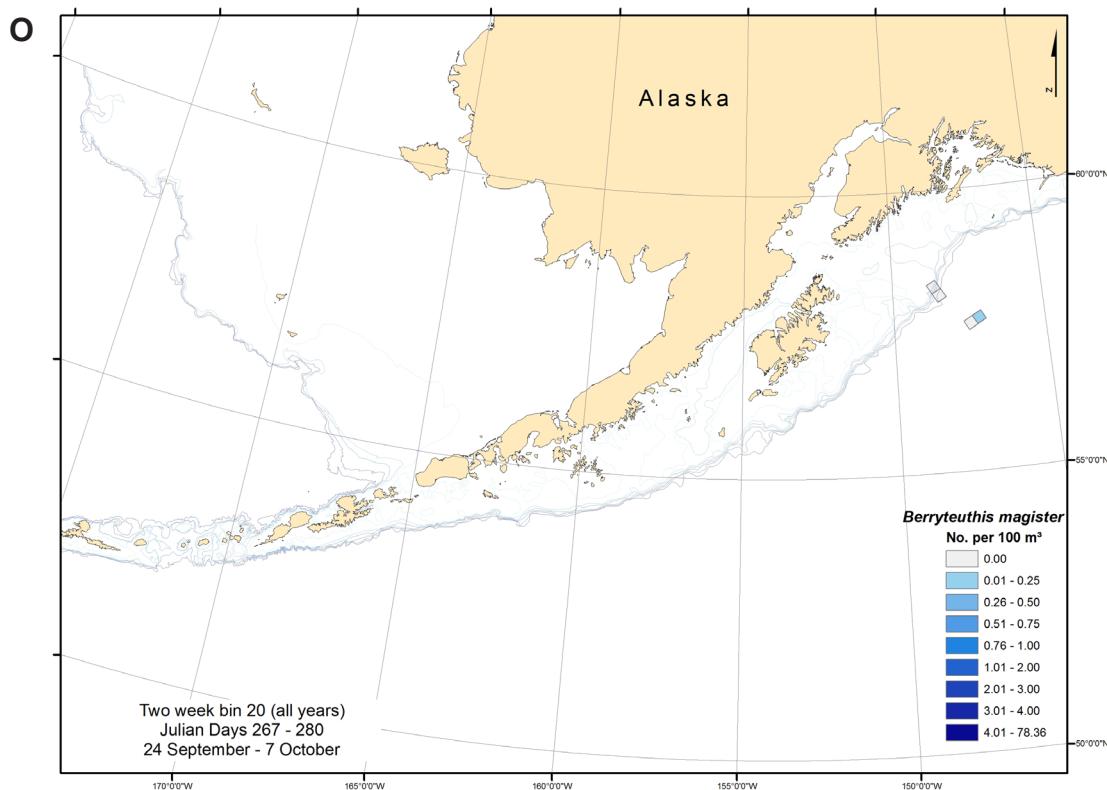
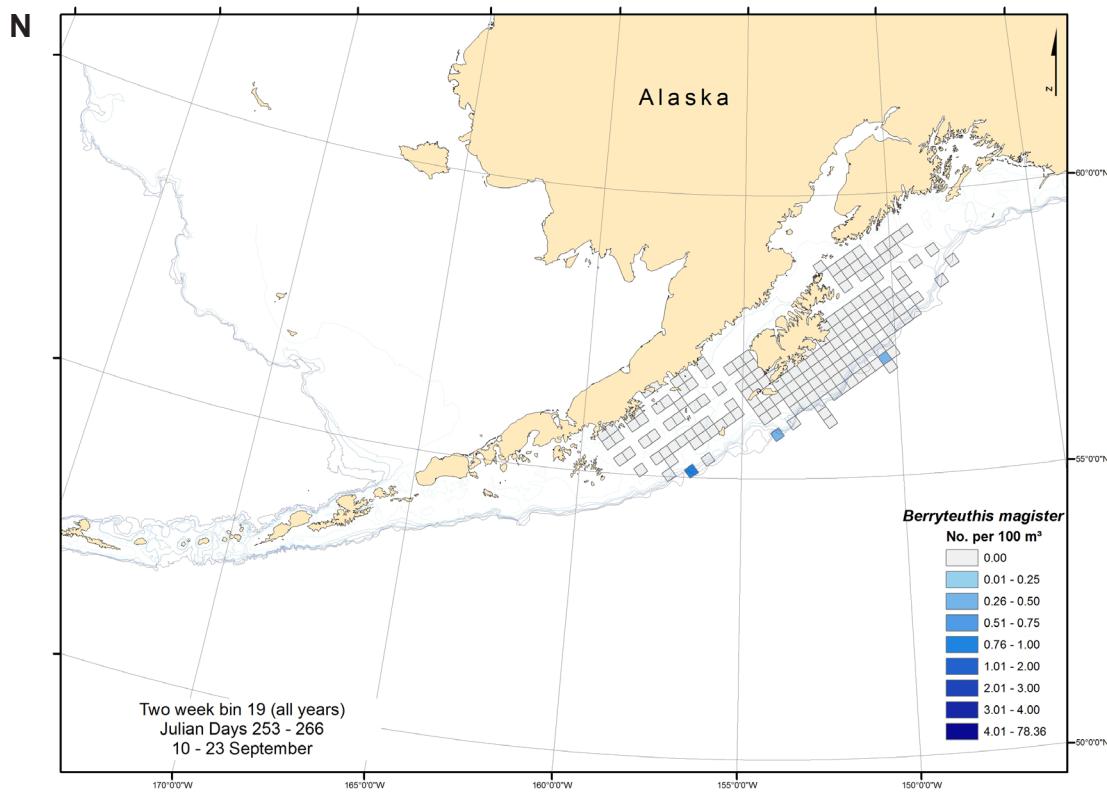
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Figures 4.10A-O continued.



Figures 4.10A-O continued.



Figures 4.10A-O continued.

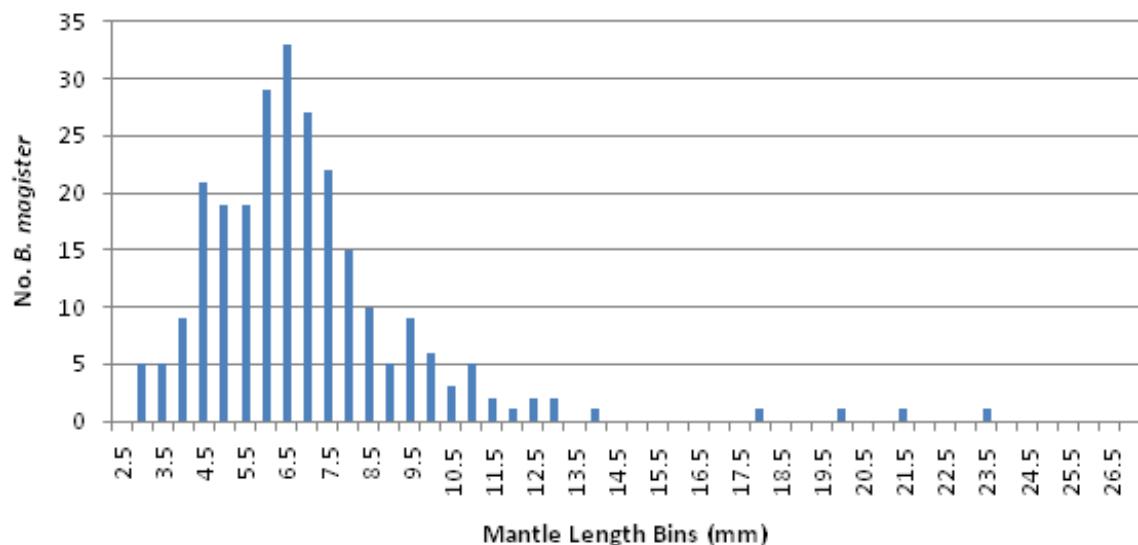


Figure 4.11. *Berryteuthis magister* mantle length frequency. Horizontal axis is mantle length bins (mm); vertical axis is the number of individuals in each bin.

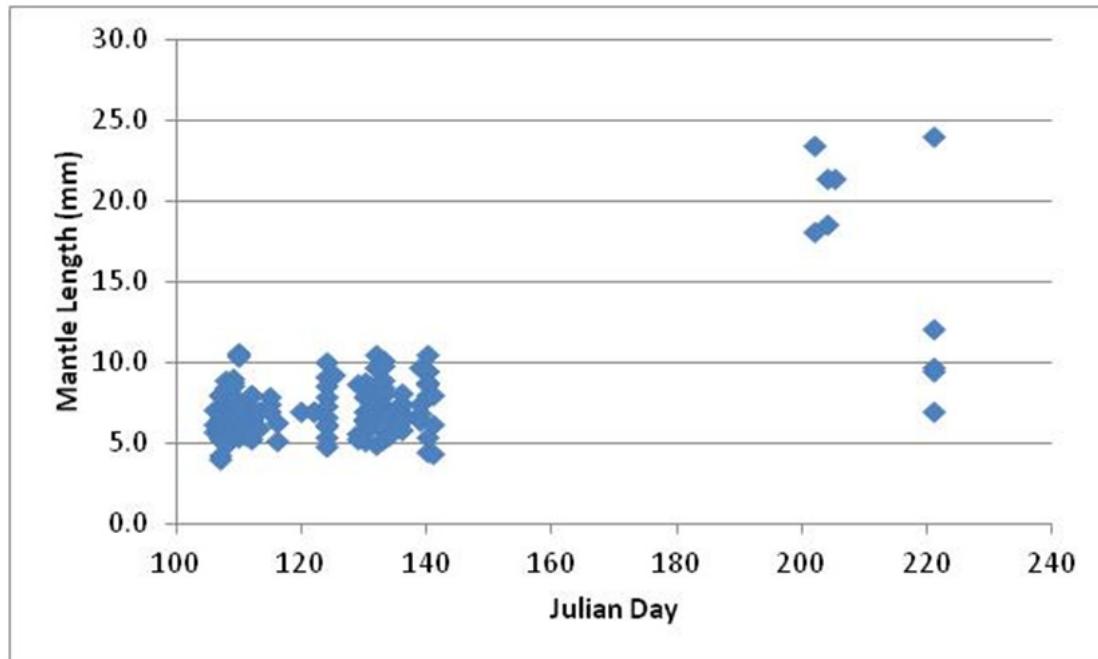


Figure 4.12A. All *Berryteuthis magister* mantle length (mm) data by Julian day for the Bering Sea.

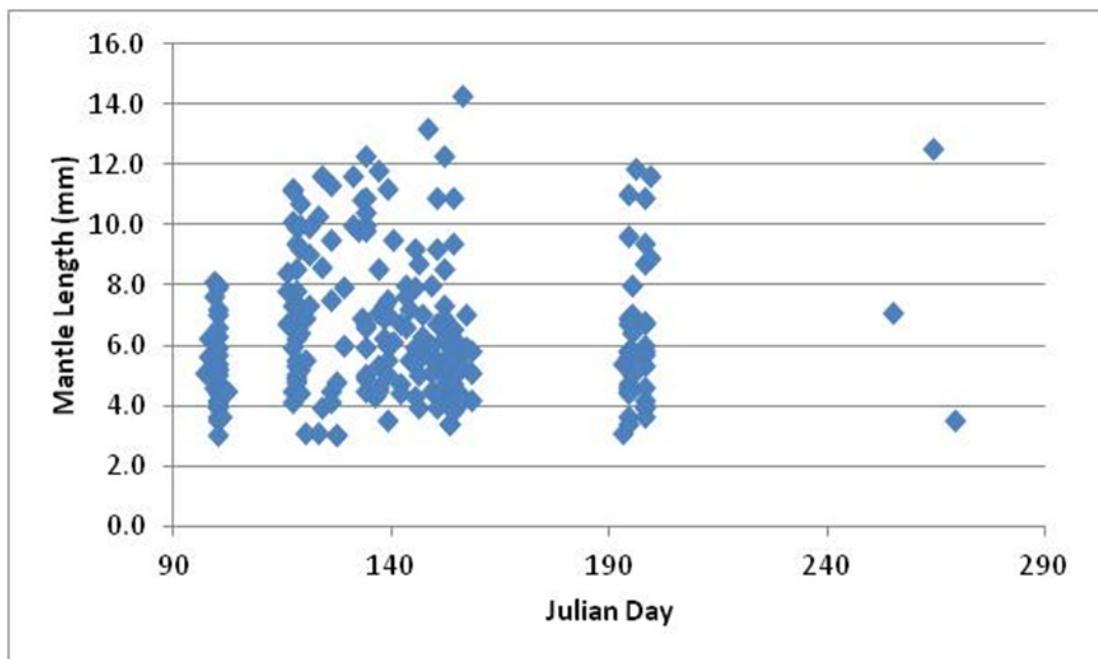


Figure 4.12B. All *Berryteuthis magister* mantle length (mm) data by Julian day for the Gulf of Alaska.

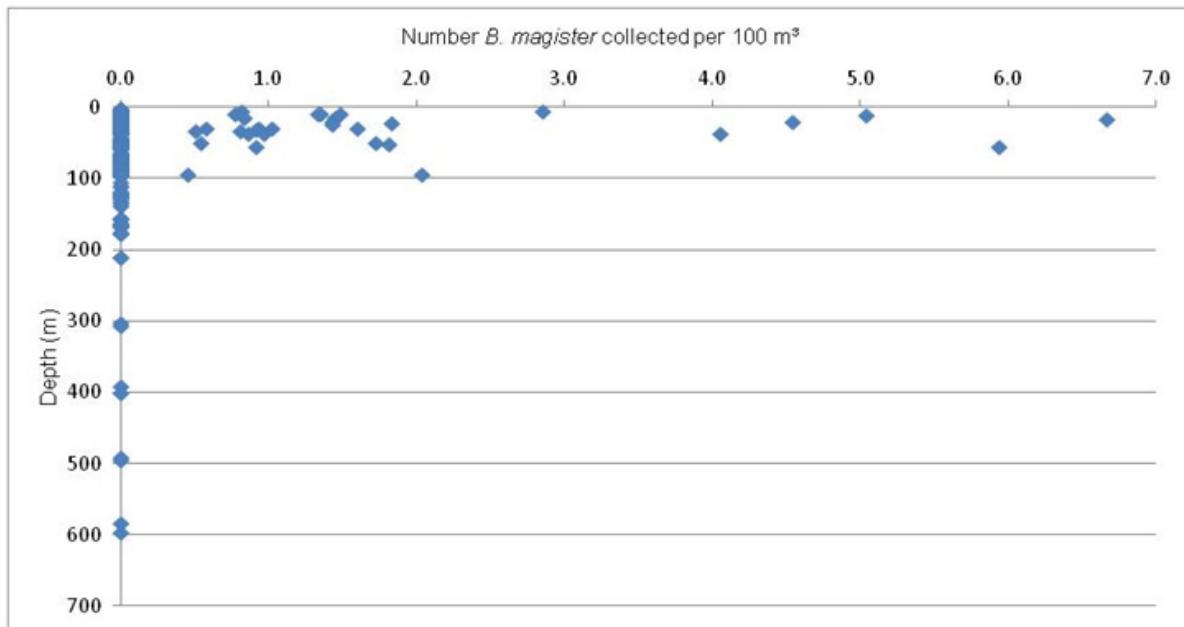
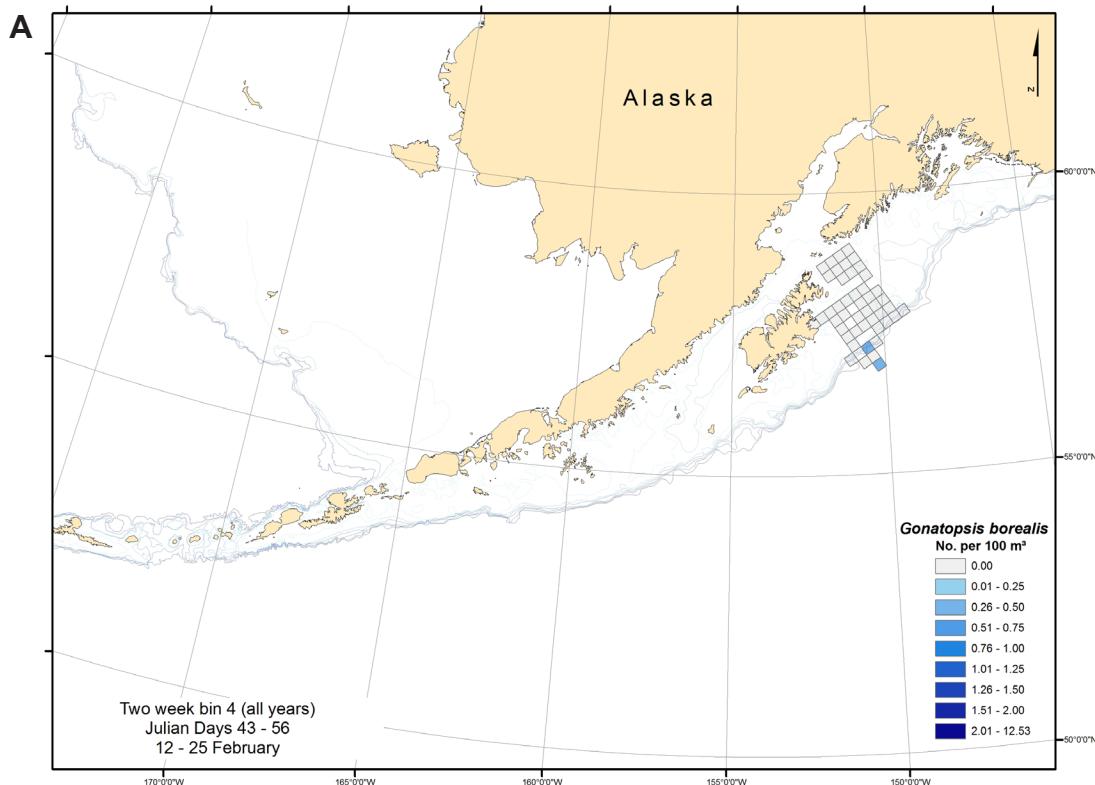
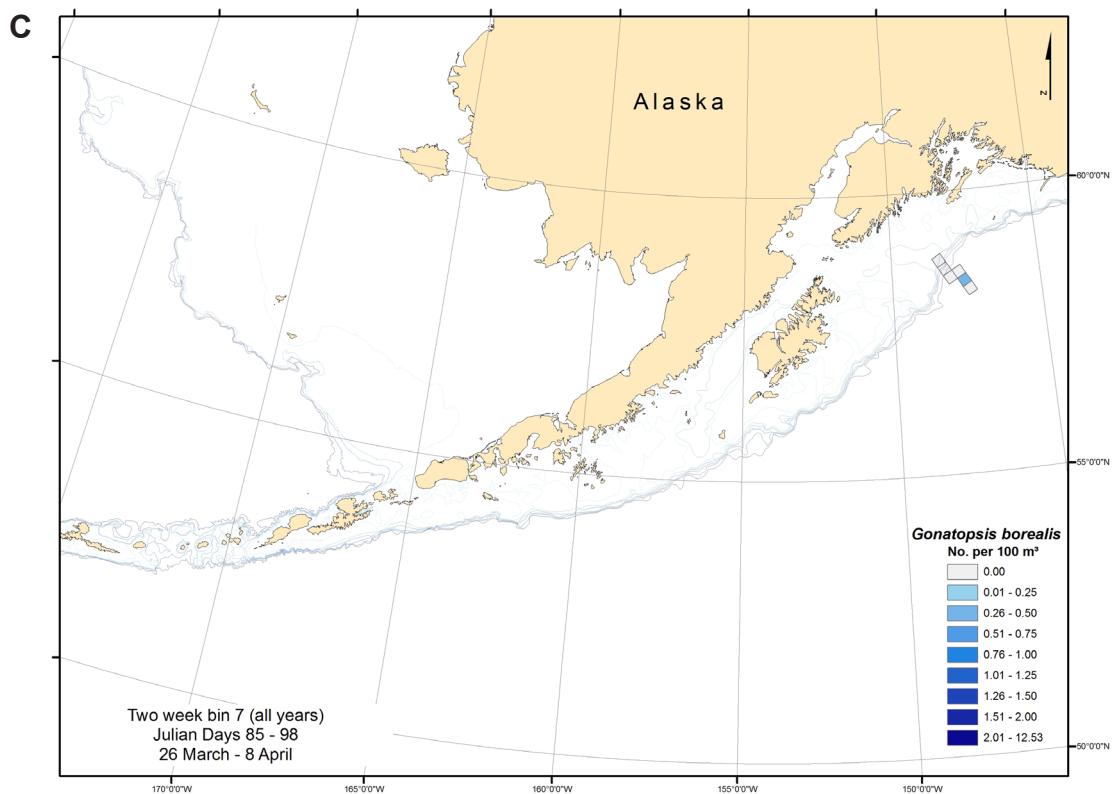
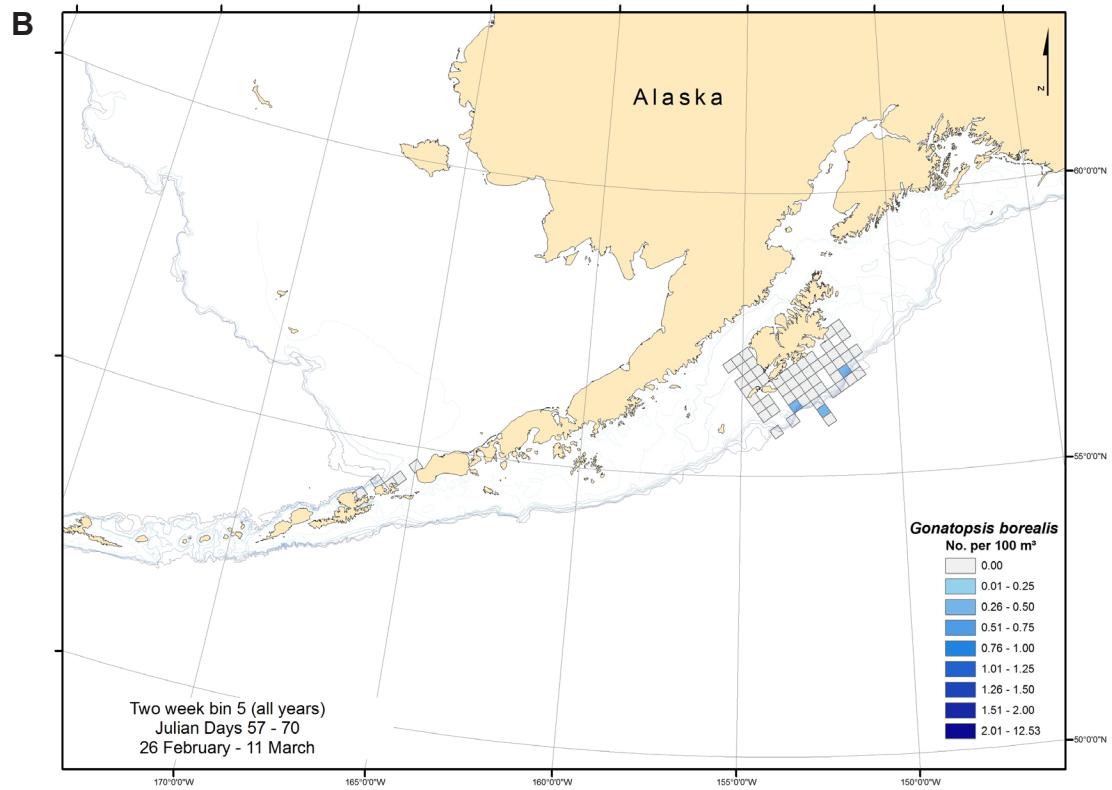


