

BOUNDARIES OF OPEN MARINE ECOSYSTEMS: AN APPLICATION TO THE PRIBILOF ARCHIPELAGO, SOUTHEAST BERING SEA

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Abstract. We applied ecosystem energetics and foraging theory to characterize the spatial extent of the Pribilof Archipelago ecosystem, located in the southeast Bering Sea. From an energetic perspective, an ecosystem is an area within which the predatory demand is in balance with the prey production. From a foraging perspective, an ecosystem boundary should at least include the foraging range of the species that live within it for a portion of their life cycle. The Pribilof Islands are densely populated by species that adopt a central place foraging strategy. Foraging theory predicts that the area traveled by central place foragers (CPF) should extend far enough so that their predatory demands are in balance with prey production. Thus, the spatial extent of an ecosystem, as defined by energetics and the foraging range of constituent species, will require a similar energy balance, and independent assessments should yield similar results. In this study, we compared the area of maximum energy balance, estimated with a food web model during the decade 1990–2000, with estimates of the foraging range of northern fur seals (the farthest traveling CPF in the Pribilof Islands community) obtained from the literature. From the food web simulations, we estimated that a circle of 100 nautical miles (NM), or 185.2 km, radius encloses the area of highest energy balance and lowest biomass import and that it represents a switch from a piscivorous-dominated (smaller areas) to a zooplanktivorous-dominated (larger areas) community. The distance from the breeding site to locations recorded at sea for lactating female fur seals, during the years 1995–1996, ranged from 5.0 to 172.2 NM (9.3–318.9 km), with a median of 97 NM (179.6 km). Thus, ~50% of the locations recorded for lactating fur seals occurred beyond the area of energy balance estimated by the model, indicating that additional factors can motivate their foraging extent. We propose that energetic constraints set the minimum extent of the Pribilof ecosystem, while the foraging distance of fur seals may indicate the maximum extent. In discussing these results, we highlight the limitations of current definitions of the spatial extent in ecosystems, when related to open oceanic environments, and discuss viable alternatives to characterize boundaries of aquatic systems that are not physically separated from adjacent areas. We believe that these arguments, though controversial, are very timely given the increased emphasis currently placed on the management and protection of entire marine ecosystems.

Key words: central place foraging; ecosystem boundary; ecosystem modeling; fur seal; mass balance; Pribilof Islands.

INTRODUCTION

The concept of an ecosystem is central in ecology, however many of its primary attributes, such as the spatial extent, are defined in such a way that limits practical applicability (Pickett and Cadenasso 2002). A common procedure in ecosystem modeling is that of

identifying the spatial extent of an ecosystem with physical features. For example, the spatial extent of terrestrial ecosystems can coincide with abrupt changes in topography (e.g., altitude, latitude, exposure), or be enclosed by conspicuous physical barriers, such as lakes, valleys, or canyons. However, similar criteria completely fail in marine environments, where most ecosystems have open boundaries, and where areas of contrasting hydrography (i.e., fronts) or abrupt topographical discontinuity (i.e., canyons, seamounts, shelf edges) have high productivity and are convergence zones for many different species (Olson et al. 1994, Allen et al. 2001; Genin, *in press*). Thus, while it is