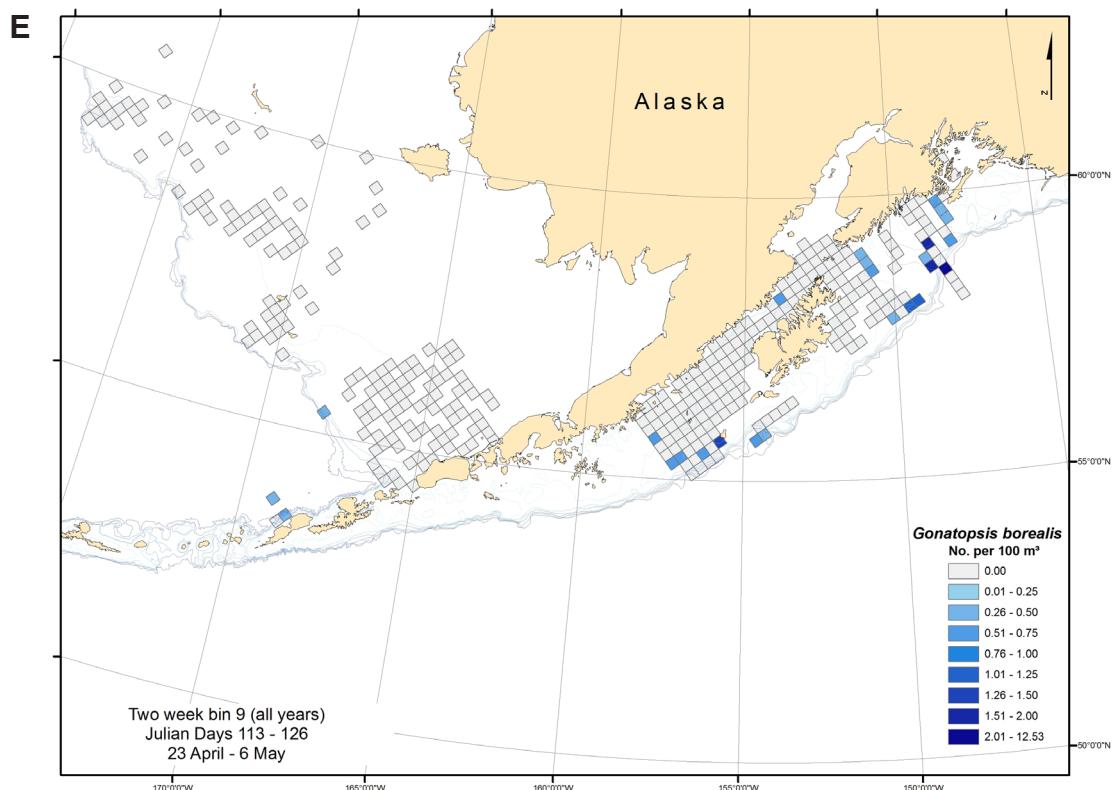
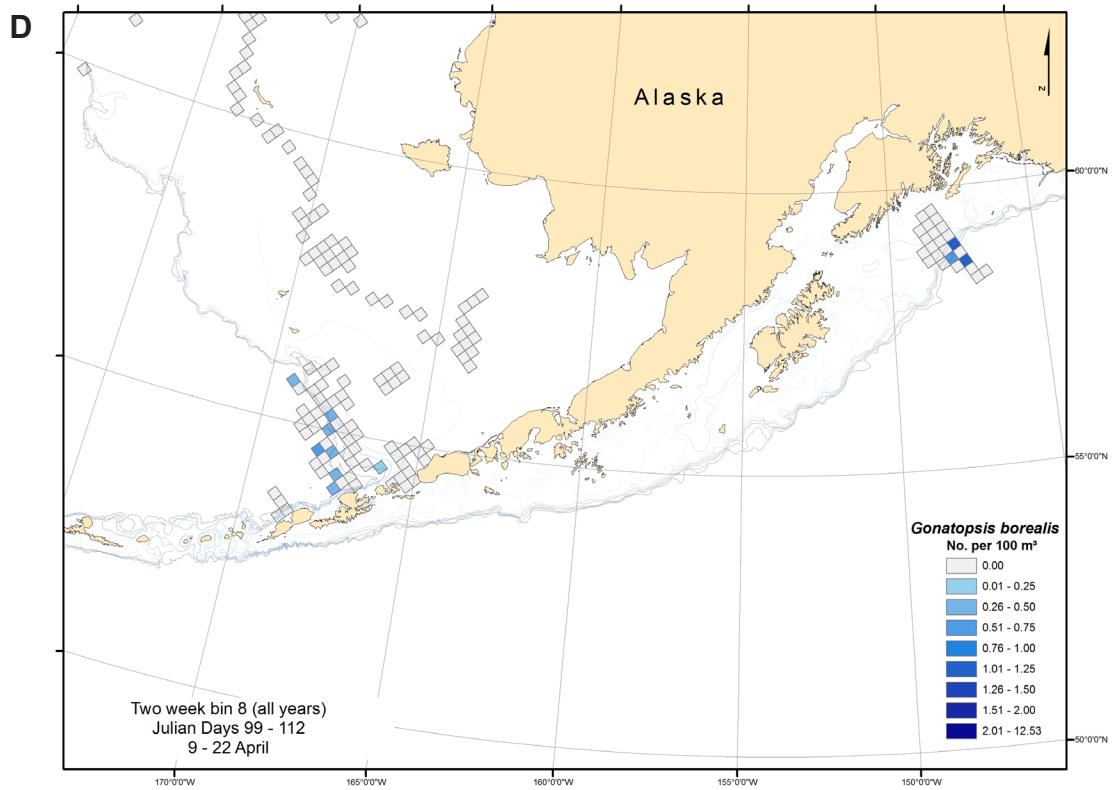
Figure 4.13. Vertical distribution of *Berryteuthis magister* (number collected per 100 m³). Includes all available data collected during the study. Depths represent the midpoint depth of each sample, e.g. a depth of 2 m represents a tow that sampled from 0 - 4 m.



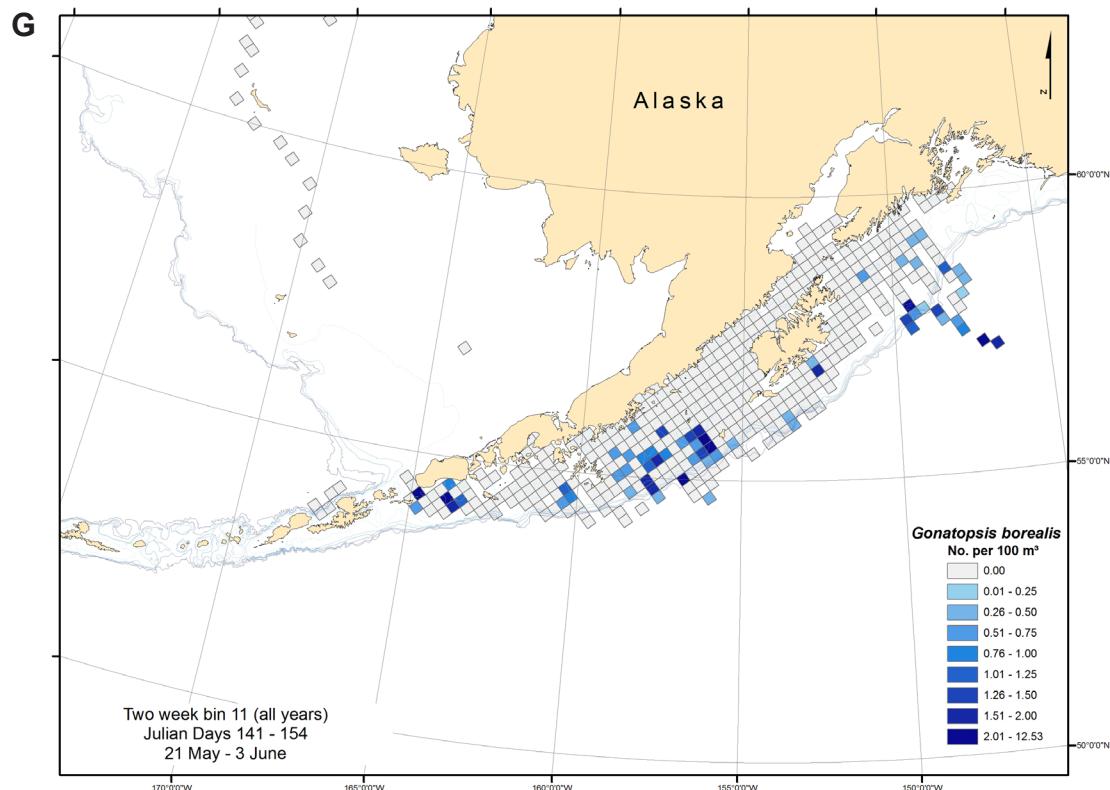
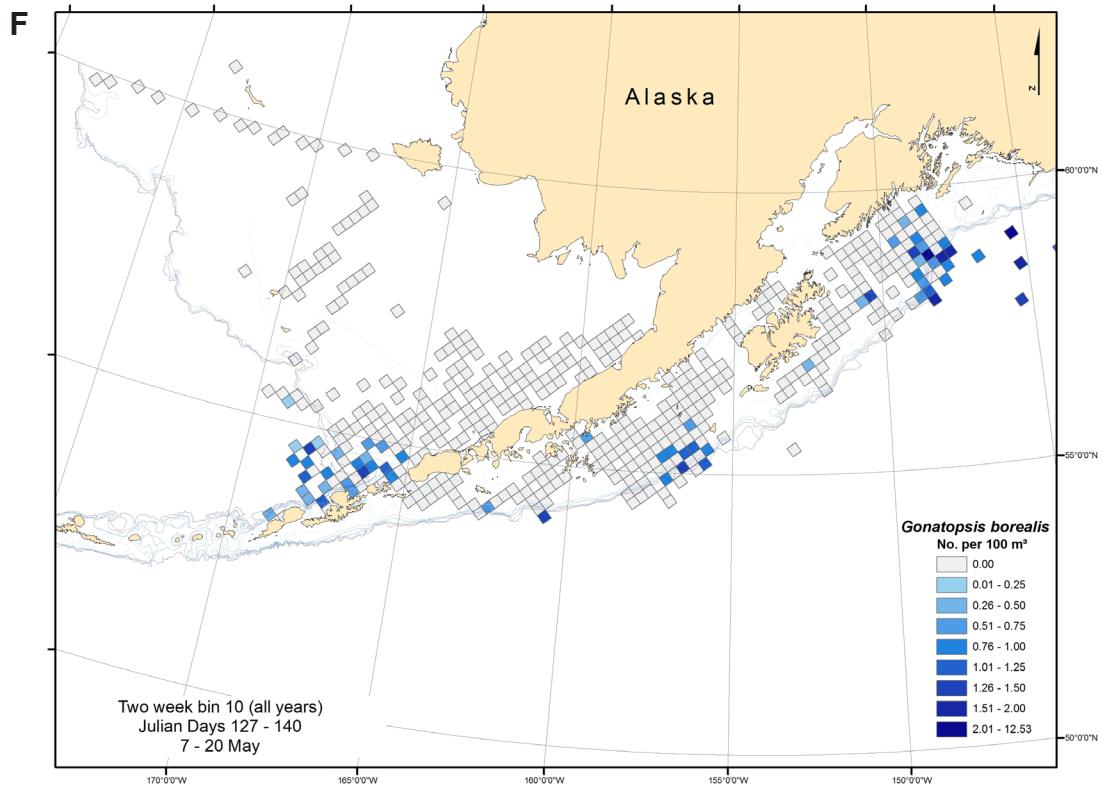
Figures 4.14A-O. Maps of *Gonatopsis borealis* distribution and abundance. Each cell represents a 20 x 20 km region within which at least one station was occupied. Grey grid cells indicate that the cell was sampled but no *G. borealis* were collected. Colors are according to legend and represent the summed number per 100 cubic meters at each station within each cell for the two-week period listed on the individual maps.



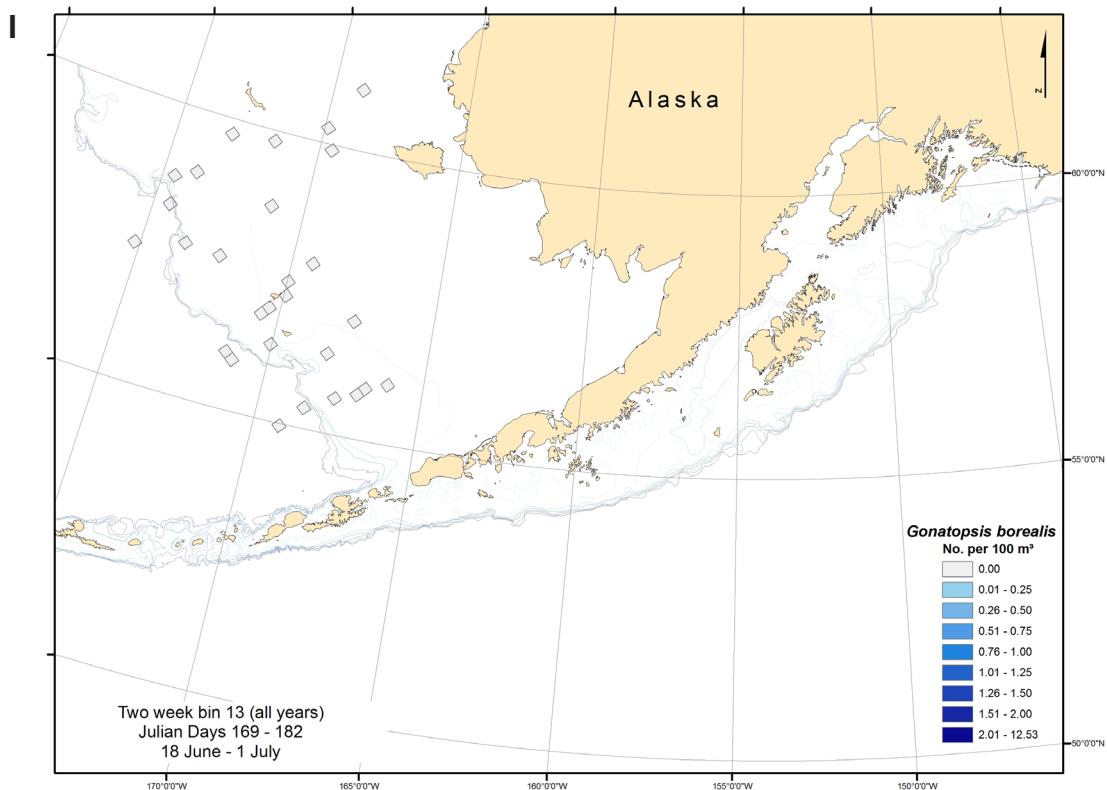
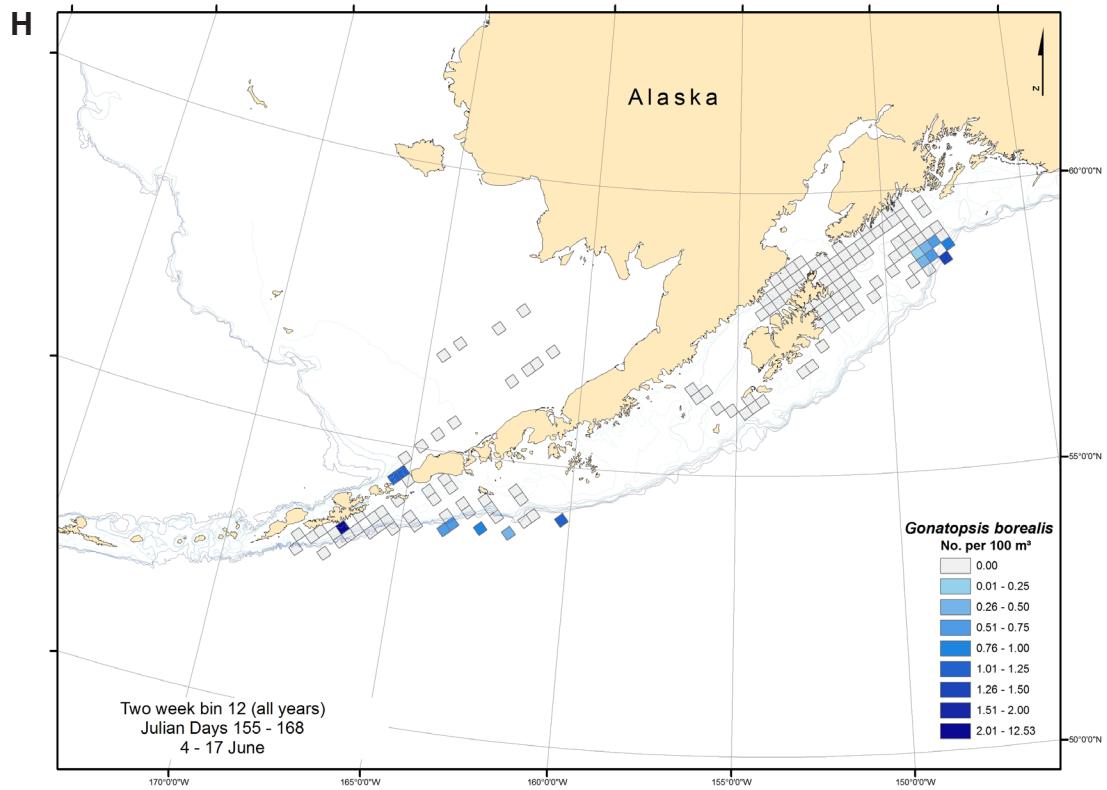
Figures 4.14A-O continued.



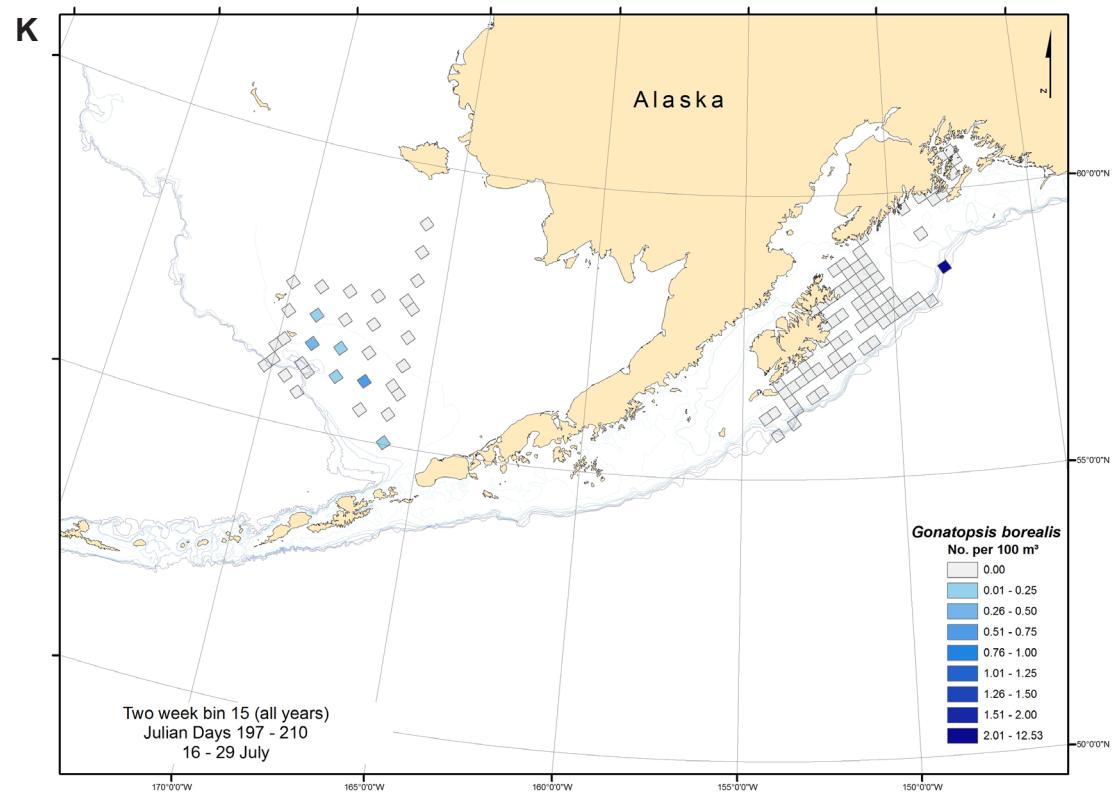
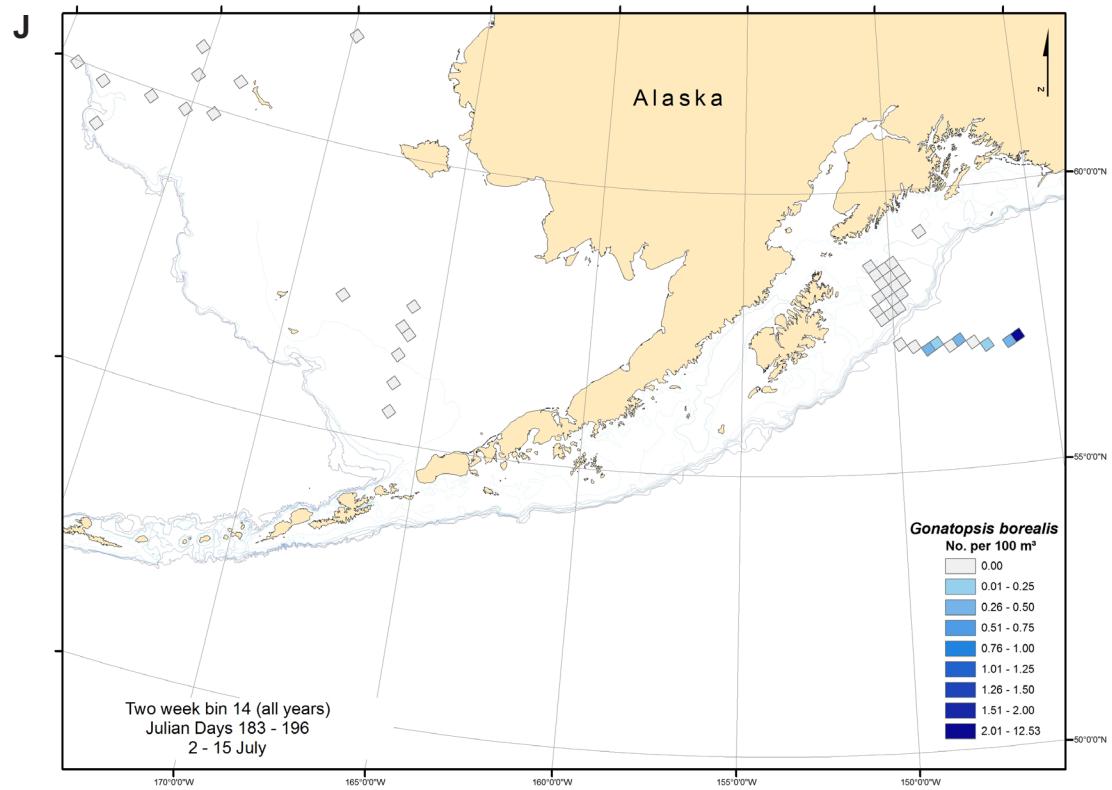
Figures 4.14A-O continued.



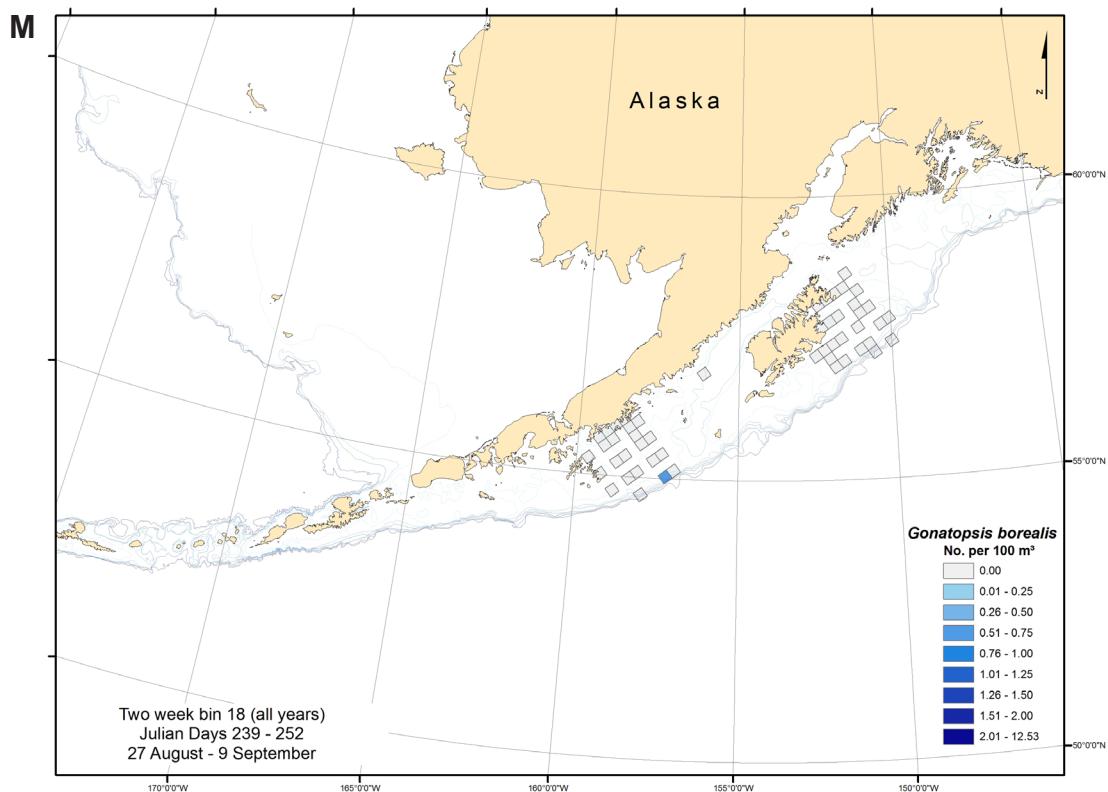
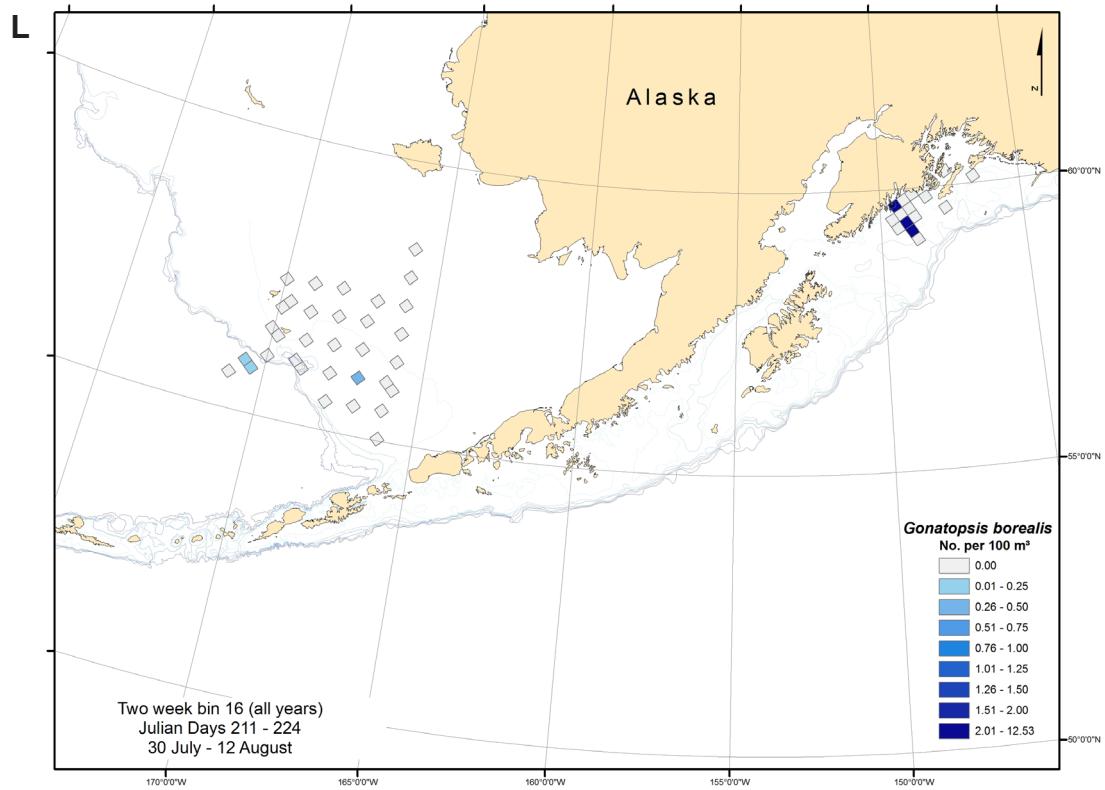
Figures 4.14A-O continued.



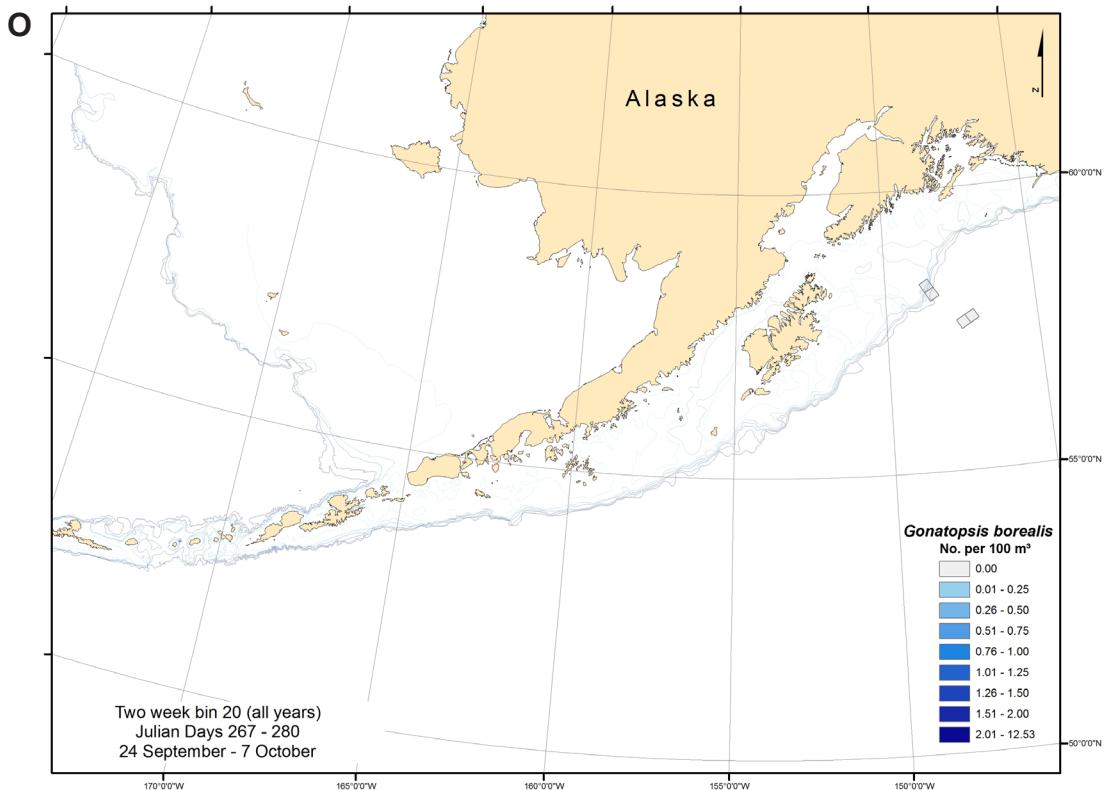
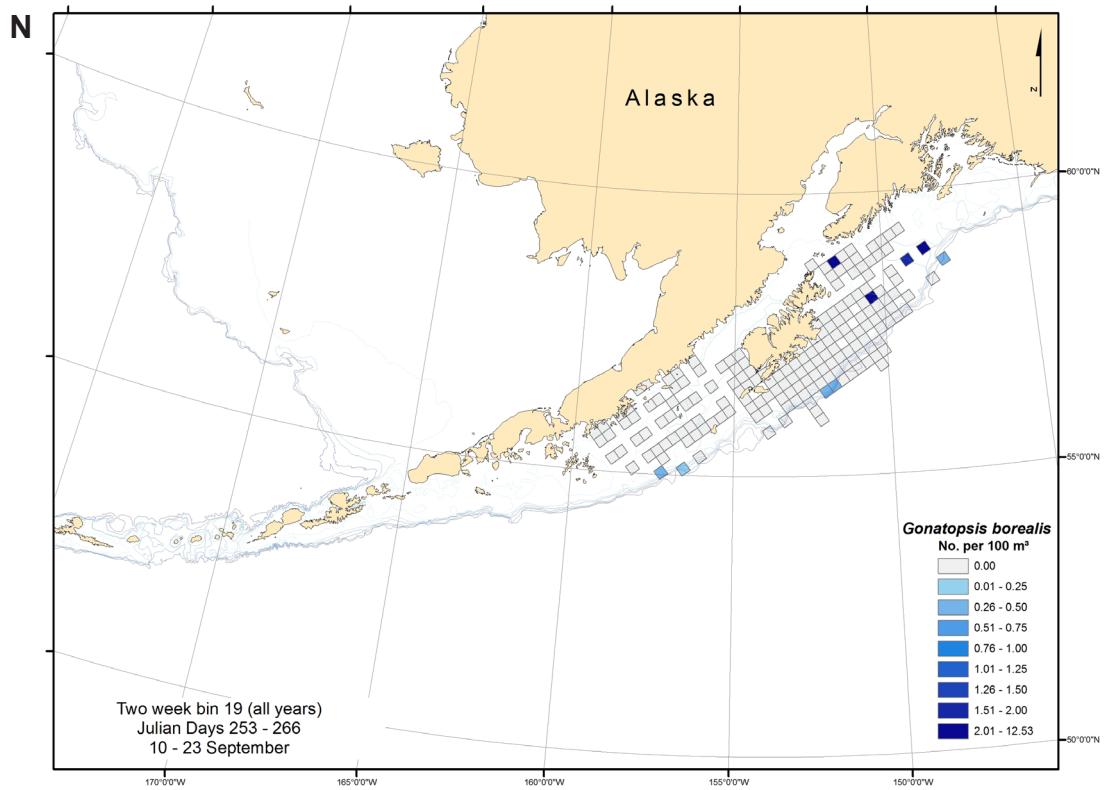
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Figures 4.14A-O continued.



Figures 4.14A-O continued.



Figures 4.14A-O continued.

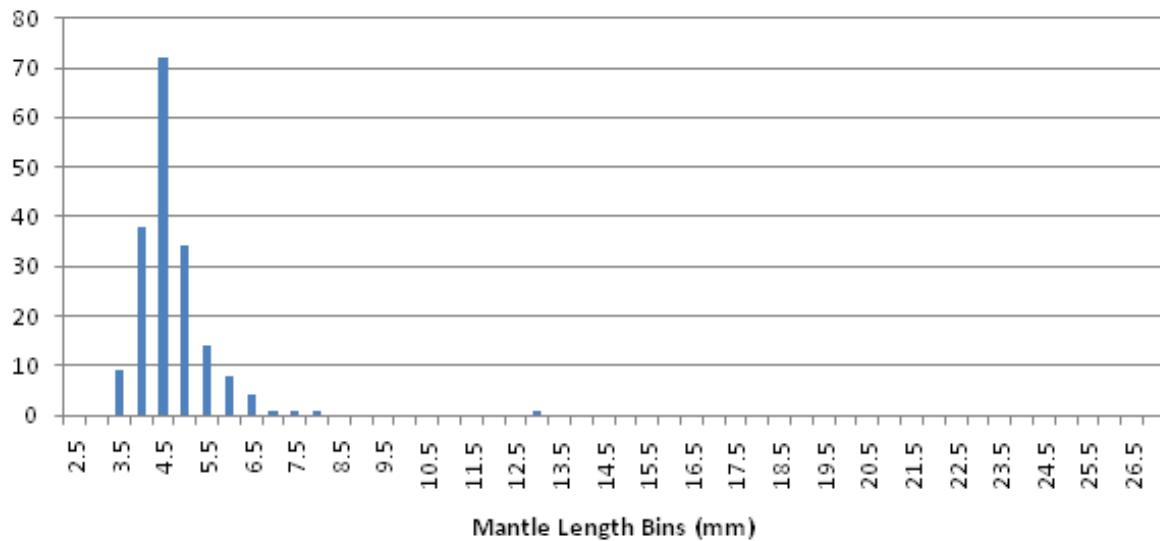


Figure 4.15. *Gonatopsis borealis* mantle length frequency. Horizontal axis is mantle length bins (mm); vertical axis is the number of individuals in each bin.

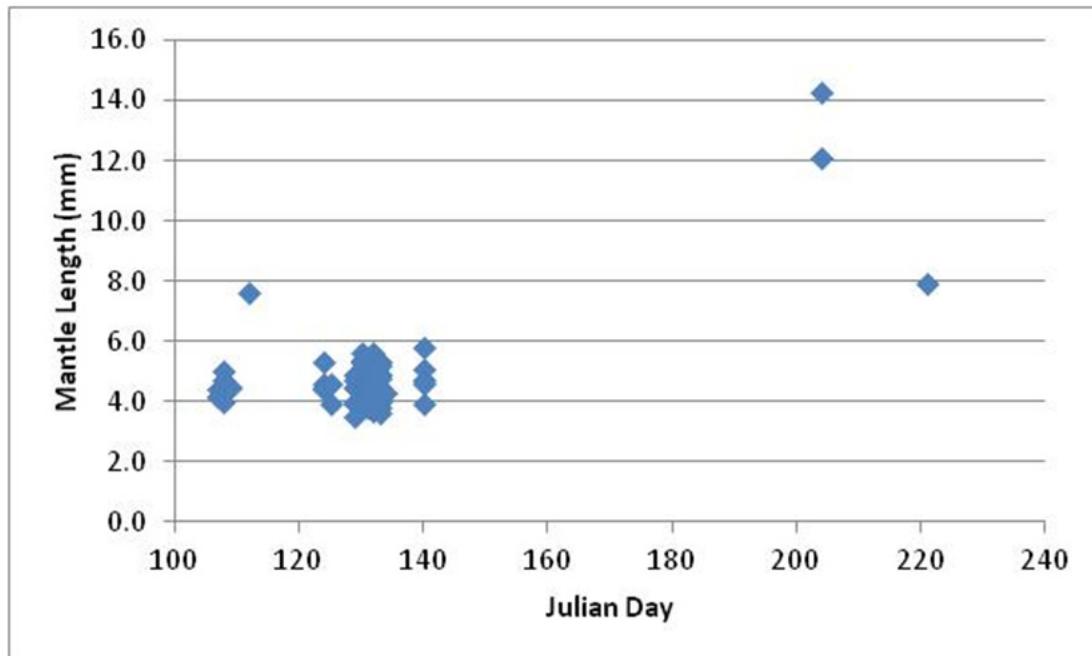


Figure 4.16A. All *Gonatopsis borealis* mantle length (mm) data by Julian day for the Bering Sea.

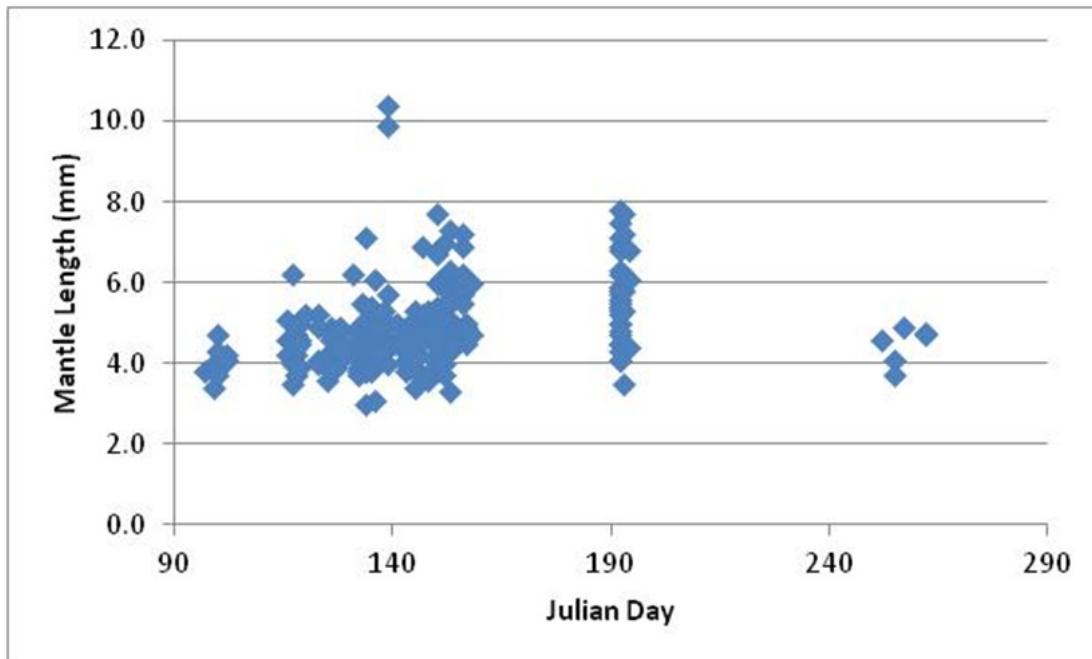


Figure 4.16B. All *Gonatopsis borealis* mantle length (mm) data by Julian day for the Gulf of Alaska.

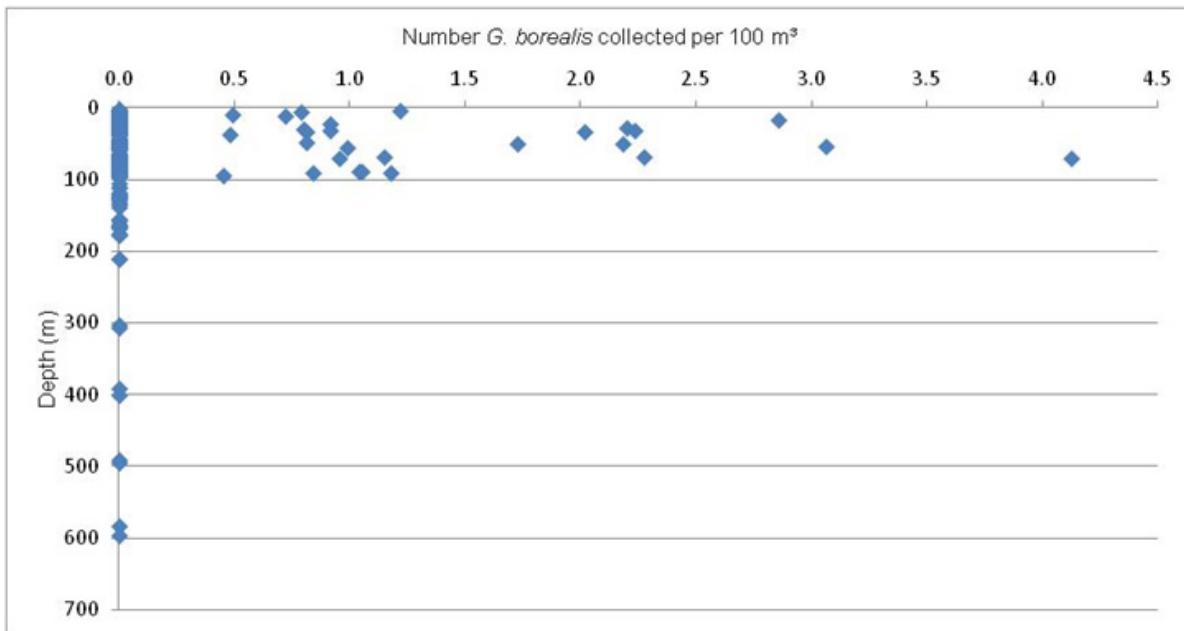


Figure 4.17. Vertical distribution of *Gonatopsis borealis* (number collected per 100 m³). Includes all available data collected during the study. Depths represent the midpoint depth of each sample, e.g. a depth of 2 m represents a tow that sampled from 0 - 4 m.

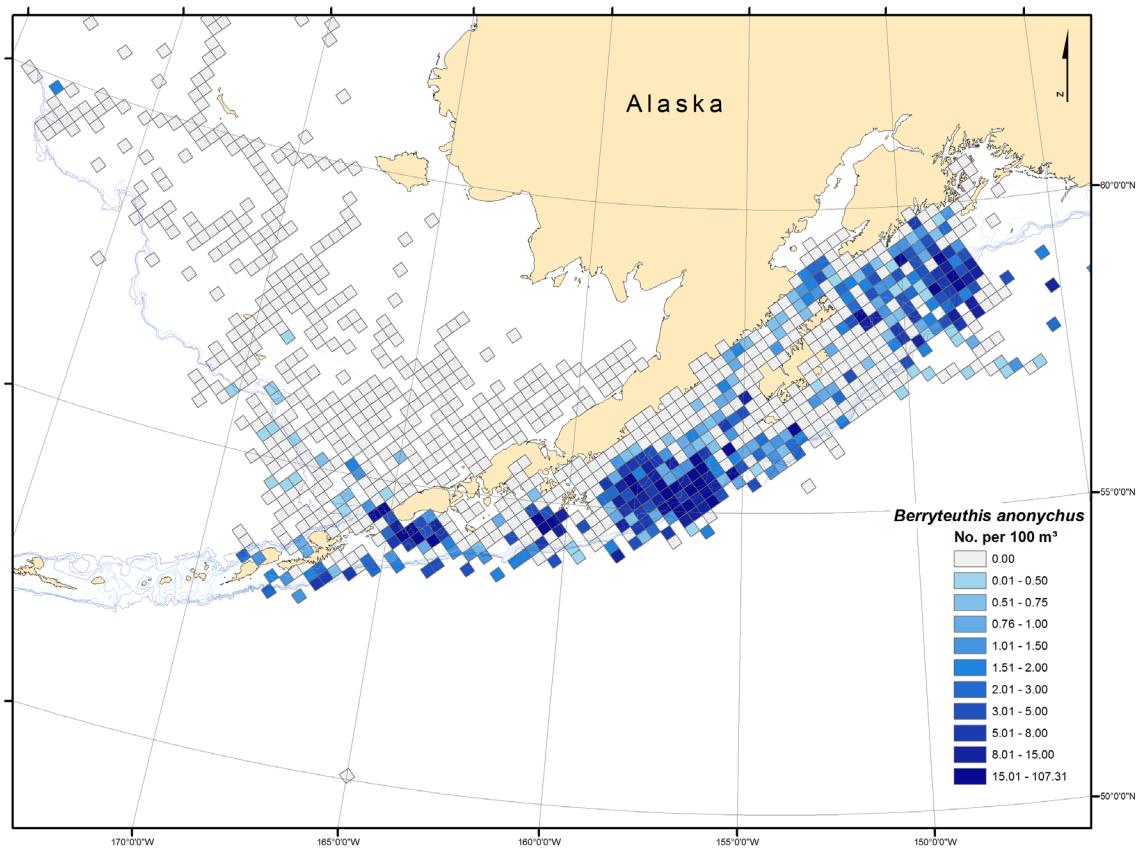


Figure 4.18. *Berryteuthis anonymus* paralarvae distribution and abundance for all years (1991 - 2009). Units are number per 100 m³.

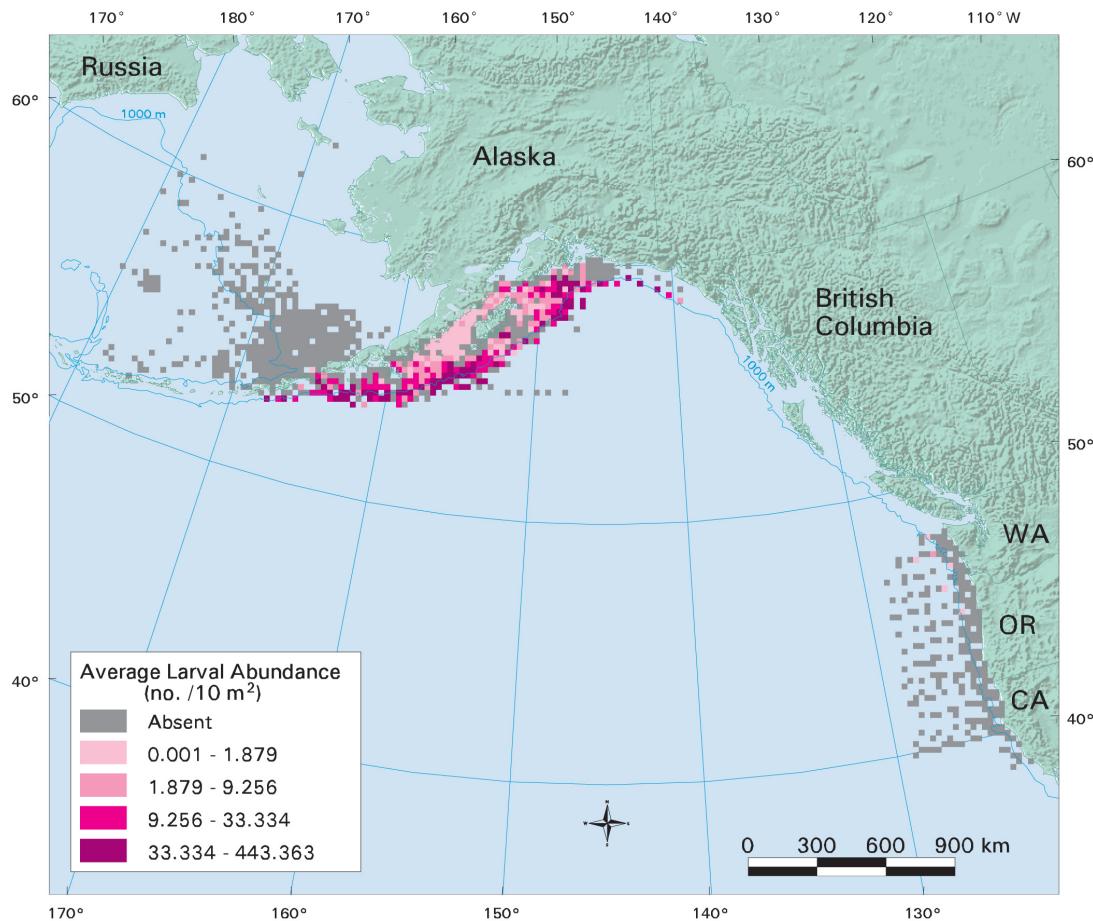


Figure 4.19. Distribution and abundance of larval arrowtooth flounder (*Atherestes stomias*) for 1979 - 2000. Units are number per 10 m². Reproduced with permission from Matarese et al. (2003).

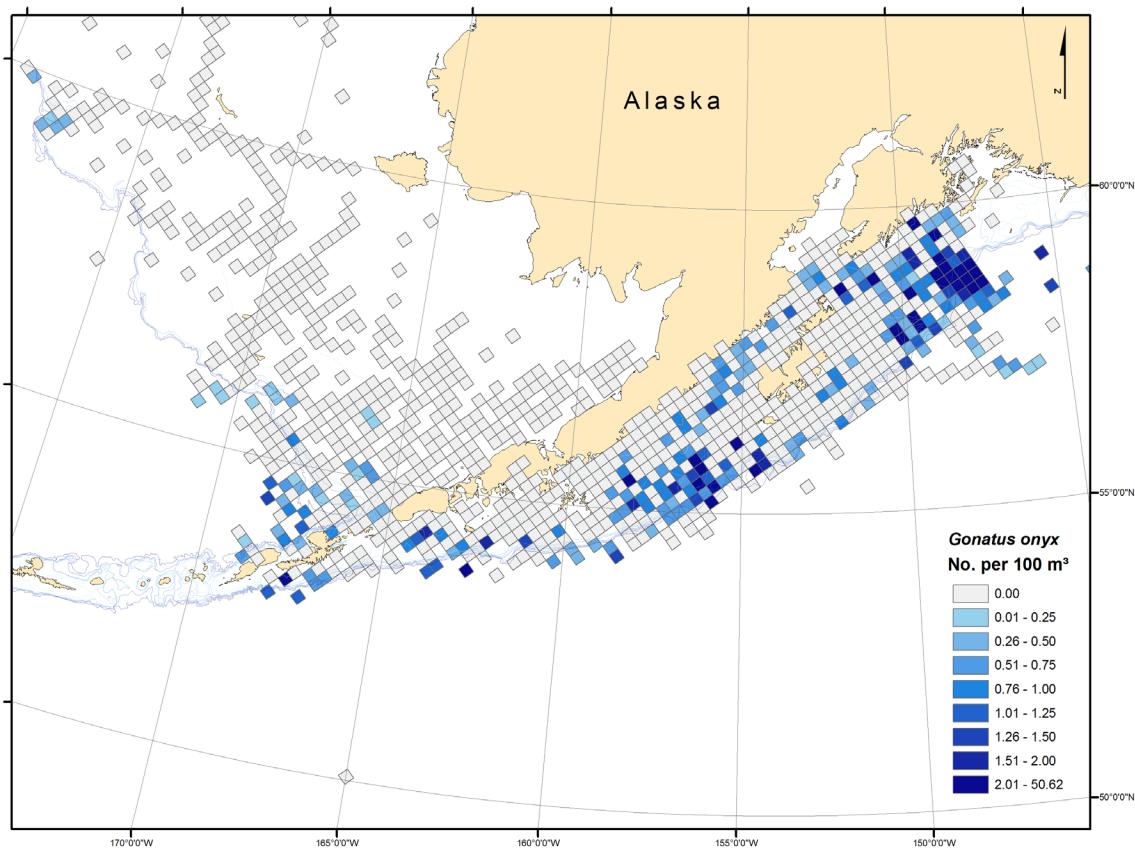


Figure 4.20. *Gonatus onyx* paralarvae distribution and abundance for all years (1991 - 2009). Units are number per 100 m³.