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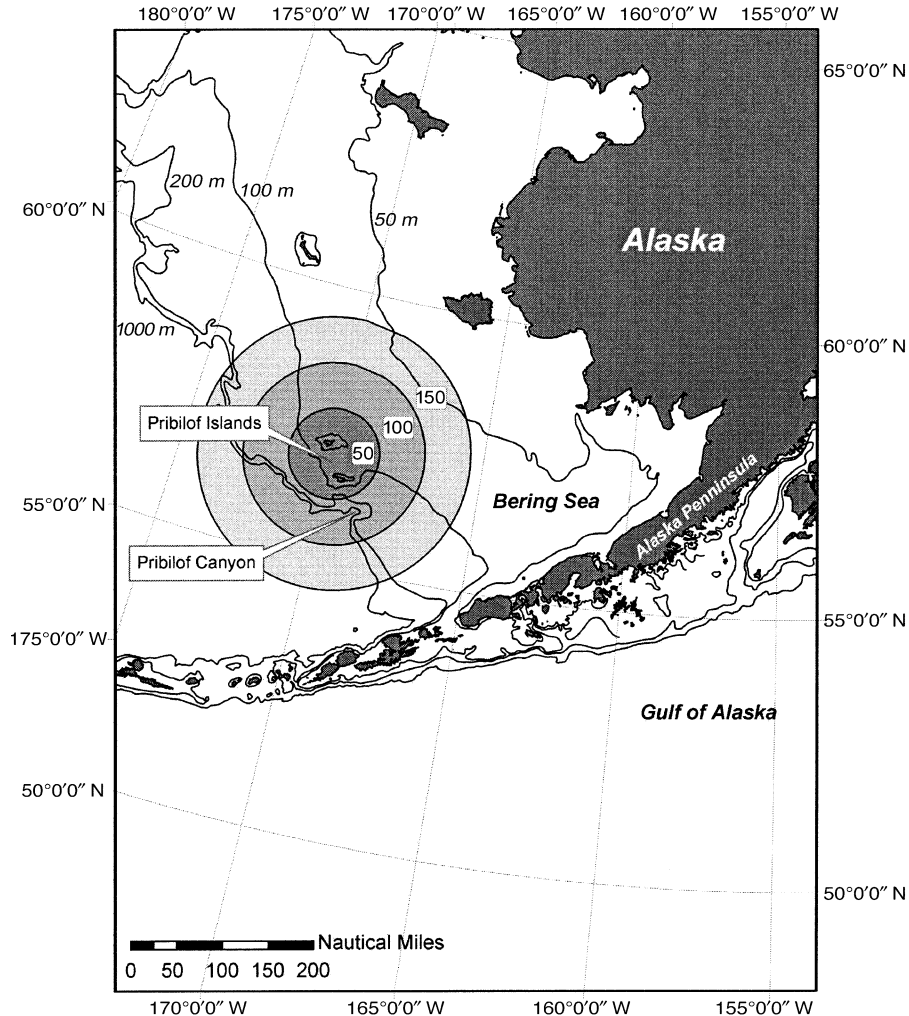


FIG 1. Map of the eastern Bering Sea, with the Pribilof Archipelago. Also shown are the simulated areas in the food web analysis around the Pribilof Archipelago. Each area has a circular shape with radius of 50, 100, and 150 NM (nautical miles; 92.6, 185.2, and 277.8 km, respectively) from a point located at approximately the center of the Pribilof Archipelago ($57^{\circ}00'00''$ N, $170^{\circ}00'00''$ W).

clear that the oceans are composed of a mosaic of many ecosystems (Longhurst 1998, Sherman and Duda 1999), there exists a lack of supporting theory to spatially identify them. This incapacity is particularly severe in light of current management practices that place greater emphasis at the ecosystem level (Griffis and Kimball 1996, Botsford et al. 1997, Mooney 1998). There is a need, particularly in marine ecology, to redefine the concept of an ecosystem boundary in such a way that it meets the distinctiveness of marine environments and can be readily applied for management purposes. Here, we attempt to characterize the spatial extent of the ecosystem around the Pribilof Archipelago in the southeastern Bering Sea. In the process, we highlight limitations of current definitions of ecosystem boundaries, when applied to oceanic systems, and discuss viable alternatives.