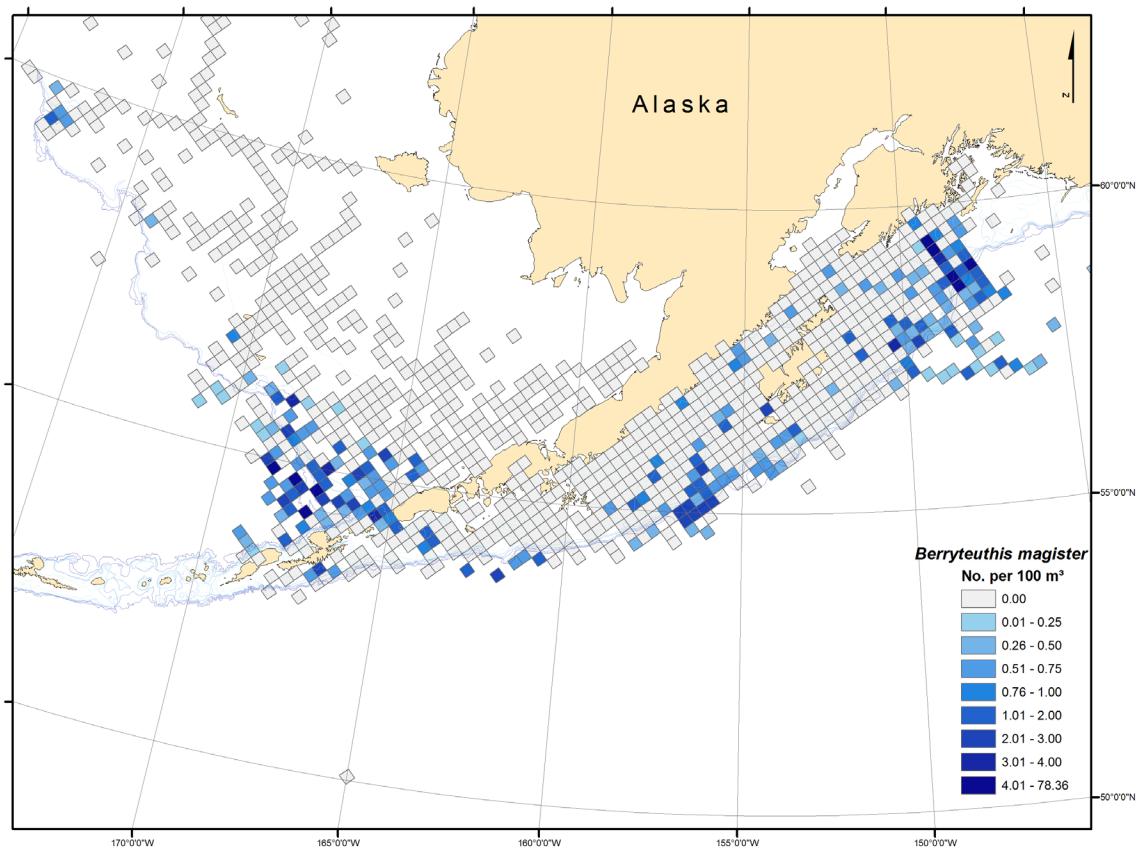


Figure 4.21. *Berryteuthis magister* paralarvae distribution and abundance for all years (1991 - 2009). Units are number per 100 m³.

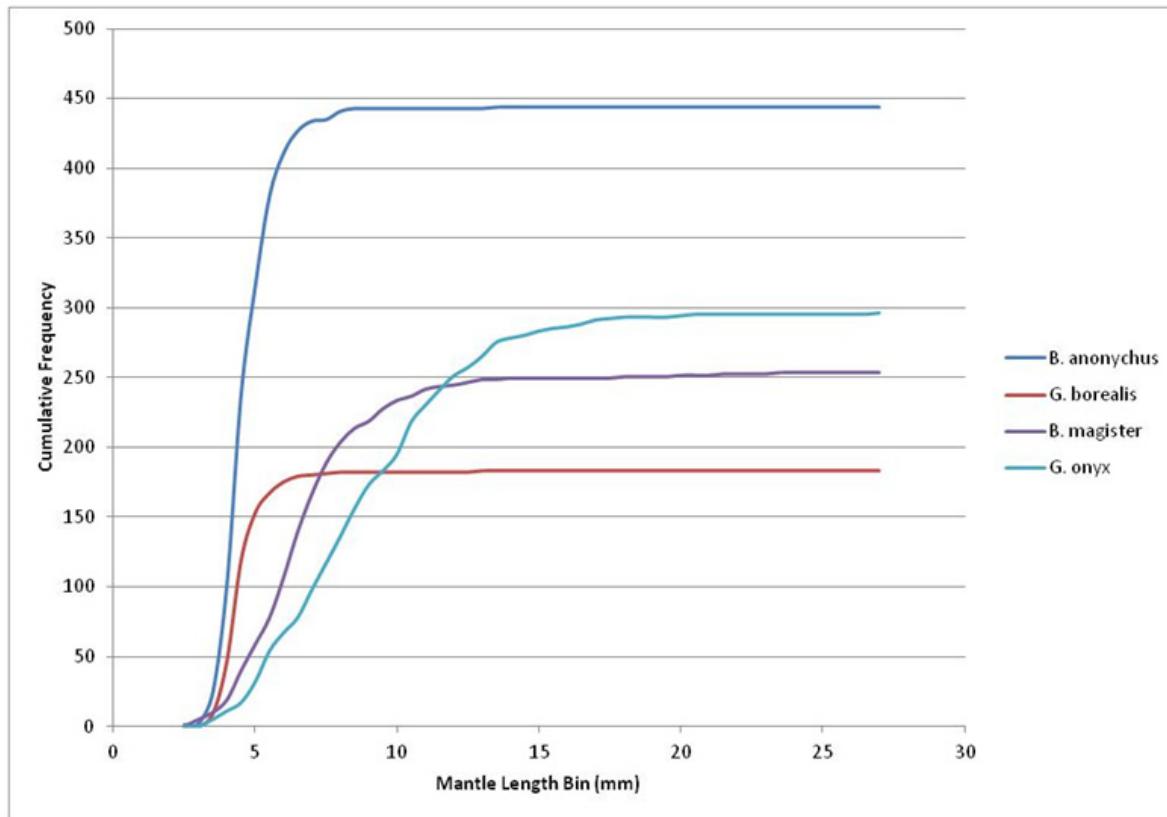


Figure 4.22. Cumulative length frequencies of each species. The x-axis is mantle length bin (0.5 mm bins, starting with 3 mm); y-axis is running total of number of individuals in each bin.

Chapter V: Investigation of bottom-up and top-down control of cephalopod paralarvae abundance in the Gulf of Alaska

Abstract

Eighteen years of cephalopod paralarvae abundance data from the Gulf of Alaska were analyzed and used in conjunction with available indices of climate and ocean as well as predator (pink salmon) abundance to investigate the factors contributing to and controlling variations in cephalopod abundance. The results of canonical correspondence analysis indicate that variations in *Berryteuthis anonymus* abundance may be due to bottom-up and top-down control.

Introduction

In the Gulf of Alaska, cephalopods are important aspects of the diets of a variety of commercially important fish, seabirds, and marine mammals. There are 23 cephalopods regularly found in the Gulf of Alaska. They are represented by 10 families in four orders. The most abundant species are from the families Gonatidae and Octopodidae.

Of the 18 described species in the family Gonatidae, one is found in Antarctica, two are found in the North Atlantic and Arctic, and the remaining 15 species are endemic to the North Pacific. In the Gulf of Alaska, the squid assemblage is dominated by *Berryteuthis magister* (Berry, 1913), *Gonatopsis borealis* Sasaki, 1923, *Berryteuthis anonymus* (Pearcy and Voss, 1963), *Gonatus onyx* Young, 1972, *Gonatus madokai* Kubodera and Okutani, 1977, and *Gonatus middendorffi* Kubodera and Okutani, 1981. Actual relative adult abundances are difficult to discern since, due to the differing life history strategies, there is no single sampling method that samples all species equally well using conventional trawling strategies. For instance, Alaska Fisheries Science Center summer

groundfish trawling reflects high numbers of *B. magister* and *G. borealis*, the two species that are mating in that area at that time and are epibenthic as adults.

The remaining species are pelagic squids, although it is possible that some may become associated with the seafloor during spawning. Spawning information is only available for a single species of gonatid, *G. onyx*. Hunt and Seibel (2000) and Seibel et al. (2005) filmed and collected specimens brooding egg sacs. The specimens were filmed between 1250 and 2250 m in Monterey Bay Canyon.

Another notable piece of missing information is the life span of any of the gonatids. Generalizations made about squid life spans are typically based on shallow-water species, i.e. loliginids, which are easier to collect and study but are in a different order (Myopsida) and therefore not the most appropriate model for the deep-sea species.

Gonatid squids of the North Pacific ocean are distributed from the California coast to Alaskan, Russian, and Japanese waters (Jorgensen, 2009). The different regions (Gulf of Alaska, Sea of Okhotsk, Sea of Japan, and California Current) have different assemblages of gonatids (Okutani et al., 1988). In the California Current, *G. onyx* is the most abundant gonatid while in the Gulf of Alaska *G. onyx* is present but *B. magister* is the most abundant in the adult stage (based on groundfish survey data).

The octopod in this study, *Enteroctopus dofleini*, is relatively well-known. It occurs from off the coast of California north to Alaska and west to Japan. It is one of two benthic incirrate octopods in the shelf region of the Gulf of Alaska and the only one with a planktonic stage; it is the highest latitude incirrate octopod with a planktonic life stage. Females deposit eggs on the underside of rocky dens and provide protection and cleaning of the eggs for the 5 - 7 months it takes them to hatch; after which the female dies. Hatchlings are 2.5 - 3.0 mm mantle length and spend the next 2 - 3 months in the plankton. Its life span is 4 - 6 years. This

information is based on laboratory studies of the same species in lower latitude, warmer waters. These estimates could be very different for animals from the cooler Alaskan waters due to the importance of water temperature on growth rate. And while bottom trawls are conducted every summer in the Gulf of Alaska and Bering Sea, adult population estimates between the two regions are likely off due to the necessity of “rock hopper” gear in the Gulf of Alaska (this gear allows the bottom trawls to fish over rocky bottoms by maneuvering the net over the rocks instead of plowing under them. For sampling fish, the discrepancy is likely fine however when sampling an animal that lives under rocks and has thousands of suckers with which to hold on to rocks, they are likely underrepresented). Even in relatively shallow areas, like Puget Sound, it is difficult to estimate the population of *E. dofleini*.

The paucity of information on these cephalopods and poor sampling make interpreting adult abundance data difficult. It was for similar reasons that Vecchione (1987) concluded that studying the paralarval stage of cephalopods would provide the most accurate information on their populations. This study, therefore, focuses on paralarval data collected during larval fish surveys in the Gulf of Alaska.

The Gulf of Alaska is a complex ecosystem (Overland et al., 2000). Despite being a downwelling, the Gulf of Alaska ecosystem is one of the most productive in the world, home to the walleye pollock (*Theragra chalcogramma* (Pallas, 1814)) fishery. It is dominated by two currents, the Alaskan Stream at the shelfbreak and the Alaska Coastal Current on the shelf (Stabeno et al., 2004). The Alaska Stream is the northern portion of the Subarctic Current that transports warm water across the Pacific from Japan. The Subarctic Current bifurcates at approximately 50°N, the southern portion becoming the California Current and the northern portion becoming the Alaska Stream. The Alaska Stream then splits into the Alaska Coastal Current and the Alaska Stream at approximately 150°W. The Alaska Stream and the Subarctic Current represent the northern and southern boundaries of the Alaska

Gyre, respectively.

Several major oceanographic and climatic phenomenon impact, to varying degrees, the Gulf of Alaska ecosystem and therefore may also influence the distribution and abundance of cephalopod paralarvae, including El Niño Southern Oscillation (ENSO) (Wolter and Timlin, 1998), the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997), Arctic Oscillation (AO) (Thompson and Wallace, 1998), East Pacific - North Pacific oscillation (EPNP) (Barnston and Livezey, 1987), the intensity of the Aleutian low pressure cell (NP) (Trenberth and Hurrell, 1994), and alongshore (ALONG) and mixing (MIX) winds (Stabeno et al., 2004). Each of these phenomena can be represented as a monthly index, representing the anomaly for that phenomenon at that time. The PDO and ENSO are closely related phenomena. ENSO is a disruption in the tropical winds of the equatorial Pacific. In the positive phase, an El Niño, tropical winds blowing east to west along the equator weaken, diminishing the normal upwelling off the coast of South America. The diminished upwelling results in warmer than normal water off the coast which in turn warms the atmosphere. In the negative phase, a La Niña, winds are stronger than normal resulting in increased upwelling and lower than normal water temperatures off the coast of South America. The effects of ENSO can be felt throughout most of the world to some degree however in Alaskan waters the effects are diminished and episodic. Despite its role as probably the climatic anomaly that is talked about the most, its role in the Gulf of Alaska ecosystem is likely secondary to the other phenomenon mentioned. The PDO is related to the ENSO, it is described as a “low pass filter” of ENSO where the warming or cooling of ENSO build up in the ocean and create the PDO (A. Hermann, personal communication) and as “rectifying and integrating the ENSO signal” (N. Bond, personal communication). Unlike the ENSO which is atmospheric in origin, the PDO is fundamentally an anomaly of sea surface temperature (SST). The PDO is also centered in the North Pacific, not the tropical

Pacific, and has, as the name suggests, decade-long cycles of warm or cool SST.

The Arctic Oscillation refers to atmospheric pressure over the North Pole. It is important because it is a dipole anomaly, meaning that when pressure is high over the North Pole it is low at the other pole, in this case, the North Pacific and vice versa. In the positive phase, the atmospheric pressure is low in the Arctic and high in the Gulf of Alaska.

The East Pacific North Pacific oscillation is also an atmospheric, dipole anomaly. The two part name refers to the fact that the poles change location depending on whether the anomaly is positive or negative. In the positive phase, the poles are centered in the Gulf of Alaska (higher than normal air pressure) and the central North Pacific (lower than normal air pressure). The negative phase poles are centered on the central North Pacific (higher than normal air pressure) and eastern North America (lower than normal air pressure). During strong positive phases, the Pacific jet stream shifts southward and intensifies. The negative phase results in a weaker Aleutian Low. This anomaly generally has the greatest effects in the Gulf of Alaska in the springtime. The result in the Gulf of Alaska is that during positive phases when atmospheric pressure is higher than normal, northeastward winds increase in intensity, intensifying the regional downwelling and resulting in warmer than normal SST and lower than normal precipitation.

The North Pacific is a monopole atmospheric phenomenon of sea level pressure in the region of 30 - 65°N and 160°E - 140°W. Its pole is centered between the positive phase poles of the EPNP. This area includes the region of the Aleutian Low, a semipermanent low pressure region near the Aleutian Islands; NP reflects the strength of the Aleutian Low. In the positive phase, sea level pressure is lower than normal, increasing westward winds. In the negative phase, sea level pressure is higher than normal. The NP is strongest in the winter months (November to March).

The alongshore winds are calculated from wind velocity data recorded at

59°N, 150°W. Mixed winds is wind speed cubed and represents the wind energy transmitted to the ocean.

In addition to the climatic and oceanographic phenomena, cephalopod paralarvae abundance could be influenced by predation. Gonatid squids are important in the diets of many fishes, including pollock, cod, halibut, but in salmon, these squids can represent 90% of the diet. Pink salmon (*Oncorhynchus gorbuscha* (Walbaum, 1792)) is a relatively small Pacific salmon with a two year life cycle. It spawns in streams and rivers from Washington State to Alaska, Russia, and Japan; however, the tag and release studies (Myers et al., 1996) indicate that individuals from the Gulf of Alaska are from North America spawning grounds. Pink salmon enter marine waters as juveniles in the summer and, in the Gulf of Alaska, feed primarily on small gelatinous zooplankton such as pteropods and larvaceans. As adults, their diet consists primarily of gonatid squids, specifically *B. anonychus*. Adult salmon return to freshwater in the fall. Salmon, like many fish, are gap and suck predators. The fish opens its mouth very quickly, creating a vacuum that sucks the prey inside. Because the prey are swallowed whole and not chewed up, salmon are very good squid samplers.

The primary objectives of this research are to 1. describe interannual trends in abundance of cephalopod paralarvae in the Gulf of Alaska in late May; 2. investigate correlations between interannual variability of cephalopod paralarvae abundance and bottom-up (climatic and oceanographic indices) and top-down (pink salmon) controls; and 3. discuss possible mechanisms for observed correlations.

Methods

Sampling for cephalopod paralarvae was conducted between 18 May and 6 June in 1991 - 2009 (Table 1) in the region southwest of Kodiak Island. There was year to year variation in the locations of sampling (Figure 1) so a minimum sampled

area was used in the analysis (Figure 2). Cephalopod paralarvae were collected using a 60 cm Bongo with either 333 or 505 µm mesh nets. The 60 cm Bongo was towed double obliquely at 2 knots. Volume filtered was recorded via calibrated flowmeters placed in the opening of each net. Net contents were fixed in a 5% formalin:buffered seawater solution. Fish and cephalopod larvae were sorted and removed. Cephalopod paralarvae were identified to species using the characters outlined in Jorgensen (2007) and their dorsal mantle length (DML) recorded. A mean weighted abundance and standard error was calculated for each year for all the stations within the minimum sampled area. The mean weighted abundance is based on the Thessian polygon represented by each station. The Thessian polygon is created by drawing a line at half the distance between each station and its closest neighbors. The result is a polygon which is assumed to be represented by the station in the center of the polygon. The area of the polygon is by how much the abundance at each station is weighted.

Pink salmon abundance data was calculated from catch and hatchery return data. There are 12 pink salmon hatcheries on the Pacific Rim. Using the known ocean distribution data from Myers et al. (1996), the pink salmon feeding in the Gulf of Alaska can be estimated to consist of animals returning to the eight hatcheries on the east side of the Pacific (fish from Japan and Russia were not found in the Gulf of Alaska). The catch and hatchery return data (Ruggerone et al., 2010) for each of these hatcheries was summed and represents the annual abundance of pink salmon.

Climatic and oceanographic indices were downloaded from perspective websites. The ENSO is calculated from six variables in the tropical Pacific (sea level pressure, zonal and meridional components of winds, SST, surface air temperature, and cloudiness) (<http://www.esrl.noaa.gov/psd/enso/mei/>). The PDO is calculated from regional SST anomalies (<http://jisao.washington.edu/pdo/PDO.latest>). The AO,

EPNP, and NP are based on modeled sea surface height data (AO: http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/monthly.ao.index.b50.current.ascii.table; EPNP: ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index_nh; and NP: <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#npmon>).

Investigation of the correlations between climatic and oceanographic indices and species abundance was performed using constrained ordination. Constrained ordination is a method by which the variation in one matrix (species abundance) is maximized while constrained by the variation in a second matrix (climate and oceanographic indices and pink salmon abundance). The species abundance data for each year (Table 2 and Table 3a) was first log ($x+1$) transformed (to account for zero values) and then row standardized (Table 3b). Climatic and oceanographic indices were organized by month (Tables 4a, 5a, 6a, 7a, and 8a) and z-score standardized (mean of zero, variance of 1) (Tables 4b, 5b, 6b, 7b, and 8b).

The first step in performing a constrained ordination is to determine whether to use redundancy analysis, based on Euclidean distance and most appropriate for response variables that exhibit a linear response, or canonical correspondence analysis which is based on Chi-squared distance and is most appropriate for unimodal response. To determine the type of response that the species abundance matrix exhibited, a detrended correspondence analysis was performed on the presence absence species matrix. Detrended correspondence analysis determines gradient lengths; the longer the gradient, the slower the turnover of the community while a shorter gradient implies rapid community turnover. Generally, gradient lengths greater than 2 indicate a unimodal response and those less than 2 indicate a linear response. In this case, the gradient length was 1.4786 which is generally considered to be short and would therefore indicate a linear response of the community to its environment however, this value is close enough to 2 to investigate both redundancy analysis and canonical correspondence analysis. Comparison of

the two methods revealed that redundancy analysis lumped all species except *B. anonychus*, therefore canonical correspondence analysis was performed. Canonical correspondence analysis was performed on the R platform (R Development Core Team, 2011).

Results

Eight species of cephalopod were collected in the study area (Figure 2) from 1981 - 2009 (Table 2). The late May larval cruise was not conducted in 1984 and 1986, and cephalopod paralarvae were either not sorted in 1988 - 1990 or the samples were lost. The abundance data for all species from 1981 to 2009 will be presented however, canonical correspondence analysis (species abundance matrix constrained by climatic and oceanographic indices) will only be conducted on the data from the contiguous years (1991 - 2009).

Berryteuthis anonychus had the highest abundances and it showed an alternating year trend, where, generally, odd years were an order of magnitude higher than even year abundances (Figure 3a). Standard error values for each year show that the values for the years of peak abundances were statistically significantly different from the values of the years of low abundances. *Enteroctopus dofleini* had the next highest abundances (Figure 3b). It was the only species which was present in the study area each year. The third most abundant species was *G. onyx*, which also showed alternating years of high and low abundances where 1 - 3 years had high abundances followed by 1 - 2 years of low abundances (Figure 4a). *Berryteuthis magister* had the highest abundances in 1991 and 1993, after which its abundance steadily decreased until 1999; it was absent for most of 2000's, present only in 2003, 2007, and 2009 (Figure 4b). *Gonatopsis borealis* was the least abundant of the abundant species. It had highest abundances in 1991 and 1992, it was present in low numbers from 1981 - 1983, 1994 - 1999, 2001 - 2004,

and 2009 and absent all other years (Figure 5a). Unknown A is a species in the family Gonatidae. It was absent for the majority years of the study except 1981, 1987, 1992, 1995, 2007, and 2009; its highest abundances were in 1981 and 2009. (Figure 5b). *Gonatus madokai* was also absent for the majority of years of the study; it was present in 1981, 1983, 1987, 1995, 1996, 2001, 2005, and 2007 with highest abundances in 1981 and 1996 (Figure 6a). Cranchiidae (cf *G. phyllura*) was the rarest of the species collected. It was present in only four years: 1985, 1991, 1996, and 1999 with a peak abundance in 1985 (Figure 6b).

Monthly climatic and oceanographic indices for January to May, 1991 to 2009 were downloaded. For ease and efficiency of representation, the five months were organized by season into winter (January, February, and March) and spring (April and May), the average of the values for each month (Table 9) were used in the graphs for each of the indices; all the data are presented in the monthly tables.

The PDO exhibited two positive phases and one negative phase during the study. In 1991 the PDO was in the last year of a negative phase, from 1992 to 1998 it was in a positive phase; 1999 to 2002 was mostly negative while 2003 to 2007 was positive. The study period ended with the PDO beginning a negative phase (Figure 7a). The ENSO was in a positive phase from 1991 to 1998 and 2003 to 2005; negative from 1999 to 2002 and 2006 to 2009, with some discrepancy between winter and spring values during the transitions (Figure 7b). The discrepancy between winter and spring values for the AO occurred throughout the time period of the study. Winter and spring values were out of phase from 1991 to 1996. After 1996 the winter values began oscillating almost annually from positive to negative through 2004 while the spring values were in a positive phase. Winter values were negative from 2004 to 2006 during which time the spring values were briefly negative before resuming positive values in 2006. From 2006 to 2009, winter values were positive while spring values began to oscillate annually (Figure 7c). The

NP winter values were lower than the spring values throughout the study (Figure 8a). The EPNP had two positive phases and two negative phases during the study (Figure 8b). The positive phases were from 1992 - 1997 and 2002 - 2005; negative phases were from 1998 - 2001 and 2006 - 2008. The winter and spring values of the alongshore winds exhibited different trends. The winter values were high from 1993 to 2000 and from 2002 to 2008 while spring values were high from 1991 to 1997 and 2000 to 2003, after 2003 the spring values oscillated annually (Figure 8c). Winter and spring wind mixing values also had different trends (Figure 9a). Winter values were generally higher and tended to have 3 - 4 years of similar high values followed by a year of low values. Spring values were less variable but oscillated almost annually; there was one anomalous year with very high values in 2007. The NPGO had two negative phases and two positive phases during the study; winter and spring values were similar (Figure 9b). The negative phases were from 1991 to 1997 and from 2004 to 2006. Positive phases were from 1998 to 2004 and from 2007 to 2009.

To investigate the bottom-up effects of environmental variation on the variation in cephalopod paralarvae abundance canonical correspondence analyses were conducted. The species abundances for May 1991 - 2009 (Table 3a) were log (x+1) transformed and then row standardized (Table 3b). Climatic and oceanographic indices for January to May 1991 to 2009 (Tables 4a, 5a, 6a, 7a, and 8a) were z-score standardized (Tables 4b, 5b, 6b, 7b, and 8b). The variation in the transformed and standardized species matrix was constrained by the variation in the standardized monthly climatic and oceanographic indices matrices in the canonical correspondence analysis such that five analyses were performed (May species abundance x January climatic and oceanographic indices; May species abundance x February indices; May species abundance x March indices; May species abundance x April indices; and May species abundance x May indices). By testing the effects

of environment in the months preceding the month of sampling, the effects on more sensitive life stages (i.e. eggs or hatchlings) can be investigated.

Of the five months of climatic and oceanographic indices, none of the months of indices constrained all of the variation in the species abundance matrix (Table 10). January indices were the most efficient at constraining the variation in the species abundance matrix however still only constrained 52.5% of the variation and the ANOVA p-value was 0.2. May indices were almost as significant in explaining variation in the species abundance matrix, 49.6% of the variation could be explained however the ANOVA p-value was 0.24.

To investigate the possible effects of top-down control, canonical correspondence analysis was performed using constraining matrices that included pink salmon abundance from the previous July. Five canonical correspondence analyses were performed using May species abundances and monthly climatic and oceanographic indices for January to May with the addition of pink salmon abundances (Table 11a) z-score standardized (Table 11b). Salmon abundance data were only available through 2005. Because the link between pink salmon and paralarval cephalopods is most likely due to the consumption of adult gonatids, primarily *Berryteuthis anonymus*, it will be the previous year's pink salmon abundances that influence the current year's paralarval abundances. For this reason, the pink salmon abundances will be given as $x + 1$, where x is year. Pink salmon abundance values of 1990 to 2005 will therefore be represented as 1991 to 2006 in the constraining matrices. With the top-down control represented in the constraining matrices, the amount of variation in the species abundance matrix explained by the constraining matrices increased, as did the significance (Table 12). May indices of bottom-up and top-down control explained the most variation in the species abundance matrix (79.7%) and was the most significant (ANOVA p-value = 0.001). Canonical correspondence axis 1 was dominated by *E. dofleini*, *B. magister*,

and *B. anonychus* and explained 48% of the variation in the matrix. While CCA 2 was dominated by the rare species, *G. madokai* and unknown A; the total variation explained by CCA 1 and CCA 2 was 64%.

The primary constraining variables in May were pink salmon abundance, wind mixing, and the North Pacific index. Canonical axis 1 and 2 explained 94% of the variation in the matrix.

Discussion

Several researchers have investigated the effects of climate on the distribution and abundance of cephalopod paralarvae (e.g. Rodhouse et al., 1992; Okutani et al., 1988; Rocha et al., 1999). Many studies concluded that different water masses or different regions had different assemblages of cephalopod paralarvae (Rodhouse et al., 1992; Okutani et al., 1988). In this study, a single region and water mass were investigated so these broader studies were less useful for interpreting these results. However, fish larvae are subject to the same physical forcings as paralarval cephalopods and in this region, much work has been done on the effects of environment on larval fish (e.g. Doyle et al., 2009). Furthermore, the historical data set used for the larval fish studies is a result of the same sampling that generated the paralarval cephalopod collection.

These data represent one of the longest, if not the longest, time series of paralarval cephalopods. Interpretation of the data benefit from the consistent location and timing of sampling as well as the use of a single gear type. However, the target of these surveys was larval fish, not cephalopods. Due to the non-targeted nature of cephalopod sampling, much of the work on this dataset was exploratory, however the results presented are very promising and provide a strong foundation on which to build and test future hypotheses.

Cephalopod species

Perhaps the most interesting result was the biannual trend in abundance of *B. anonychus*. This is the first published record of a strong biannual trend in the abundance of any paralarval cephalopod. A biannual trend would be difficult to determine in short time series data or from data sets that did not sample in a spatially and temporally consistent manner. Previous work on cephalopod paralarvae from the northern North Pacific first focused on identification and systematics (Kubodera and Okutani, 1981; Jorgensen, 2007) and distribution (Jefferts, 1988; Okutani et al., 1988). Kubodera and Jefferts (1984a, 1984b) and Jorgensen (2007) published on the relative abundances of cephalopod paralarvae from the region. Kubodera and Jefferts (1984a, 1984b) computed abundance seasonally for all time so would not have been able to determine interannual variation. Jorgensen (2007) analyzed abundance for the May 2001 - 2003 in the Amatuli Trough region and noted interannual variation in abundance in *B. anonychus* however included only three years of data in the study.

The trend in abundance of *B. anonychus* was most obvious and statistically significant in this study. It can be concluded that while *B. anonychus* was sampled well at this time of the year, location, and spatial scale, the other four species (*E. dofleini*, *G. onyx*, *B. magister*, and *G. borealis*) may not have been.

The poor representation in the samples by the majority of species is likely due to the nature of the surveys. The surveys were designed to assess the population of larval fish species, primarily walleye pollock, which is a shelf-spawning species whose larvae are most abundant in May. On the other hand, all the squids in the region are likely hatching off the shelfbreak and many species may be hatched earlier in the year than May (Chapter 4), making the minimally sampled area, well into the shelf domain, a poor location for sampling squid paralarvae, and the late-May timing of the surveys too limited in scope for accurately sampling many of the

squid paralarvae in the region. Despite the limitations in available data, the trend in *B. anonychus* is significant and presents some novel insights into the life history of high latitude squids.

The life history of squids has been based primarily on warm-water species such as the members of the family Loliginidae, and is assumed to be one year or less. In the case of the family Gonatidae, no life span information is known definitely however Kubodera (1982) hypothesized a two-year life cycle for *B. magister* and Bjørke (1995) concluded that *Gonatus fabricii* from the North Atlantic has a two-year life cycle. The strong biannual trend in the abundance of *B. anonychus* may be due to a two-year life span.

Bottom-up and top-down controls

Major indices of climate and ocean for the region were investigated in conjunction with paralarval abundances. Although these environmental indices are presented individually, their affects on the organisms are cumulative. To account for the cumulative nature of the environmental indices and their effect on the presence and relative abundance of the cephalopod paralarvae, canonical correspondence analysis (constrained ordination technique) was chosen. Canonical correspondence analysis maximizes the variation in the species abundance matrix while constraining it to the variation in the environmental indices matrix. Monthly environmental indices for January through May were used to constrain the variation in the May species abundance matrix. The hypothesis was that environment in the months leading up to May sampling would influence the abundances if fragile life stages (eggs and hatchlings) were released during these months went on to be sampled in May. None of the months leading up to May sampling were found to statistically significantly explain the observed variation in May species abundance. There are many possible explanations for this result. Doyle et al. (2009) using GAM technique discovered that

for many larval fish species, local environmental variables (sea surface temperature, salinity, alongshore and mixing winds, retention index, and flow through Shelikof Strait) were more important than basin variables (PDO, ENSO, NP, AO, and EPNP). In this study, only two local variables (alongshore and mixing winds) were available. However, it is important to note that it was previously shown (Chapter 3) that similar spawning strategies in fish and cephalopods resulted in similar larval distributions and based on this, the four most abundant squid in this study were determined to be most similar in spawning strategy (spawning in the deep-sea at the shelfbreak) to arrowtooth flounder (Chapter 4). Doyle et al. (2009) included arrowtooth flounder in their study and discovered that the most important environmental variables for this species were PDO, NP, AO, EPNP, alongshore and mixing winds, and salinity, all except salinity were investigated here and did not significantly explain the variation.

It is probable that there are other environmental factors that need to be included in this study to make it complete however no published combination of environmental indices for the region has resulted in a biannual cycle, like that seen for *B. anonychus*. Because the environmental indices were not able to explain the trends seen in the species, top-down control was incorporated into the analysis.

Pink salmon prey heavily on *B. anonychus* sub-adults and have a two-year life cycle. The 145°W latitude line in the Gulf of Alaska is sampled each summer for returning salmon by Japanese research vessels (Aydin et al., 2000). Pink salmon have long been known to consume squid (LeBrasseur, 1966). Kaeriyama et al. (2004) found that from 1994 - 1998, pink salmon stomach contents consisted of 40 - 80% squid and Aydin et al. (2000) found that 90% of the squid in pink salmon stomachs were *B. anonychus*. *Berryteuthis anonychus* is an important prey item for pink salmon.

The canonical correspondence analysis was performed with pink salmon abundance (catch and return data) included in the constraining matrix. May values

of environment plus salmon abundance for the previous summer were found to statistically significantly explain the majority of variation in May species abundance (Table 5.12). It appears that pink salmon predation is driving the trend seen in *B. anonychus* abundance however, these results simply mean there is a strong correlation between pink salmon abundance and *B. anonychus* abundance. In the analysis, a strong positive correlation was found between *B. anonychus* and MIX and a strong negative correlation between *B. anonychus* and NP (Figure 5.19).

There are four hypotheses that would explain the correlations discovered in the species abundance matrix and the constraining matrix:

Hypothesis 1: Top-down control of *B. anonychus* by pink salmon. Returning pink salmon (adults) prey on *B. anonychus* in the 60 - 90 mm ML range (N. Davis, personal communication). Assuming these animals are the cohort of May-caught paralarvae (and no other peak in abundances were found for *B. anonychus* as indicated by Chapter 4 results), then if the life history was one year, this would require an estimated 35 mm mantle length per month growth rate (assuming an average mantle length of 4.5 mm in May and 75 mm in July). These growth rates can be found in warm-water loliginids (Bettencourt et al., 1996) but are unlikely for cold-water species (M. Vecchione, personal communication). The biannual trend in abundance of *B. anonychus* in this scenario only occurs if *B. anonychus* has a one year life cycle.

Aydin (2000) found an alternating year cycle in squid abundance in pink salmon stomach contents from 1993 - 1998. The highest abundances were in even years (highest paralarval abundances were in odd years). If pink salmon predation were controlling the population of *B. anonychus*, the alternating year trend in abundance of *B. anonychus* would not be expected to be reflected in the predator stomach contents. Also, high abundances of individuals in the 60 - 90 mm ML range a year later than that seen for the paralarval sampling corresponds well to the size

expected given an estimated 5 - 7 mm per month growth rate and two-year life cycle.

Hypothesis 2: *Berryteuthis anonychus* has a two-year life cycle. Of the 19 species in the family, *B. magister* and *G. fabricii* (Kubodera, 1982 and Bjørke, 1995, respectively) are hypothesized to have a two-year life cycle. Furthermore, Kubodera and Shimazaki (1989) estimated the growth rate of *B. anonychus* to be 10 mm mantle length per month, based on the presence of 10 - 30 mm mantle length juveniles collected in June and July. Given an average mantle length of 4.5 mm in May, mantle lengths of 10 - 30 mm would result in a growth rate of 5 - 15 mm mantle length per month. A growth rate of 5 - 7 mm per month would place the following year's July size class at 74.5 to 102.5 mm mantle length. With a maximum size of 150 mm mantle length (Nesis, 1987), a growth rate of 5 - 7 mm mantle length would place mature adults in January - March, almost two years after the May cohort was collected. The size range of individuals collected in the stomachs of pink salmon and the alternating year peak abundance seen in pink salmon stomachs also support this scenario.

Hypothesis 3: Increased transport by increased intensity of the Aleutian Low increases the number of *B. anonychus* moved into the study area. The North Pacific index reflects the relative strength of the Aleutian Low (N. Bond, personal communication). Miller (1996) found that intensification of the Aleutian Low led to an intensification of the Alaska Coastal Current however, no correlation was found between NP index values and *B. anonychus* abundance.

Hypothesis 4: Wind mixing (MIX) decreases survival of *B. anonychus* paralarvae. Bailey and Macklin (1994) found that high wind mixing events had a negative affect on survival of first feeding larval walleye pollock. The authors did not provide a mechanism for the correlation. Over the entire study period, there was no correlation between MIX and *B. anonychus* abundances. If *B. anonychus* has a similar ability to withstand starvation as *E. dofleini* then first feeding would be in

June so wind mixing events in May may not have the same relevance to paralarval *B. anonychus* as they do to larval walleye pollock. Furthermore, wind mixing is very episodic and the index used here is for the entire month. It is possible that the conditions experienced by the paralarvae on a daily scale are not reflected in a monthly index.

Enteroctopus dofleini was negatively correlated with wind mixing, which was the only constraining variable with which it was strongly correlated. It was also negatively correlated with alongshore winds but to a lesser extent. *Enteroctopus dofleini* is the only species in the study known to be associated with the shelf, where spawning and hatching occurs. Its preferred adult habitat is the rocky bottom of the shelf and shelfbreak. Increased wind activity would have the deleterious effect of moving individuals away from their preferred habitat. Destabilizing the water column would also decrease prey availability by dispersing patches of prey. It should be noted that the variability in the abundance of this species was very low, making the results tentative.

The results do not point to a strong environmental control on the abundance of the paralarval cephalopods in the Gulf of Alaska. In addition to investigating the effect of more local variables it may also be prudent to investigate subsets of time. Bailey (2000) found that prior to the mid-1980's, recruitment of walleye pollock was correlated with larval mortality and that larval mortality was subject to bottom-up control; after the mid-1980's, bottom-up control relaxed and juvenile mortality due to predation became more critical to recruitment. Unfortunately, the same investigations cannot be made using the paralarval cephalopod dataset because of missing samples in the 1980s however it speaks to the importance of time series biological data when attempting to understand the effects of decadal-long temporal patterns in the environment.

Conclusions

The results of this work have important ramifications for not only the Gulf of Alaska ecosystem but high-latitude squids. The results presented here strongly support a two year life cycle of *Berryteuthis anonymus*, the population of which may be controlled not only by bottom-up effects such as alongshore winds and wind mixing but top-down control by pink salmon. However, it is also obvious that while the results are interesting, they leave more questions than answers and illustrate the need for targeted cephalopod research. The results should present a starting point of when, where, and how to sample as well as a justification for their study due to the connection to commercially important fish.

Year	Cruise	Begin Date	End Date
1981	3SH81	20-May	28-May
1981	4MF81	20-May	24-May
1982	2DA82	21-May	31-May
1983	1CH83	21-May	30-May
1985	2PO85	16-May	8-Jun
1987	3MF87	19-May	27-May
1991	4MF91	18-May	25-May
1992	4MF92	18-May	28-May
1993	5MF93	23-May	3-Jun
1994	6MF94	24-May	1-Jun
1995	8MF95	21-May	28-May
1996	8MF96	24-May	1-Jun
1997	8MF97	24-May	30-May
1998	5MF98	22-May	30-May
1999	2WE99	24-May	5-Jun
1999	5MF99	22-May	2-Jun
2000	6MF00	26-May	4-Jun
2001	3MF01	25-May	2-Jun
2002	4MF02	24-May	1-Jun
2003	5MF03	26-May	2-Jun
2004	5MF04	23-May	3-Jun
2005	6MF05	22-May	3-Jun
2006	4MF06	22-May	1-Jun
2007	5MF07	20-May	28-May
2008	4DY08	24-May	30-May
2009	4DY09	28-May	6-Jun

Table 5.1. Late May larval cruise begin and end dates.

Year	<i>B. anonychus</i>		<i>E. dofleinii</i>		<i>G. onyx</i>		<i>B. magister</i>		<i>G. borealis</i>		<i>Unknown A</i>		<i>G. madokai</i>		<i>Cranchiidae</i>	
	CPUA	SE	CPUA	SE	CPUA	SE	CPUA	SE	CPUA	SE	CPUA	SE	CPUA	SE	CPUA	SE
1981	0.2129	0.1003	0.0191	0.0057	0.0077	0.0077	0.0218	0.0218	0.0039	0.0039	0.0417	0.0417	0.0295	0.0295	0	0
1982	0.0616	0.0347	0.0897	0.0659	0	0	0	0	0	0	0	0	0	0	0	0
1983	0.4646	0.1281	0.1390	0.0613	0.0203	0.0150	0.0179	0.0126	0.0068	0.0068	0	0	0.0148	0.0104	0	0
1984	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1985	0.5700	0.2148	0.0300	0.0172	0.0157	0.0118	0.0987	0.0627	0	0	0	0	0	0	0.0315	0.0315
1986	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1987	0.0073	0.0073	0.0587	0.0214	0.0073	0.0073	0	0	0	0	0.0077	0.0077	0.0080	0.0080	0	0
1988	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1989	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1990	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1991	1.8692	0.7631	0.0667	0.0271	0.0595	0.0414	0.0617	0.0276	0.0704	0.0704	0.0422	0	0	0	0	0.0118
1992	0.0724	0.0486	0.0806	0.0439	0.0585	0.0234	0	0	0.0406	0.0406	0.0252	0.0101	0.0101	0	0	0
1993	2.6349	1.2691	0.1396	0.0618	0.0474	0.0321	0.0455	0.0231	0	0	0	0	0	0	0	0
1994	0.1887	0.0718	0.0318	0.0162	0.0089	0.0065	0.0402	0.0298	0.0201	0.0201	0	0	0	0	0	0
1995	1.0652	0.3544	0.0296	0.0127	0.0132	0.0081	0.0212	0.0114	0.0114	0.0110	0.0053	0.0057	0.0046	0.0050	0	0
1996	0.0730	0.0345	0.0713	0.0209	0.0406	0.0217	0.0132	0.0093	0.0316	0.0162	0	0	0.0255	0.0162	0.0058	0.0058
1997	0.7341	0.3748	0.1027	0.0304	0.0057	0.0057	0.0063	0.0063	0.0179	0.0102	0	0	0	0	0	0
1998	0.0172	0.0100	0.0835	0.0297	0.0073	0.0073	0.0063	0.0063	0.0073	0.0073	0	0	0	0	0	0
1999	0.4075	0.2185	0.0993	0.0281	0.0064	0.0064	0.0195	0.0146	0.0067	0.0067	0	0	0	0	0	0.0068
2000	0.0145	0.0145	0.0761	0.0253	0	0	0	0	0	0	0	0	0	0	0	0
2001	0.9140	0.3688	0.0304	0.0151	0.0366	0.0366	0	0	0	0	0	0	0	0.0065	0.0065	0
2002	0	0	0.0325	0.0231	0	0	0	0	0	0	0	0	0	0	0	0
2003	0.4896	0.1937	0.0965	0.0407	0	0	0.0058	0.0058	0.0346	0.0346	0	0	0	0	0	0
2004	0.0369	0.0260	0.0308	0.0195	0.0075	0.0075	0	0	0.0241	0.0170	0	0	0	0	0	0
2005	0.7850	0.2259	0.0730	0.0258	0.0340	0.0291	0	0	0	0	0	0	0.0053	0.0053	0	0
2006	0.0151	0.0151	0.0451	0.0215	0.0298	0.0234	0	0	0	0	0	0	0	0	0	0
2007	0.1273	0.0548	0.0868	0.0452	0.0572	0.0266	0.0213	0.0151	0	0	0.0109	0.0109	0.0078	0.0078	0	0
2008	0.0167	0.0122	0.0584	0.0218	0.0105	0.0074	0	0	0	0	0	0	0	0	0	0
2009	0.9389	0.5998	0.0459	0.0175	0.0071	0.0071	0.0125	0.0089	0.0378	0.0264	0.0289	0.0135	0	0	0	0

Table 5.2. Original (not transformed or standardized) species abundance (weighted mean abundances) matrix.

Year	<i>B. anonychus</i>	<i>E. dofleini</i>	<i>G. onyx</i>	<i>B. magister</i>	<i>G. borealis</i>	Unknown A	<i>G. madokai</i>	Cranchiidae
1991	1.8692	0.0667	0.0595	0.0617	0.0704	0	0	0.0118
1992	0.0724	0.0806	0.0585	0	0.0406	0.0101	0	0
1993	2.6349	0.1396	0.0474	0.0455	0	0	0	0
1994	0.1887	0.0318	0.0089	0.0402	0.0201	0	0	0
1995	1.0652	0.0296	0.0132	0.0212	0.0171	0.0053	0.0046	0
1996	0.0730	0.0713	0.0406	0.0132	0.0316	0	0.0255	0.0058
1997	0.7341	0.1027	0.0057	0.0063	0.0179	0	0	0
1998	0.0172	0.0835	0.0073	0.0063	0.0073	0	0	0
1999	0.4075	0.0993	0.0064	0.0195	0.0067	0	0	0.0068
2000	0.0145	0.0761	0	0	0	0	0	0
2001	0.9140	0.0304	0.0366	0	0	0	0.0065	0
2002	0	0.0325	0	0	0	0	0	0
2003	0.4896	0.0965	0	0.0058	0.0346	0	0	0
2004	0.0369	0.0308	0.0075	0	0.0241	0	0	0
2005	0.7850	0.0730	0.0340	0	0	0	0.0053	0
2006	0.0151	0.0451	0.0298	0	0	0	0	0
2007	0.1273	0.0868	0.0572	0.0213	0	0.0109	0.0078	0
2008	0.0167	0.0584	0.0105	0	0	0	0	0
2009	0.9389	0.0459	0.0071	0.0125	0.0378	0.0289	0	0

Table 5.3a. Species abundance matrix (1991 - 2009).