The Pribilof Archipelago, in the Bering Sea, is composed of two larger islands, St. Paul and St. George, and two smaller islands, Walrus and Otter Islands (Fig. 1). Despite the absence of defined physical boundaries, the area around the archipelago is ecologically bounded from the rest of the Bering Sea. A favorable combination of physical events makes it one of the most productive regions in the Bering Sea (Cooney and Coyle 1982, Coyle and Cooney 1993, Traynor and Smith 1996, Flint et al. 2002). High production in the water column permeates to higher trophic levels, in both benthic and pelagic systems, and contributes to the formation of a unique and abundant community of species. More than 2.5 million seabirds nest and breed on the islands during the summer months, including Thick-billed Murres (*Uria lomvia*), Common Murres (*Uria aalge*), Red-legged Kittiwakes (*Rissa brevirostris*),

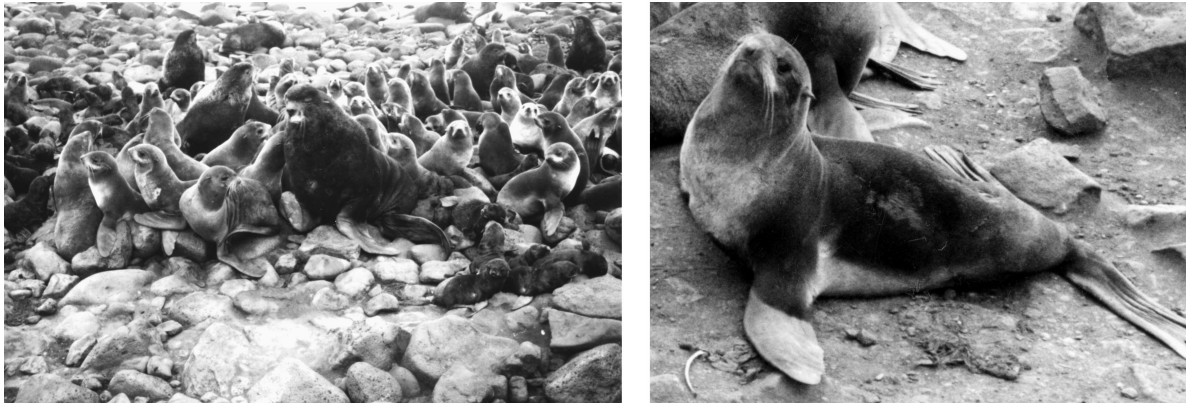


PLATE 1. Northern fur seal (*Callorhinus ursinus*) breeding colony on St. Paul Island, Alaska. The image on the left shows a typical breeding aggregation consisting of the larger adult male fur seals, smaller adult females, and newborn pups. The image on the right shows a close-up of an adult female northern fur seal. Photo credit: Bruce Robson.

Black-legged Kittiwakes (*Rissa tridactyla*), Tufted Puffins (*Fratercula cirrata*), and Horned Puffins (*Fratercula corniculata*) (Craighead and Oppenheim 1985). Approximately 72% of the worldwide population of northern fur seals (*Callorhinus ursinus*; see Plate 1) breeds on the islands from May through October (Gentry 1998; based on 1994 estimates). Walrus and Otter Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina richardsi*) (Ferrero et al. 2000).

To our knowledge, there are no studies that explicitly address the issue of ecosystem boundaries in marine environments, and only a few are available for terrestrial environments. A first characterization of ecosystem boundaries, based on energetic arguments, can be derived from the pioneering work of E. P. Odum: namely, an ecosystem is an area within which the energy flow is balanced (Odum 1969). Therefore, the problem of spatially defining an ecosystem, which is not physically bounded, is equivalent to finding the smallest area that can accommodate the energetic demands of all the species that reside within it, or the area of energy balance between prey production and predator consumption. Another indication of the spatial extent of an ecosystem can be derived from the foraging range of the species that reside within it for a portion of their life cycle. The Pribilof Islands are densely populated by species that adopt a central place foraging strategy, such as fur seals and sea birds. By definition, central place foragers (CPF) are animals that reside within a portion of a system (the central place), but feed at a greater distance (foraging range) and periodically come back to the central place to provision their offspring (Orlans and Pearson 1979). Theoretical (Hamilton et al. 1967, Orlans and Pearson 1979, Carins 1989), as well as empirical (Furness and Birkhead 1984, Lewis et al. 2001), studies suggest that the dispersal of CPF is motivated by intraspecific competition for food. This is particularly true of colonial CPF in marine environ-