Year	<i>B. anonychus</i>	<i>E. dofleini</i>	<i>G. onyx</i>	<i>B. magister</i>	<i>G. borealis</i>	Unknown A	<i>G. madokai</i>	Cranchiidae
1991	0.8009	0.0490	0.0439	0.0455	0.0517	0	0	0.0089
1992	0.2749	0.3050	0.2238	0	0.1566	0.0397	0	0
1993	0.8536	0.0864	0.0306	0.0294	0	0	0	0
1994	0.6349	0.1151	0.0324	0.1448	0.0729	0	0	0
1995	0.8895	0.0358	0.0161	0.0257	0.0208	0.0065	0.0057	0
1996	0.2771	0.2706	0.1563	0.0516	0.1223	0	0.0991	0.0229
1997	0.8120	0.1441	0.0084	0.0093	0.0262	0	0	0
1998	0.1443	0.6789	0.0617	0.0533	0.0617	0	0	0
1999	0.7186	0.1990	0.0134	0.0407	0.0141	0	0	0.0143
2000	0.1638	0.8362	0	0	0	0	0	0
2001	0.8997	0.0416	0.0498	0	0	0	0.0089	0
2002	0	1	0	0	0	0	0	0
2003	0.7513	0.1737	0	0.0109	0.0641	0	0	0
2004	0.3702	0.3103	0.0763	0	0.2433	0	0	0
2005	0.8415	0.1023	0.0485	0	0	0	0.0077	0
2006	0.1691	0.4985	0.3323	0	0	0	0	0
2007	0.4014	0.2789	0.1865	0.0707	0	0.0363	0.0262	0
2008	0.1974	0.6782	0.1243	0	0	0	0	0
2009	0.8359	0.0566	0.0089	0.0157	0.0468	0.0360	0	0

Table 5.3b. Species abundance matrix (1991 - 2009) transformed ($\log(x+1)$) and row standardized.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-2.02	0.723	7.7	0.309	-0.45	1.01	506.1	-0.7442
1992	0.05	0.55	-1.1	1.747	-0.17	1.794	386.5	0.4931
1993	0.05	3.495	10.8	0.689	-0.65	-1.469	379.6	-2.8170
1994	1.21	-0.288	8.3	0.349	2.38	1.294	358.8	-1.8540
1995	-0.49	-0.154	2.2	1.211	1.03	2.823	514.4	-0.4990
1996	0.59	-1.2	8.3	-0.641	0.26	3.493	328.3	-0.6390
1997	0.23	-0.457	2	-0.486	0.22	4.207	717.6	-1.6402
1998	0.83	-2.081	0.7	2.5	0.62	4.35	649.9	0.5279
1999	-0.32	0.11	8	-1.109	-0.89	1.34	711.1	1.0828
2000	-2	1.27	13.5	-1.172	-0.92	0.674	545.4	1.4045
2001	0.6	-0.959	2	-0.514	-0.9	0.262	559.8	2.8619
2002	0.27	1.381	7.9	-0.041	-0.11	1.048	781	1.8642
2003	2.09	-0.472	-0.4	1.195	2.07	4.2	720.5	1.9692
2004	0.43	-1.686	5.1	0.315	0.66	4.861	977.6	0.2650
2005	0.44	0.356	4	0.307	0.73	4.533	571.2	-1.4484
2006	1.03	-0.17	8	-0.449	-1.07	2.794	423	-0.2915
2007	0.01	2.034	8.5	0.997	-1.14	-0.591	373.3	0.0342
2008	-1	0.819	9.3	-0.984	-1.25	0.357	415.2	0.9800
2009	-1.4	0.8	9.6	-0.729	-0.18	1.831	475.5	0.7217

Table 5.4a. Climatic and oceanographic indices for January 1991 - 2009.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-1.9384	0.3853	0.4078	0.1229	-0.4430	-0.5544	-0.2355	-0.5949
1992	0.0174	0.2543	-1.7295	1.5356	-0.1749	-0.1335	-0.9226	0.2573
1993	0.0174	2.4849	1.1606	0.4962	-0.6345	-1.8853	-0.9622	-2.0224
1994	1.1134	-0.3804	0.5535	0.1622	2.2670	-0.4019	-1.0817	-1.3592
1995	-0.4928	-0.2789	-0.9280	1.0090	0.9742	0.4189	-0.1878	-0.4260
1996	0.5276	-1.0712	0.5535	-0.8104	0.2369	0.7786	-1.2569	-0.5224
1997	0.1875	-0.5084	-0.9766	-0.6581	0.1986	1.1619	0.9795	-1.2120
1998	0.7544	-1.7385	-1.2923	2.2753	0.5816	1.2387	0.5906	0.2812
1999	-0.3322	-0.0790	0.4806	-1.2701	-0.8643	-0.3772	0.9421	0.6634
2000	-1.9195	0.7997	1.8164	-1.3320	-0.8931	-0.7348	-0.0097	0.8850
2001	0.5371	-0.8887	-0.9766	-0.6856	-0.8739	-0.9560	0.0730	1.8887
2002	0.2253	0.8837	0.4563	-0.2209	-0.1174	-0.5340	1.3437	1.2016
2003	1.9449	-0.5198	-1.5594	0.9933	1.9701	1.1582	0.9961	1.2739
2004	0.3764	-1.4393	-0.2237	0.1288	0.6199	1.5130	2.4731	0.1002
2005	0.3859	0.1074	-0.4908	0.1209	0.6869	1.3369	0.1385	-1.0799
2006	0.9433	-0.2911	0.4806	-0.6217	-1.0367	0.4033	-0.7129	-0.2831
2007	-0.0204	1.3783	0.6020	0.7988	-1.1037	-1.4139	-0.9984	-0.0588
2008	-0.9747	0.4580	0.7963	-1.1473	-1.2091	-0.9050	-0.7577	0.5926
2009	-1.3526	0.4437	0.8692	-0.8968	-0.1845	-0.1136	-0.4113	0.4147

Table 5.4b. Climatic and oceanographic indices for January 1991 - 2009 z-scores standardized.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-1.19	-0.876	2.7	0.303	0.31	2.368	472.1	-0.3045
1992	0.31	1.122	7	1.87	0.7	2.093	287.3	-0.4565
1993	0.19	0.184	2.4	0.99	2.12	1.735	642.7	-2.1408
1994	0.59	-0.862	10.4	0.192	0.47	5.296	930.1	-1.9787
1995	0.46	1.429	6.6	0.957	0.05	2.362	526.9	-1.5609
1996	0.75	0.163	8	-0.597	0.27	0.106	398.4	-1.0529
1997	0.28	1.889	4.2	-0.607	-0.03	1.426	412.4	-1.1131
1998	1.56	-0.183	0.2	2.788	-0.33	4.563	493.2	1.9001
1999	-0.66	0.482	6.9	-1.219	-1.12	2.54	994.6	2.3042
2000	-0.83	1.076	0.9	-1.228	-0.55	0.683	301.1	2.1235
2001	0.29	-0.622	9.5	-0.699	0.26	0.002	362.5	2.9561
2002	-0.64	1.304	10.1	-0.206	-0.89	0.069	452.3	2.1774
2003	1.75	0.128	7.5	0.925	0.94	-1.246	221.1	0.9926
2004	0.48	-1.528	1.8	0.334	-0.5	1.949	451.5	0.6672
2005	0.81	-1.271	8.1	0.794	-0.29	1.192	327.1	-1.3975
2006	0.66	-0.156	14.4	-0.443	0.57	-0.702	390.3	-0.6196
2007	0.04	-1.307	8.2	0.526	0.93	3.853	634.5	0.3491
2008	-0.77	0.938	5.8	-1.389	-0.4	3.946	725.4	1.6177
2009	-1.55	-0.672	14.8	-0.705	0.32	0.471	352.8	1.1892

Table 5.5a. Climatic and oceanographic indices for February 1991 - 2009.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-1.5087	-0.9185	-0.9984	0.1520	0.2145	0.3602	-0.1023	-0.3736
1992	0.2016	1.0313	0.0447	1.5796	0.7338	0.2070	-0.9859	-0.4680
1993	0.0648	0.1160	-1.0712	0.7779	2.6246	0.0076	0.7134	-1.5133
1994	0.5209	-0.9048	0.8695	0.0509	0.4275	1.9911	2.0876	-1.4127
1995	0.3727	1.3309	-0.0523	0.7478	-0.1318	0.3568	0.1598	-1.1534
1996	0.7033	0.0955	0.2873	-0.6679	0.1612	-0.8998	-0.4547	-0.8381
1997	0.1674	1.7798	-0.6346	-0.6770	-0.2383	-0.1645	-0.3877	-0.8755
1998	1.6269	-0.2422	-1.6049	2.4159	-0.6378	1.5828	-0.0014	0.9946
1999	-0.9044	0.4068	0.0204	-1.2345	-1.6897	0.4560	2.3960	1.2454
2000	-1.0982	0.9865	-1.4351	-1.2427	-0.9307	-0.5784	-0.9199	1.1333
2001	0.1788	-0.6706	0.6512	-0.7608	0.1479	-0.9577	-0.6263	1.6500
2002	-0.8816	1.2090	0.7967	-0.3117	-1.3834	-0.9204	-0.1969	1.1667
2003	1.8435	0.0613	0.1660	0.7187	1.0534	-1.6528	-1.3024	0.4314
2004	0.3955	-1.5547	-1.2168	0.1803	-0.8641	0.1268	-0.2008	0.2295
2005	0.7717	-1.3039	0.3115	0.5993	-0.5845	-0.2949	-0.7956	-1.0520
2006	0.6007	-0.2158	1.8398	-0.5276	0.5607	-1.3498	-0.4934	-0.5692
2007	-0.1062	-1.3391	0.3358	0.3552	1.0400	1.1873	0.6742	0.0320
2008	-1.0298	0.8518	-0.2464	-1.3894	-0.7310	1.2391	1.1089	0.8194
2009	-1.9191	-0.7194	1.9369	-0.7662	0.2278	-0.6965	-0.6727	0.5534

Table 5.5b. Climatic and oceanographic indices for February 1991 - 2009 z-scores standardized.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-0.74	-0.527	14.7	0.387	-0.38	-1.71	246.8	-0.8070
1992	0.67	0.984	10.3	1.993	1.28	-1.752	280.6	-0.8208
1993	0.76	0.764	7.6	0.972	0.21	1.809	429.8	-1.7419
1994	0.8	1.881	12.4	0.157	-1.06	1.229	731.3	-1.8558
1995	0.75	0.393	11.9	0.853	0.61	4.28	790.2	-2.0547
1996	1.01	-1.483	10.9	-0.267	2.41	1.839	340.8	-1.1488
1997	0.65	1.091	15	-0.252	-0.06	4.476	670.2	-0.6180
1998	2.01	-0.254	8.1	2.765	1.31	2.242	434.3	0.8933
1999	-0.33	-1.492	12	-1.043	-0.73	1.874	356.1	1.9743
2000	0.29	-0.451	5.9	-1.117	-0.4	1.763	461.5	2.1493
2001	0.45	-1.687	11.6	-0.591	-1.16	1.601	572.2	2.3888
2002	-0.43	0.902	14.5	-0.187	1.99	2.622	377.9	1.8983
2003	1.51	0.933	10.4	0.819	0.56	4.577	744.5	1.4907
2004	0.61	0.318	14	-0.116	-1.28	0.339	491	0.3829
2005	1.36	-1.348	8.4	1.017	0.31	1.11	265.3	-1.1601
2006	0.05	-1.604	14.8	-0.581	0.2	3.681	647.9	-0.1901
2007	-0.36	1.182	12.7	0.082	-1.27	4.494	825.6	-0.0466
2008	-0.71	0.586	13.2	-1.619	-1.62	0.965	232.8	1.6521
2009	-1.59	0.121	17.4	-0.702	-1.12	1.052	429.3	0.2276

Table 5.6a. Climatic and oceanographic indices for March 1991 - 2009.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-1.2381	-0.4894	0.9536	0.2322	-0.3172	-1.9627	-1.2622	-0.6456
1992	0.3550	0.8718	-0.5365	1.7139	1.1078	-1.9854	-1.0875	-0.6551
1993	0.4567	0.6736	-1.4509	0.7720	0.1893	-0.0603	-0.3161	-1.2847
1994	0.5019	1.6800	0.1747	0.0201	-0.9009	-0.3739	1.2425	-1.3625
1995	0.4454	0.3394	0.0053	0.6622	0.5327	1.2755	1.5470	-1.4984
1996	0.7392	-1.3507	-0.3333	-0.3711	2.0778	-0.0441	-0.7762	-0.8792
1997	0.3324	0.9682	1.0552	-0.3573	-0.0425	1.3815	0.9267	-0.5165
1998	1.8690	-0.2435	-1.2816	2.4261	1.1336	0.1738	-0.2929	0.5166
1999	-0.7748	-1.3588	0.0392	-1.0870	-0.6176	-0.0252	-0.6971	1.2555
2000	-0.0743	-0.4210	-2.0266	-1.1553	-0.3343	-0.0852	-0.1523	1.3751
2001	0.1064	-1.5345	-0.0963	-0.6700	-0.9867	-0.1728	0.4200	1.5388
2002	-0.8878	0.7980	0.8859	-0.2973	1.7173	0.3792	-0.5844	1.2035
2003	1.3041	0.8259	-0.5026	0.6308	0.4898	1.4361	1.3108	0.9249
2004	0.2872	0.2718	0.7165	-0.2318	-1.0898	-0.8550	0.0002	0.1677
2005	1.1346	-1.2291	-1.1800	0.8135	0.2751	-0.4382	-1.1666	-0.8870
2006	-0.3455	-1.4597	0.9875	-0.6608	0.1807	0.9517	0.8114	-0.2240
2007	-0.8087	1.0502	0.2763	-0.0491	-1.0812	1.3912	1.7300	-0.1258
2008	-1.2042	0.5133	0.4456	-1.6184	-1.3816	-0.5166	-1.3346	1.0352
2009	-2.1984	0.0944	1.8680	-0.7724	-0.9524	-0.4696	-0.3187	0.0615

Table 5.6b. Climatic and oceanographic indices for March 1991 - 2009 z-scores standardized.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-1.01	0.53	14	0.444	-0.14	3.448	554.8	-0.2064
1992	0.75	-0.521	13.9	2.27	1.46	4.459	361.7	-1.4336
1993	1.21	-0.435	9.7	1.388	0.71	3.805	498	-0.7588
1994	1.05	0.225	14	0.423	0.98	2.114	287.9	-1.4471
1995	0.83	-0.963	13.9	0.419	1.13	3.231	444.9	-1.8250
1996	1.46	-1.525	9.6	-0.506	0.07	4.612	473.1	-0.4361
1997	1.05	0.324	11.4	0.493	1.7	3.751	515.5	-0.5061
1998	1.27	-0.038	15.1	2.67	-0.49	0.083	405.6	0.5215
1999	-0.41	0.284	17.1	-1.026	-0.57	0.86	434.5	1.6464
2000	0.35	-0.279	15.1	-0.525	0.08	2.379	243.4	2.3653
2001	-0.31	0.906	16.1	-0.149	0.06	1.272	321.7	2.2039
2002	-0.32	0.748	18.4	0.337	0.45	1.651	311.3	0.8974
2003	1.18	-0.178	14.5	0.307	0.34	2.402	452.2	1.1017
2004	0.57	-0.409	11.6	0.215	1.23	1.512	428.6	0.1253
2005	1.03	-0.046	14	0.558	0.81	1.967	276.3	-1.4295
2006	0.4	0.138	15.5	-0.69	-1.57	0.738	238.2	-0.1676
2007	0.16	0.544	9.9	-0.051	-0.19	4.967	819	0.4903
2008	-1.52	-0.455	18.2	-0.945	-0.5	0.043	285	1.6089
2009	-1.65	0.973	15.9	-0.161	0.49	0.904	294.8	0.3473

Table 5.7a. Climatic and oceanographic indices for April 1991 - 2009.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-1.4017	0.8435	-0.0377	0.1606	-0.5635	0.7310	1.0882	-0.2935
1992	0.4524	-0.8003	-0.0754	2.0397	1.4032	1.3897	-0.2910	-1.2682
1993	0.9370	-0.6658	-1.6594	1.1320	0.4813	0.9636	0.6825	-0.7322
1994	0.7685	0.3665	-0.0377	0.1390	0.8132	-0.1383	-0.8182	-1.2789
1995	0.5367	-1.4916	-0.0754	0.1349	0.9975	0.5896	0.3032	-1.5791
1996	1.2004	-2.3705	-1.6971	-0.8170	-0.3053	1.4894	0.5047	-0.4759
1997	0.7685	0.5213	-1.0182	0.2110	1.6982	0.9284	0.8075	-0.5315
1998	1.0002	-0.0449	0.3771	2.4513	-0.9937	-1.4617	0.0225	0.2847
1999	-0.7696	0.4587	1.1314	-1.3522	-1.0920	-0.9554	0.2289	1.1783
2000	0.0310	-0.4218	0.3771	-0.8366	-0.2931	0.0344	-1.1360	1.7492
2001	-0.6642	1.4316	0.7543	-0.4497	-0.3176	-0.6869	-0.5768	1.6211
2002	-0.6748	1.1844	1.6216	0.0505	0.1617	-0.4400	-0.6510	0.5833
2003	0.9054	-0.2638	0.1509	0.0196	0.0265	0.0494	0.3554	0.7456
2004	0.2628	-0.6251	-0.9428	-0.0751	1.1205	-0.5305	0.1868	-0.0300
2005	0.7474	-0.0574	-0.0377	0.2779	0.6042	-0.2341	-0.9010	-1.2650
2006	0.0837	0.2304	0.5280	-1.0064	-2.3211	-1.0349	-1.1732	-0.2626
2007	-0.1691	0.8654	-1.5839	-0.3488	-0.6249	1.7208	2.9753	0.2599
2008	-1.9390	-0.6971	1.5462	-1.2688	-1.0060	-1.4878	-0.8389	1.1484
2009	-2.0759	1.5363	0.6788	-0.4620	0.2109	-0.9267	-0.7689	0.1463

Table 5.7b. Climatic and oceanographic indices for April 1991 - 2009 z-scores standardized.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-0.51	0.486	14.5	0.708	-1.13	2.006	369.1	-0.0595
1992	1.54	1.341	15.9	2.138	1.02	1.815	231.4	-1.7956
1993	2.13	-1.607	12.5	1.976	0.37	1.993	238.7	-1.0894
1994	1.23	-0.115	13.6	0.51	-0.76	2.381	321.6	-0.3014
1995	1.46	-0.891	13.8	0.503	0.72	2.275	281.2	-1.5042
1996	2.18	-0.226	15.8	-0.201	1.15	0.6	161.2	-1.2748
1997	1.83	-0.961	12.9	1.114	2.43	1.316	149	-0.8772
1998	0.7	0.429	15.8	2.148	-1.36	-1.03	150.9	0.2776
1999	-0.68	0.226	15.7	-0.727	-0.69	1.475	276.7	1.6046
2000	-0.05	0.969	16.3	0.118	-0.62	2.737	196.2	2.2203
2001	-0.3	0.452	15.5	0.151	-1.42	2.627	274	1.9539
2002	-0.63	0.401	14.4	0.766	1.52	1.384	120.4	1.1026
2003	0.89	1.017	15.9	0.027	-0.57	1.618	171	0.9193
2004	0.88	-0.094	15.2	0.462	1.92	0.721	189.8	0.2074
2005	1.86	-0.763	11.9	0.735	0.09	2.491	168.3	-0.7554
2006	0.48	0.156	16.5	-0.055	-0.31	1.835	195.1	-0.0445
2007	-0.1	0.894	15.5	0.156	-0.67	3.4	346.4	0.8234
2008	-1.37	-1.205	14.1	-0.39	0.21	2.088	415.1	1.7465
2009	-0.88	1.194	16	0.355	1.31	2.067	164.9	0.3041

Table 5.8a. Climatic and oceanographic indices for May 1991 - 2009.

YEAR	PDO	AO	NP	ENSO	EPNP	ALONG	MIX	NPGO
1991	-0.9624	0.4644	-0.2433	0.1923	-1.1345	0.2369	1.6222	-0.1993
1992	0.8796	1.4662	0.7841	1.9583	0.7433	0.0377	-0.0153	-1.6320
1993	1.4098	-1.9879	-1.7111	1.7583	0.1756	0.2233	0.0715	-1.0492
1994	0.6011	-0.2398	-0.9038	-0.0523	-0.8113	0.6280	1.0573	-0.3989
1995	0.8078	-1.1490	-0.7571	-0.0609	0.4813	0.5174	0.5769	-1.3916
1996	1.4547	-0.3698	0.7107	-0.9304	0.8568	-1.2295	-0.8500	-1.2022
1997	1.1402	-1.2310	-1.4176	0.6937	1.9748	-0.4828	-0.9951	-0.8741
1998	0.1249	0.3976	0.7107	1.9707	-1.3354	-2.9295	-0.9725	0.0789
1999	-1.1152	0.1598	0.6373	-1.5800	-0.7502	-0.3169	0.5234	1.1740
2000	-0.5491	1.0303	1.0776	-0.5364	-0.6891	0.9992	-0.4338	1.6821
2001	-0.7737	0.4246	0.4905	-0.4956	-1.3878	0.8845	0.4913	1.4623
2002	-1.0702	0.3648	-0.3167	0.2639	1.1800	-0.4118	-1.3352	0.7597
2003	0.2956	1.0866	0.7841	-0.6488	-0.6454	-0.1678	-0.7335	0.6085
2004	0.2866	-0.2152	0.2704	-0.1115	1.5294	-1.1033	-0.5100	0.0209
2005	1.1672	-0.9990	-2.1514	0.2256	-0.0690	0.7427	-0.7656	-0.7736
2006	-0.0728	0.0778	1.2244	-0.7500	-0.4183	0.0585	-0.4469	-0.1869
2007	-0.5940	0.9425	0.4905	-0.4895	-0.7327	1.6907	1.3522	0.5293
2008	-1.7352	-1.5169	-0.5369	-1.1638	0.0359	0.3224	2.1692	1.2911
2009	-1.2949	1.2940	0.8575	-0.2437	0.9966	0.3005	-0.8060	0.1008

Table 5.8b. Climatic and oceanographic indices for May 1991 - 2009 z-scores standardized.

Year	PDO		AO		NP		ENSO	
	winter ave	spring ave						
1991	-1.317	-0.760	-0.227	0.508	8.367	14.250	0.333	0.576
1992	0.343	1.145	0.885	0.410	5.400	14.900	1.870	2.204
1993	0.333	1.670	1.481	-1.021	6.933	11.100	0.884	1.682
1994	0.867	1.140	0.244	0.055	10.367	13.800	0.233	0.467
1995	0.240	1.145	0.556	-0.927	6.900	13.850	1.007	0.461
1996	0.783	1.820	-0.840	-0.876	9.067	12.700	-0.502	-0.354
1997	0.387	1.440	0.841	-0.319	7.067	12.150	-0.448	0.804
1998	1.467	0.985	-0.839	0.196	3.000	15.450	2.684	2.409
1999	-0.437	-0.545	-0.300	0.255	8.967	16.400	-1.124	-0.877
2000	-0.847	0.150	0.632	0.345	6.767	15.700	-1.172	-0.204
2001	0.447	-0.305	-1.089	0.679	7.700	15.800	-0.601	0.001
2002	-0.267	-0.475	1.196	0.575	10.833	16.400	-0.145	0.552
2003	1.783	1.035	0.196	0.420	5.833	15.200	0.980	0.167
2004	0.507	0.725	-0.965	-0.252	6.967	13.400	0.178	0.339
2005	0.870	1.445	-0.754	-0.405	6.833	12.950	0.706	0.647
2006	0.580	0.440	-0.643	0.147	12.400	16.000	-0.491	-0.373
2007	-0.103	0.030	0.636	0.719	9.800	12.700	0.535	0.053
2008	-0.827	-1.445	0.781	-0.830	9.433	16.150	-1.331	-0.668
2009	-1.513	-1.265	0.083	1.084	13.933	15.950	-0.712	0.097

Year	EPNP		ALONG		MIX		NPGO	
	winter ave	spring ave						
1991	-0.173	-0.635	0.556	2.727	408.333	461.950	-0.619	-0.133
1992	0.603	1.240	0.712	3.137	318.133	296.550	-0.261	-1.615
1993	0.560	0.540	0.692	2.899	484.033	368.350	-2.233	-0.924
1994	0.597	0.110	2.606	2.248	673.400	304.750	-1.896	-0.874
1995	0.563	0.925	3.155	2.753	610.500	363.050	-1.372	-1.665
1996	0.980	0.610	1.813	2.606	355.833	317.150	-0.947	-0.855
1997	0.043	2.065	3.370	2.534	600.067	332.250	-1.124	-0.692
1998	0.533	-0.925	3.718	-0.474	525.800	278.250	1.107	0.400
1999	-0.913	-0.630	1.918	1.168	687.267	355.600	1.787	1.626
2000	-0.623	-0.270	1.040	2.558	436.000	219.800	1.892	2.293
2001	-0.600	-0.680	0.622	1.950	498.167	297.850	2.736	2.079
2002	0.330	0.985	1.246	1.518	537.067	215.850	1.980	1.000
2003	1.190	-0.115	2.510	2.010	562.033	311.600	1.484	1.010
2004	-0.373	1.575	2.383	1.117	640.033	309.200	0.438	0.166
2005	0.250	0.450	2.278	2.229	387.867	222.300	-1.335	-1.092
2006	-0.100	-0.940	1.924	1.287	487.067	216.650	-0.367	-0.106
2007	-0.493	-0.430	2.585	4.184	611.133	582.700	0.112	0.657
2008	-1.090	-0.145	1.756	1.066	457.800	350.050	1.417	1.678
2009	-0.327	0.900	1.118	1.486	419.200	229.850	0.713	0.326

Table 5.9. Climatic and oceanographic indices for winter (averaged over values from January, February, and March) and spring (averaged over values from April and May).

Month	P-value	Total Inertia	Constrained	Unconstrained
January	0.2	0.7902	0.415	0.3752
February	0.84	0.7902	0.2674	0.5228
March	0.56	0.7902	0.356	0.4342
April	0.61	0.7902	0.335	0.4552
May	0.24	0.7902	0.3921	0.3981

Table 5.10. Results of canonical correspondence analysis on transformed and standardized May species abundances and monthly indices of climate and ocean for 1991 to 2009. Total inertia is the total variation in the species matrix.

Year	Year of Effect	PINKS
1990	1991	175.71
1991	1992	206.47
1992	1993	132.06
1993	1994	186.92
1994	1995	187.95
1995	1996	223.06
1996	1997	213.5
1997	1998	147.39
1998	1999	186.44
1999	2000	260.78
2000	2001	144.84
2001	2002	240.65
2002	2003	182.49
2003	2004	230.04
2004	2005	194.18
2005	2006	273.62

Table 5.11a. Pink salmon abundance data (millions of fish) for the eastern North Pacific.

Year	Year of Effect	PINKS
1990	1991	-0.582
1991	1992	0.1824
1992	1993	-1.667
1993	1994	-0.304
1994	1995	-0.278
1995	1996	0.5949
1996	1997	0.3572
1997	1998	-1.286
1998	1999	-0.316
1999	2000	1.5326
2000	2001	-1.35
2001	2002	1.0322
2002	2003	-0.414
2003	2004	0.7684
2004	2005	-0.123
2005	2006	1.8518

Table 5.11b. Pink salmon abundance data for the eastern North Pacific, z-scores standardized.

Month	p-value	Total Inertia	Constrained	Unconstrained
January	0.07	0.8347	0.6213	0.2134
February	0.42	0.8347	0.5294	0.3053
March	0.05	0.8347	0.6198	0.2149
April	0.135	0.8347	0.5928	0.2419
May	0.001	0.8347	0.6655	0.1692

Table 5.12. Results of canonical correspondence analysis on transformed and standardized May species abundances and monthly indices of climate and ocean and pink salmon abundances for 1991 to 2006. Total inertia is the total variation in the species matrix.

SPECIES	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
anon	-0.5246	-0.1106	0.04075	-0.02336	0.02859	-0.001463
dof	0.8583	-0.2167	-0.03998	0.02861	0.01252	0.004658
onyx	0.4901	0.8161	0.59535	-0.03841	-0.1706	-0.022863
mag	-0.5668	0.248	-0.45032	0.3165	-0.82301	0.076418
bor	0.1112	0.8271	-0.77836	-0.14844	0.10937	-0.027158
unkA	0.3611	1.7147	0.20562	-2.49273	0.294	0.189519
mad	-0.3333	1.6141	0.19321	1.3526	0.86996	0.260565
cran	-0.4094	0.9144	-0.14389	1.05888	0.17401	-0.74091

INDEX	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
PDO	-0.3137	0.48055	0.049709	-0.0007954	0.15701	0.68399
AO	0.501	0.12631	-0.156464	-0.2654413	-0.04947	-0.18981
NP	0.5591	0.35839	0.003519	0.102733	0.02133	-0.34334
ENSO	0.1041	0.02167	-0.109267	-0.605181	-0.18877	0.43278
EPNP	0.1388	0.25761	-0.208256	-0.1202227	0.57071	0.04024
ALONG	-0.3959	-0.27858	0.421843	-0.3525669	-0.0159	-0.05235
MIX	-0.6057	0.06024	0.044811	-0.2575419	-0.54517	-0.46204
NPGO	0.2861	-0.62254	-0.145803	0.2081704	0.04315	-0.31098
PINKS	0.6586	0.19707	0.106091	0.1537776	0.12215	-0.11978

Table 5.13. Results of canonical correspondence analysis on transformed and standardized May species abundances and monthly indices of climate and ocean and pink salmon abundances for 1991 to 2006, organized by relative contribution of each variable to each canonical axis.

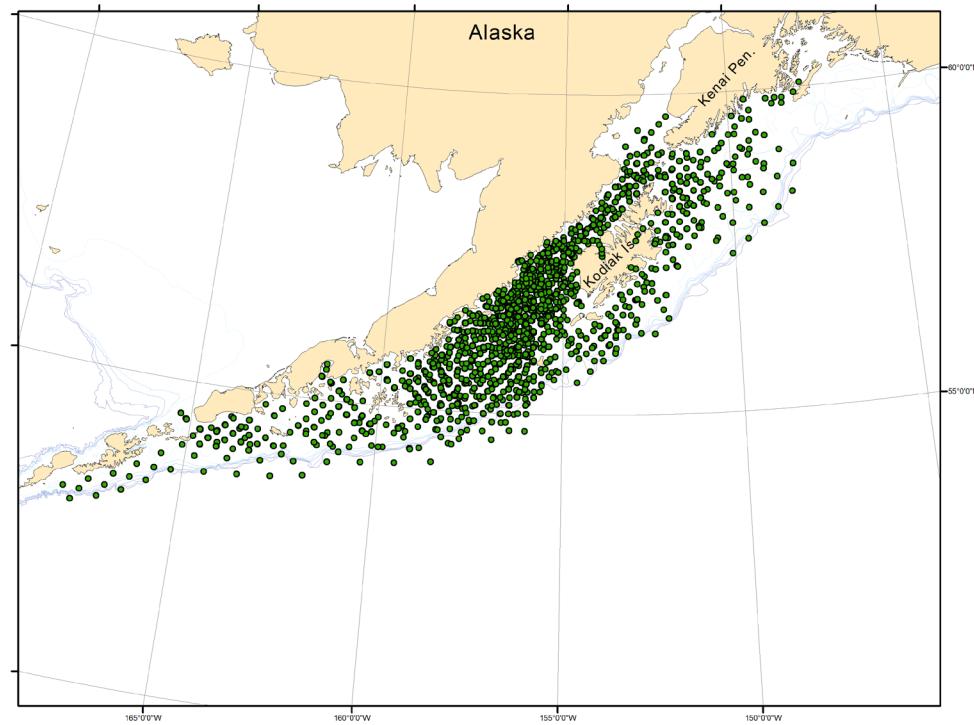


Figure 5.1. Map of study area showing all stations sampled from 1981 to 2009.

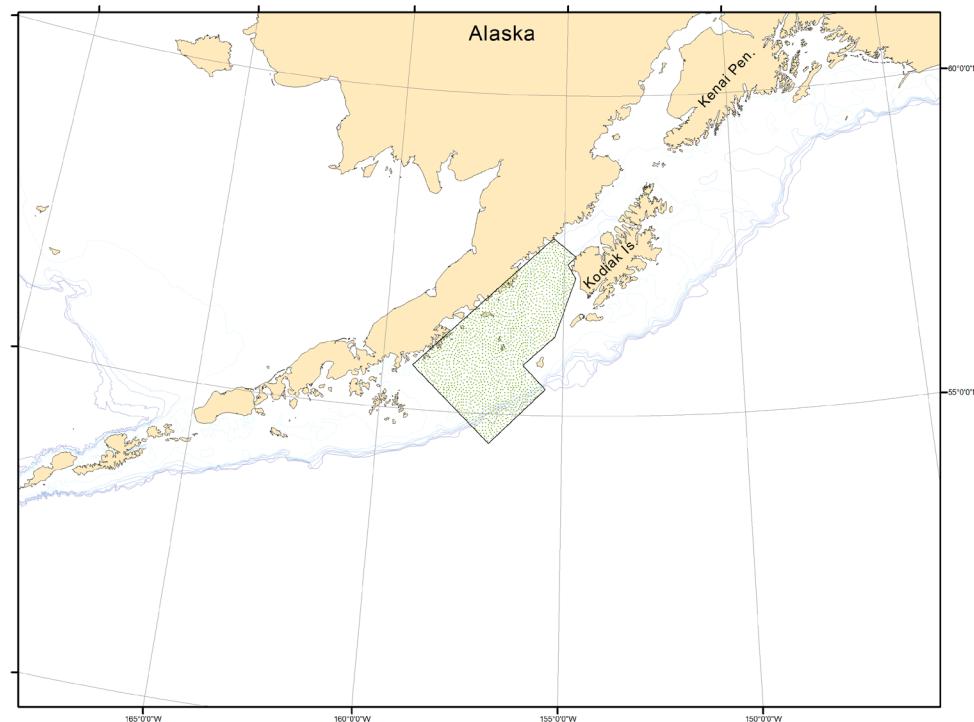


Figure 5.2. Map of study area showing minimal sampled region.

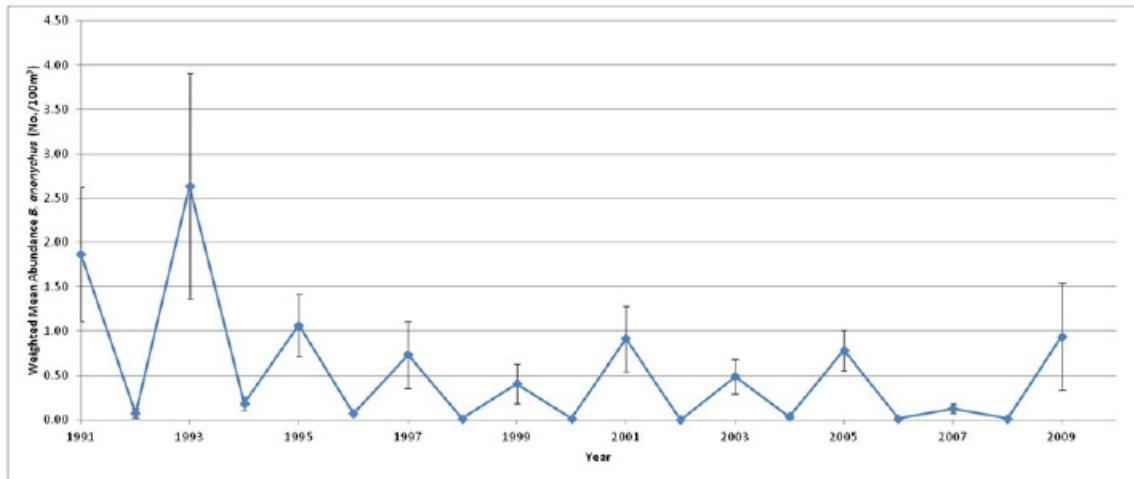


Figure 5.3. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of *Berryteuthis anonymus*.

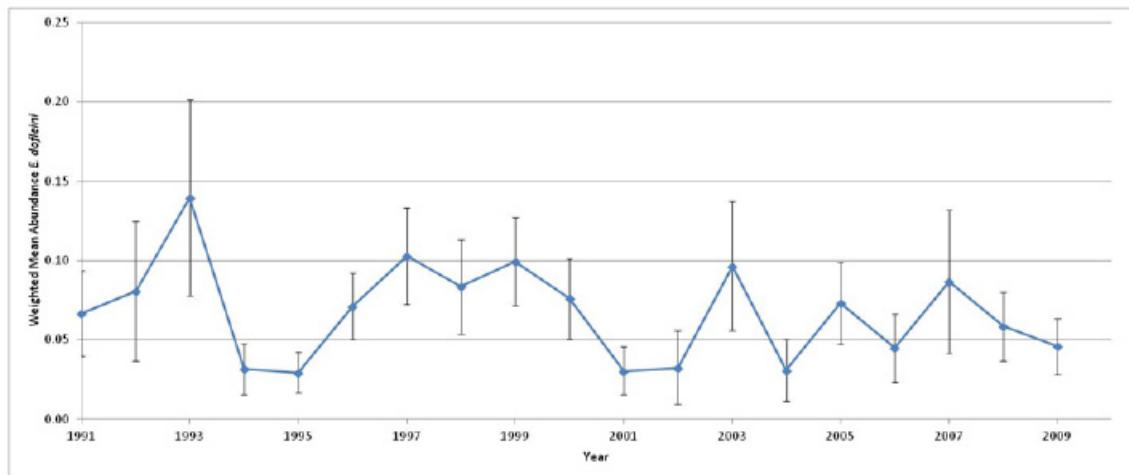


Figure 5.4. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of *Enteroctopus dofleini*.

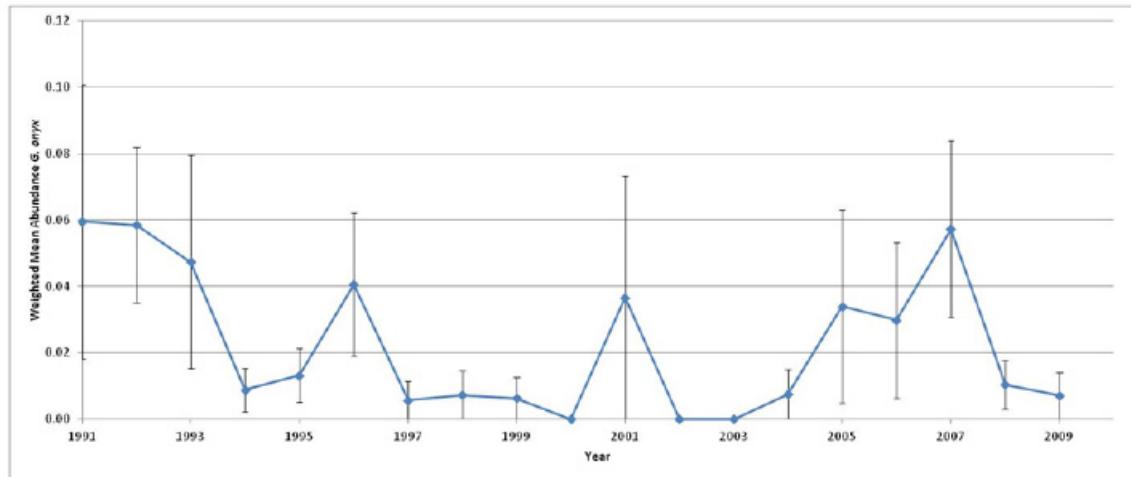


Figure 5.5. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of *Gonatus onyx*.

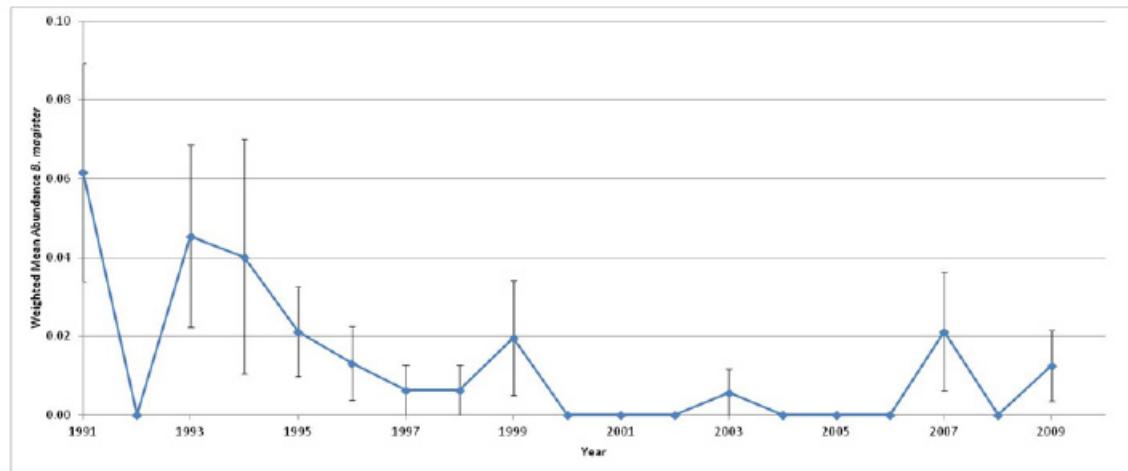


Figure 5.6. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of *Berryteuthis magister*.

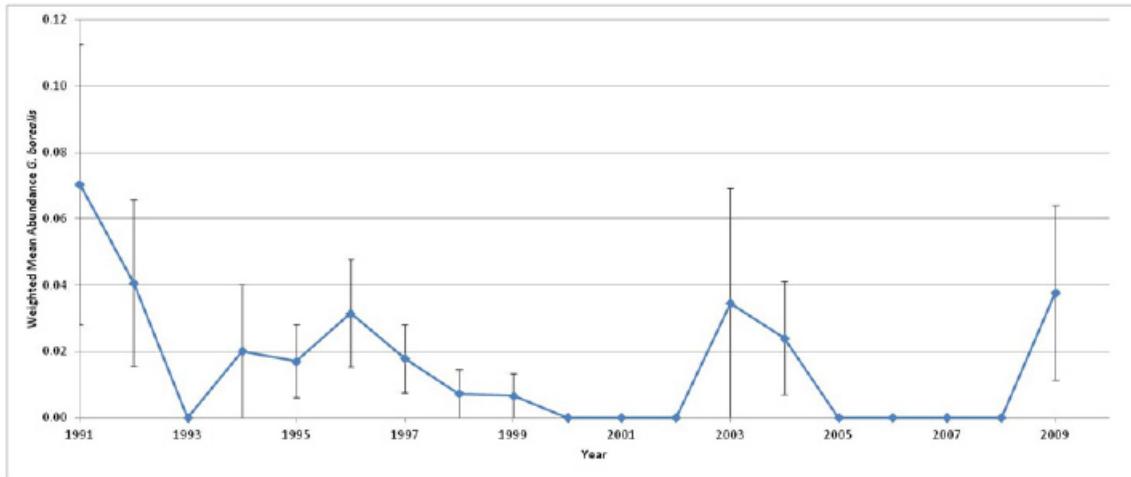


Figure 5.7. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of *Gonatopsis borealis*.

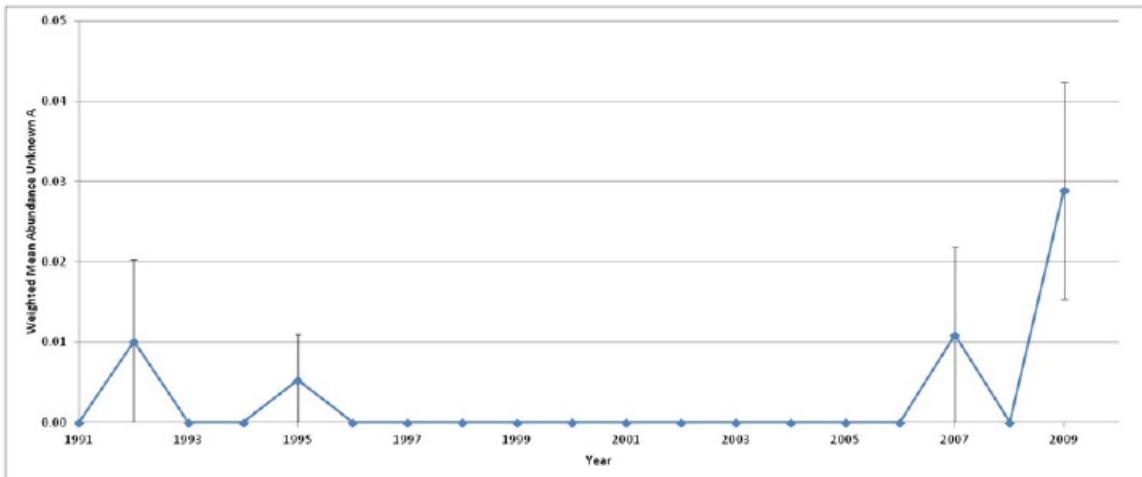


Figure 5.8. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of Unknown A.

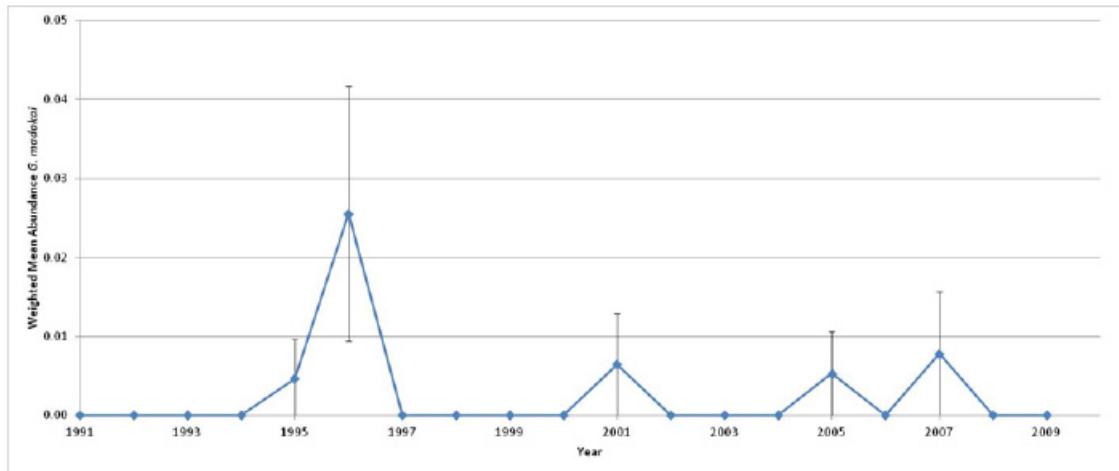


Figure 5.10. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of *Gonatus madokai*.

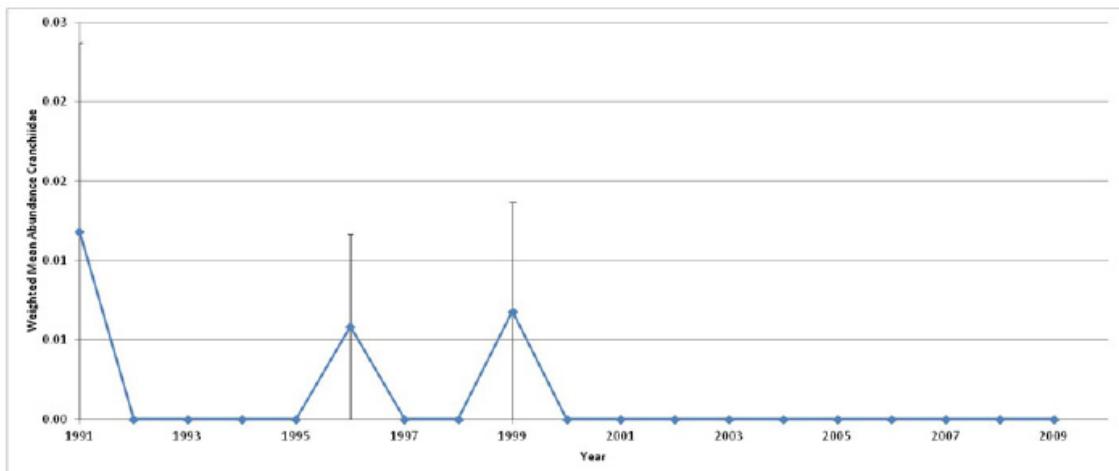


Figure 5.11. Weighted mean abundances (number collected per 100 m³, weighted by polygonal area) of Cranchiidae (cf *Galiteuthis phyllura*).

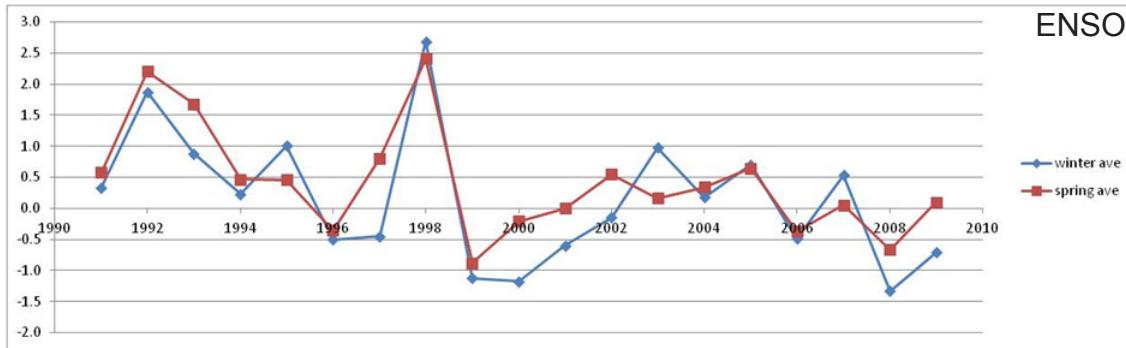


Figure 5.12. Average seasonal values of El Niño Southern Oscillation (ENSO) index for 1991 - 2009. Winter is the average of January, February, and March values; Spring is the average of April and May values.

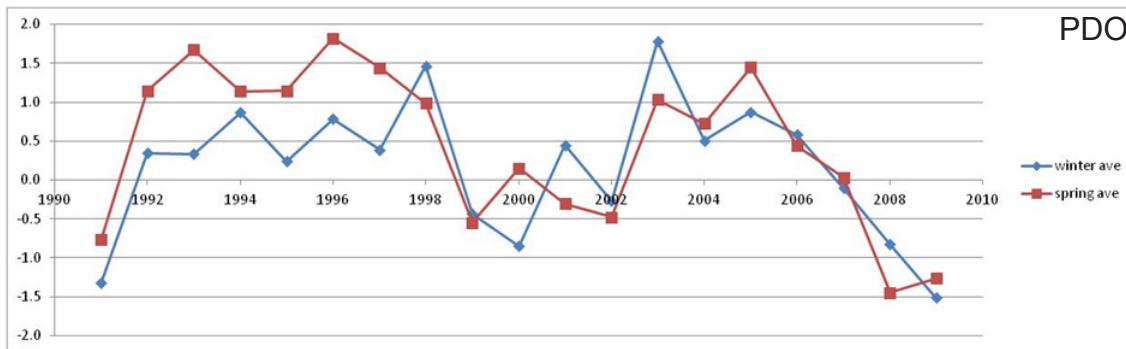


Figure 5.13. Average seasonal values of Pacific Decadal Oscillation (PDO) index for 1991 - 2009. Winter is the average of January, February, and March values; Spring is the average of April and May values.

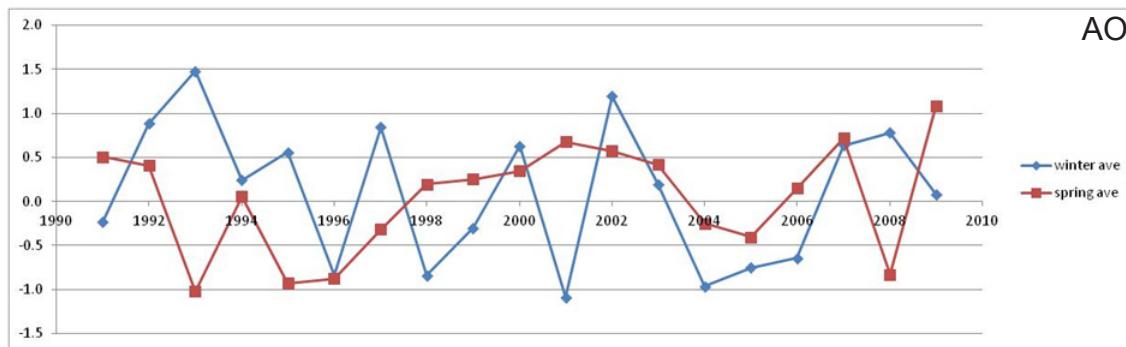


Figure 5.14. Average seasonal values of Arctic Oscillation (AO) index for 1991 - 2009. Winter is the average of January, February, and March values; Spring is the average of April and May values.

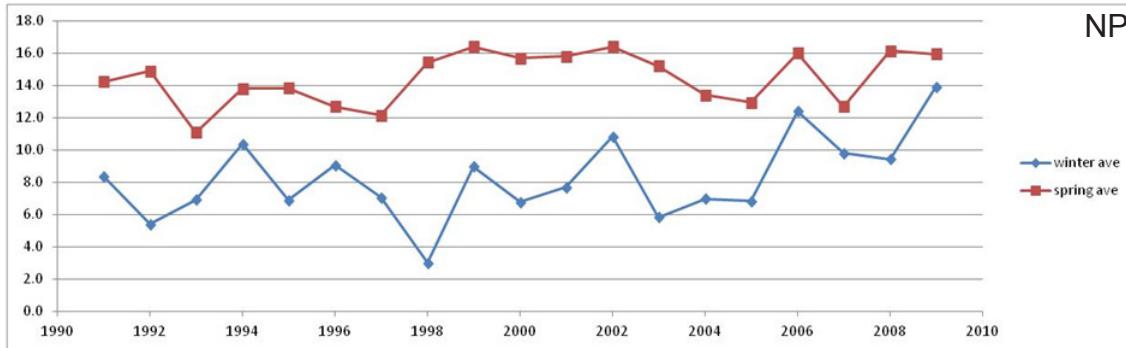


Figure 5.15. Average seasonal values of North Pacific Oscillation (NP) index for 1991 - 2009. Winter is the average of January, February, and March values; Spring is the average of April and May values.

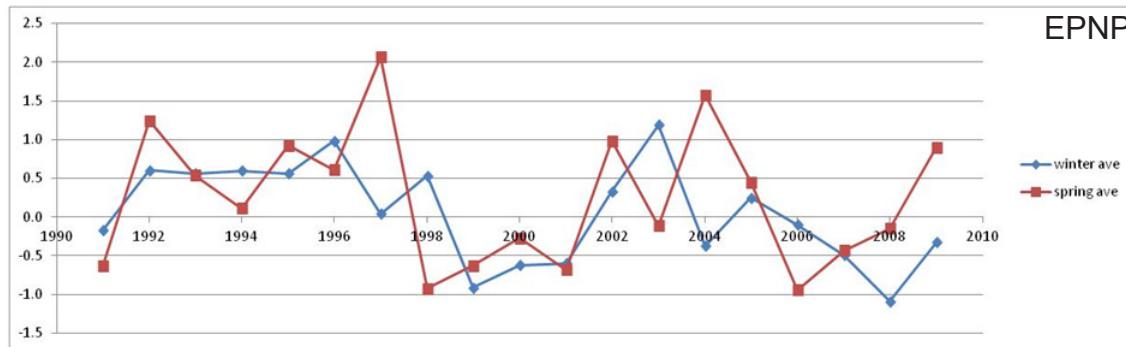


Figure 5.16. Average seasonal values of East Pacific-North Pacific (EPNP) index for 1991 - 2009. Winter is the average of January, February, and March values; Spring is the average of April and May values.

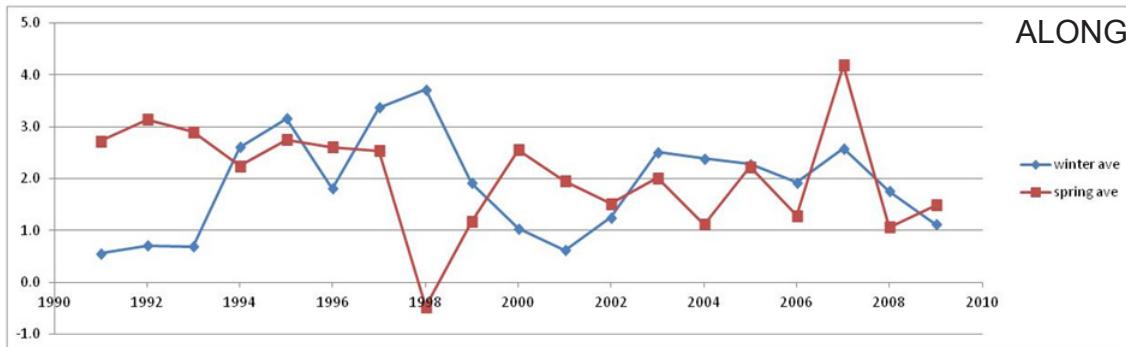


Figure 5.17. Average seasonal values of alongshore wind (ALONG) index for 1991 - 2009. Winter is the average of January, February, and March values; Spring is the average of April and May values.

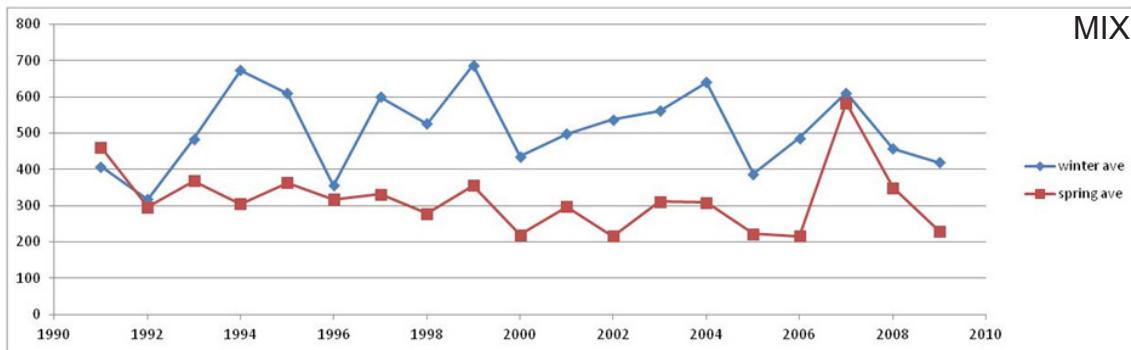


Figure 5.18. Average seasonal values of wind mixing (MIX) index for 1991 - 2009. Winter is the average of January, February, and March values; Spring is the average of April and May values.

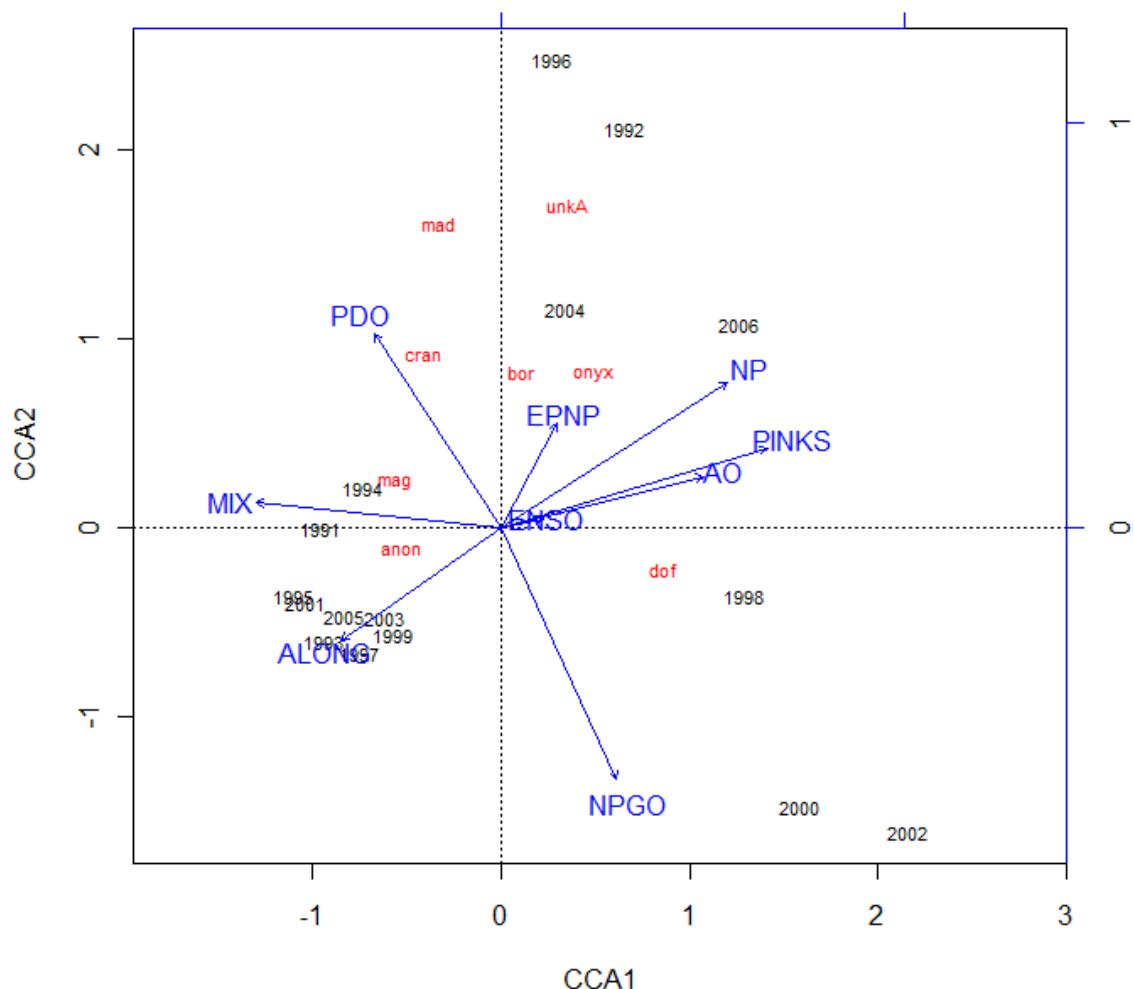


Figure 5.19. Canonical correspondence analysis of species abundance matrix constrained by matrix of May values of climatic and oceanographic indices and previous year pink salmon abundance (catch + return). AVONA = 0.001.

References

- Andrewartha, H. G. 1961. *Introduction to the Study of Animal Populations*. Univ. of Chicago Press, Chicago. 281 pp.
- Aydin, K.Y. 2000. Trophic feedback and carrying capacity of Pacific salmon (*Oncorhynchus* spp.) on the high seas of the Gulf of Alaska. Doc. Diss. Univ. Wa., 392 pp.
- Aydin, K.Y., Myers, K.W., and R.V. Walker. 2000. Variation in summer distribution of the prey of Pacific salmon (*Oncorhynchus* spp.) in the offshore Gulf of Alaska in relation to oceanographic conditions, 1994-98. NPAFC Bull. 2: 43-54.
- Bailey, K.M., 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Mar. Ecol. Prog. Ser. 198: 215-224.
- Bailey, K.M. and S.A. Macklin, 1994. Analysis of patterns in larval walleye pollock *Theragra chalcogramma* survival and wind mixing events in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 113, 1-12.
- Barnston, A.G. and R.E. Livezey, 1987. Classification, seasonality and persistence of low frequency atmospheric circulation patterns. Monthly Weather Review 115, 1083–1126.
- Beamish, R. J., and D.R. Bouillon, 1993. Pacific salmon trends in relation to climate. Canadian J. Fish. and Aquatic Sci., 50: 1002–1016.
- Bettencourt, V., Coelho, L., Andrade, J.P., and A. Guerra. 1996. Age and growth of the squid *Loligo vulgaris* off the south coast of Portugal, using statolith analysis. J. Moll. Stud. 62(3): 359 - 366.
- Bidder, A. M. 1957 Evidence for absorptive function in the 'liver' of *Octopus vulgaris* Lam. Pubbl. Staz. Zool. Napoli 29, 139-150.
- Bjørke, H. 1995. Norwegian investigations of *Gonatus fabricii* (Lichtenstein). ICES Council Meeting 1995/K: 12 (Ref. N). 13 pp.
- Blood, D. M., A. C. Matarese, and M. S. Busby. 2007. Spawning, egg development, and early life history dynamics of arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska. U.S. Dep. Commer., NOAA Prof. Pap. NMFS 7, 28 pp.

- Botsford, L. W. 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. ICES J. Mar. Sci., 58: 1081–1091.
- Boucaud-Camou, E. 1982. Localization of some hydrolytic enzymes in digestive organs of juvenile *Sepia officinalis* (Mollusca: Cephalopoda). Malacologia 22 (1–2), 685–690.
- Boucaud-Camou, E. and R. Boucher-Rodoni. 1983. Feeding and digestion in cephalopods. In: Saleudin, A.S.M., Wilbur, K.M. (Eds.), *The Mollusca, Physiology* Vol. 5, part 2, 149–187. Academic Press, New York.
- Boucaud-Camou, E. and M. Yim. 1980. Fine structure and function of the digestive cell of *Sepia officinalis* (Mollusca: Cephalopoda). J. Zool., Lond. 191, 89–105.
- Boucaud-Camou, E. and C.F.E. Roper. 1995a. Digestive enzymes in paralarval cephalopods. Bull. Mar. Sci. 57 (2), 313–327.
- Boucaud-Camou, E. and C.F.E. Roper. 1995b. The digestive gland of young (post-embryonic) cephalopods: structural and functional relationships. In: Guerra, A., Rola'n, E., Rocha, F. (Eds.), Abstracts—Int. Malacological Congress, 12th, Instituto de Investigaciones Marinas, Vigo, Spain, pp. 62–63.
- Boucher-Rodoni, R., Boucaud-Camou, E., and K. Mangold. 1987. Feeding and digestion. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles: Comparative Reviews*. Vol. 2, 85–108. Academic Press, London.
- Bower, J.R., Seki, M.P., Young, R.E., Bigelow, K.A., Hirota, J., and P. Flament. 1999. Cephalopod paralarvae assemblages in Hawaiian Islands waters. Mar. Ecol. Prog. Ser. 185, 203–212.
- Bower, J.R. and S. Takagi. 2004. Summer vertical distribution of paralarval gonatid squids in the northeast Pacific. J. Plank. Res. 26(8): 851–857.
- Boyle P. R. and P.G. Rodhouse. 2005. *Cephalopods: ecology and fisheries*. Oxford: Blackwell Science, 452 pp.
- Castro, B.G., Garrido, J.L., and C.G. Sotelo. 1992. Changes in the composition of digestive gland and mantle muscle of cuttlefish *Sepia officinalis* during starvation. Mar. Biol. 114 (1), 11–20.
- Castro, B.G. and P.G. Lee. 1994. The effect of semi-purified diets on growth and condition of *Sepia officinalis* (Mollusca: Cephalopoda). Comp. Biochem. Physiol. 109A (4), 1007–1016.
- Crow, K.D., Powers, D.A., and G. Bernardi. 1997. Evidence for multiple

- maternal contributors in nests of kelp greenling (*Hexagrammos decagrammus*, Hexagrammidae). Copia, 1: 9-15.
- Darmaillacq, A.-S., Chichery, R. and L. Dickel. 2006. Food imprinting, new evidence from the cuttlefish *Sepia officinalis*. Biology Letters, 2: 345-347.
- Darmaillacq A.-S., Lesimple C., and L. Dickel. 2008. Embryonic visual learning in the cuttlefish, *Sepia officinalis*. Animal Behaviour, 76(1): 131-134.
- Doyle, M.J., Picquelle, S.J., K.L. Mier, M.C. Spillane, and N.A. Bond. 2009. Larval fish abundance and physical forcing in the Gulf of Alaska, 1981-2003. Prog. Ocean. 80, 163-187.
- Fields, W.G. 1965. The structure, development, food relations, reproduction, and life history of *Loligo opalescens* Berry. Cal. Fish Game Fish. Bull. 131, 1-108.
- Hartwick, B. 1983. *Octopus dofleini*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles: Species Accounts*. Vol. 1, 277-291. Academic Press, London.
- Hayashi, S. 1993. Growth and maturation of the firefly squid, *Watasenia scintillans* (Berry), in Toyama Bay and adjacent waters of the Sea of Japan. In Okutani, T., O'Dor, R.K., and T. Kubodera (Eds.), *Recent advances in cephalopod fisheries biology*, 173-178. Tokai University Press, Tokyo.
- Hunt, J. C. and B.A. Seibel. 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): ontogenetic changes in habitat, behavior, and physiology. Mar. Biol. 136, 543-552.
- Jefferts, K. 1988. Zoogeography of cephalopods from the northeastern Pacific Ocean. Bull. Ocn. Res. Inst., 26: 123-157.
- Jereb, P., Roper, C.F.E., and M. Vecchione. 2005. Introduction. In: Jereb, P. and C.F.E. Roper (Ed.), *Cephalopods of the World*. Rome, FAO pp. 1-19.
- Jorgensen, E.M., 2007. Identification, distribution, and relative abundance of paralarval gonatid squids (Cephalopoda:Oegopsida:Gonatidae) from the Gulf of Alaska, 2001-2003. J. Moll. Stud. 73, 155-165.
- Jorgensen, E.M. 2009. *Identification guide to the squids and octopods of the eastern North Pacific and Bering Sea*. Alaska Sea Grant Fairbanks Alaska. 99 pp.
- Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R.V., and K. W. Myers. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska

- in relation to climate events. Fish Ocn. 13(3): 197-207.
- Kanamaru, S. 1964. The octopods off the coast of Rumoi and the biology of mizudako (*Paroctopus dofleini*). Monthly Rep. Hokkaido Fish. Exp. Stat. 21, 189-210. [In Japanese]
- Kanamaru, S. and Y. Yamashita. 1967. The octopus mizudako. Part 1. Ch. 12, Investigations of the marine resources of Hokkaido and developments of the fishing industry, 1961-1965. [In Japanese]
- Krebs, C.J. 1994. *Ecology: The experimental analysis of distribution and abundance*. 4th edition, Harper Collins, New York. 801 pp.
- Kubodera, T. 1982. Ecological studies of pelagic squids in the subarctic Pacific region. Doctoral Diss., Hokkaido Univ., Hakodate, 255 pp.
- Kubodera, T. 1991. Distribution and abundance of the early life stages of Octopus, *O. dofleini* Wülker, 1910 in the North Pacific. Bull of Mar Sci 49(1-2): 235-243.
- Kubodera, T. and T. Okutani, 1981. The systematics and identification of larval cephalopods from the northern North Pacific. Res. Inst. N. Pac. Fish., Hokkaido Univ. Sp. Vol., 131-159.
- Kubodera, T. and K. Jefferts, 1984a. Distribution and abundance of the early life history stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific, part 1. Bull. Nat. Sci. Mus., 10(3): 91-106.
- Kubodera, T. and K. Jefferts, 1984a. Distribution and abundance of the early life history stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific, part 2. Bull. Nat. Sci. Mus., 10(4): 165-193.
- Kubodera, T. and K. Shimazaki. 1989. Cephalopods from the stomach contents of the pomfret (*Brama japonica* Hilgendorf) caught in surface gillnets in the northern North Pacific. J. Ceph. Biol. 1(1): 71 - 83.
- Lasker, R. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In: Lasker, R. (Ed.), *Marine fish larvae morphology, ecology, and relation to fisheries*. 80-87. University of Washington Press, Seattle and London.
- LeBrasseur, R.J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Bd. Canada 23(1): 85-100.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and R.C. Francis, 1997. A Pacific

- interdecadal climate oscillation with impacts on salmon production. Bull. Amer. Meteor. Soc. 78, 1069–1079.
- Matarese, A. C., D. M. Blood, S. J. Picquelle, and J. L. Benson. 2003. Atlas of abundance and distribution patterns of ichthyoplankton from the Northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center 1972–1996. U.S. Dep. Commer., NOAA Prof. Pap. NMFS 1, 281 pp.
- Mecklenburg, C.W., Mecklenburg, T.A., and L.K. Thorsteinson. 2002. *Fishes of Alaska*. American Fisheries Society, Bethesda, MD. 1116 pp.
- Melzner, F., Forsythe, J.W., Lee, P.G., Wood, J.B., Piatkowski, U., and C. Clemmesen. 2005. Estimating recent growth in the cuttlefish *Sepia officinalis*: are nucleic acid-based indicators for growth and condition the method of choice? J. Exp. Mar. Bio. Eco. 317, 37-51.
- Miller, A.J. 1996. Recent advances in California Current modeling: decadal and interannual thermocline variations. CalCOFI Report, 37: 69-79.
- Mottet, M.G. 1975. The fishery biology of *Octopus dofleini*. Wash. Dept. of Fish., Tech. Rep. No. 16, 39 pp.
- Myers, K.W., Aydin, K.Y., Walker, R.V., Fowler, S., and M.L. Dahlberg. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956-1995. (NPAFC Doc. 192.) 4 p. + figs. and appends. FRI-UW-9614. University of Washington, Fisheries Research Institute, Box 357980, Seattle, WA 98195-7980.
- Nesis, K. 1987. *Cephalopods of the World*. TFH Publications, Neptune City, NJ. 351 pp.
- Nesis, K. 1997. Gonatid squids in the subarctic North Pacific: Ecology, biogeography, niche diversity and role in the ecosystem. Advances in Marine Biology, 37: 243 - 324.
- O'Dor, R.K. 1983. *Illex illecebrosus*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles: Species Accounts*. Vol. 1, 175-200. Academic Press, London.
- Okutani, T. 1966. Studies on early life history of decapodan Mollusca - II. Planktonic larvae of decapodan cephalopods from the northern North Pacific in summer seasons during 1952-1959. Bull. Tokai Reg. Fish. Res. Lab. 45, 61-79.
- Okutani, T. 1983. *Todarodes pacificus*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles: Species Accounts*. Vol. 1, 201-216. Academic Press, London.

- Okutani, T. 1988. Evidence of spawning of *Berryteuthis magister* in the northwestern Pacific (Cephalopoda:Gonatidae). Bull. Ocn. Res. Inst., 26(1): 193-200.
- Okutani, T., Kubodera, T. and K. Jefferts. 1988. Diversity, distribution, and ecology of gonatid squids in the subarctic Pacific: a review. Bull. Ocn. Res. Inst., 26: 159–192.
- Otero, J., Alvarez-Salgado, X.A., Gonzalez, A.F., Miranda, A., Groom, S.B., Cabanas, J.M., Casas, G., Wheatley, B., and A. Guerra. 2008. Bottom-up control on common octopus *Octopus vulgaris* in the Galician upwelling system, northeast Atlantic Ocean. Mar. Ecol. Prog. Ser. 362, 181-192.
- Overland, J. E., J. M. Adams, and H. O. Mofjeld. 2000. Chaos in the North Pacific: Spatial modes and temporal irregularity, Prog. Oceangr., 47, 337– 354.
- Radchenko, V.I. 1992. The role of squids in the pelagic ecosystem of the Bering Sea. Okeanologiya, 32: 1093–1101. [In Russian]
- Raskoff, K.A., Sommer, F.A., Hamner, W.M., and K.M. Cross. 2004. Collection and culture techniques for gelatinous zooplankton. Bio. Bull. 2004, 68-80.
- Rigby, P.R. and Y. Sakurai. 2005. Multidimensional tracking of giant Pacific octopuses in northern Japan reveals unexpected foraging behavior. Mar. Tech. Soc. Journal. 39(1): 64-67.
- Rocha, F., Guerra, A., Prego, R., and U. Piatkowski. 1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). J. Plank. Res. 21(1): 21-33.
- Rodhouse, P.G., Dawe, E.G., and R.K. O'Dor. 1998. Squid recruitment dynamics. The genus *Ilex* as a model, the commercial *Ilex* species and influences on variability. FAO Fish. Tech. Paper 376. Rome, FAO, 273 pp.
- Royer, T.C. 1981. Baroclinic transport in the Gulf of Alaska. Part II. Fresh water driven coastal current. J. Mar. Res. 39, 251–266.
- Ruggerone, G.T., Peterman, R.M., Dorner, B., Myers, K.W., and N.J. Mantua. 2010. Abundance of adult hatchery and wild salmon by region of the North Pacific. School of Aquatic and Fishery Sciences, University of Washington, Seattle WA. A report to the Gordon and Betty Moore Foundation. July 2010. 24 pp.
- Sakurai, Y. Bower, J.R., Nakamura, Y., Yamamoto, S. and K. Watanabe. 1996. Effect of temperature on development and survival of *Todarodes pacificus* embryos

- and paralarvae. Amer. Malacological Bull. 13, 89-95.
- Sakurai, Y., Kiyofuji, H., Saitoh, S., Goto, T. and Y. Hiyama. 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda:Ommastrephidae) due to changing environmental conditions. ICES J. Mar. Sci. 57, 24-30.
- Seibel, B.A., Robison, B.H., and S.D.H. Haddock. 2005. Post-spawning egg-care by a squid. Nature 438, 929.
- Stabeno, P.J., Bond, N.A, Hermann, A.J., Kachel, N.B, Mordy, C.W, and J.E. Overland. 2004. Meteorology and oceanography of the Northern Gulf of Alaska. Cont. Shelf Res. 24, 859-897.
- Thompson, D.W.J., Wallace, J.M., 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. Geophys. Res. Letters 25, 1297–1300.
- Trenberth, K.E. and J.W. Hurrell, 1994. Decadal atmosphere–ocean variations in the Pacific. Climate Dynamics 9, 303–319.
- Vecchione, M. 1987. Juvenile ecology. In: Boyle, P.R. (Ed.), Cephalopod Life Cycles, Vol. 2: Comparative Reviews. Academic Press, London, pp. 61 - 84.
- Vecchione, M. and V.A. Hand. 1989. Digestive gland histology in paralarval squids (Cephalopoda:Loliginidae). Fish. Bull. 87, 995-1000.
- Vidal, E.A.G., DiMarco, P.F., Wormuth, J.H., and P.G. Lee. 2002. Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. Bull. Mar. Sci. 71, 915–931.
- Wolter, K. and M.S. Timlin. 1998. Measuring the strength of ENSO – how does 1997/98 rank? Weather 53, 315–324.
- Yamashita, Y. 1975. Octopus fisheries of Hokkaido. Prog. Rep. Squid Fish. Survey World, 5, 59-64.
- Yang, W.T., Hixon, R.F, Turk, P.E, Krejci, M.E., Hulet, W.H., and R.T. Hanlon. 1986. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. Fish. Bull. 84, 771-798.
- Young, R.E. and R.F. Harman. 1988. “Larva,” “paralarva” and “subadult” in cephalopod terminology. Malacologia 29(1): 201-207.

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Jorgensen, E.M. 2009. Identification guide to the squids and octopods of the eastern North Pacific and Bering Sea. Alaska Sea Grant Fairbanks Alaska. 99 pp.

Jorgensen, E.M., Strugnell, J., A.L. Allcock. 2010. Description and phylogenetic relationships of a new genus of octopus, *Sasakiopus* (Cephalopoda:Octopodidae), from the Bering Sea, with a redescription of *Sasakiopus salebrosus* (Sasaki, 1920) nov. comb. *J. Moll. Stud.* 76(1): 57-66.