ments (Boyd et al. 2002). Other species can also have an effect, either direct or indirect, on the relationship between the CPF and their foraging range (Schoener 1971, Furness and Birkhead 1984, Loughlin et al. 1987). Specifically, the foraging range should, at minimum, extend far enough such that the energetic demand of the CPF is fulfilled in conjunction with the production and consumption of the other species that reside within the same area. Such a definition of the minimum foraging range is the spatial analogy of the energetic definition of an ecosystem boundary derived from the Odum's work, in that both require a balance between community production and consumption. Therefore, the foraging range of a CPF community should also provide an indirect estimate of an ecosystem's spatial extent, and should yield similar results to those derived from energetic calculations. In our study, we developed a mass-balance food web model to characterize the ecosystem boundary of the Pribilof Archipelago for comparison with field observations of the foraging range of CPF. In examining the foraging range of CPF, we only considered that of fur seals in detail, since, based on current knowledge, they undertake the most distant foraging excursions in the community of CPF on the Pribilof Islands (cf. Schneider and Hunt 1982, Flint and Golovkin 2002, Robson et al. 2004).

METHODS

The energetic approach was carried out using a mass-balance food web model, while the foraging range of fur seals residing on the Pribilof Archipelago was available from previous studies (Loughlin et al. 1987, Robson 2001). Therefore, we expand on the description of the mass-balance model and its application to the area around the Pribilof Archipelago, and refer to Robson (2001) for information regarding the estimation of foraging range for fur seals during the period covered in the model.

Food web ecosystem model

The energy balance between predator demand and prey availability was estimated using a mass-balance analysis on different geographic scales, each representative of a progressively larger concentric region with the Pribilof Archipelago at its center. Our fundamental assumption was that the smallest system reaching energetic balance was representative of the ecosystem boundary. The model used to calculate the energy flow within a community was ECOPATH (Polovina 1984, Christensen and Pauly 1992, Christensen et al. 2000), distributed online by the Fisheries Centre at the University of British Columbia, British Columbia, Canada.⁶ Henceforth, we briefly reiterate the main characteristics of the model structure, and emphasize the major aspects of relevance to this study.

ECOPATH is a static mass-balance model that describes the flow of energy within a trophic web. Assuming a mass balance and a steady state, the production from a trophic group i , is partitioned as follows:

$$P_i = \sum_{j=1}^n Q_{ij} + \text{Ex}_i + L_i \quad (1)$$

where P_i indicates production of group i and is calculated as the product of the production to biomass ratio (P/B_i) and biomass (B_i),

$$P_i = (P/B_i)B_i.$$

Q_{ij} indicates the consumption by predator j of prey i and is calculated as the product of the fraction of prey i in the diet of predator j (diet composition, DC_{ij}), the predator consumption to biomass ratio (Q/B_j), and the predator biomass (B_j):

$$Q_{ij} = \text{DC}_{ij}(Q/B_j)B_j.$$

L_i indicates the amount of production of group i that is left over after predation (Q_{ij}) and export or fishing (Ex_i). In ECOPATH, L_i is calculated as the product between production and 1 minus the ecotrophic efficiency (EE_i):

$$L_i = (1 - \text{EE}_i) \times (P/B_i) \times B_i.$$

EE_i is the fraction of production that remains in the system (i.e., depredated) or is removed by fishing. By substitution into Eq. 1 and rearranging,

$$(P/B_i)B_i\text{EE}_i = \text{Ex}_i - \sum_{j=1}^n \text{DC}_{ji}(Q/B_j)B_j \quad (2)$$

where n is the total number of trophic groups included in the model.

In ECOPATH, the total mortality fraction of a group (Z) is composed of predation mortality ($M2$), fishing mortality (F), and "other mortality" ($M0$) due to diseases or senescence. For each group, the three sources of mortality are derived as follows:

$$M2_i = \frac{\sum_j Q_{ij}}{B_i} \quad (3)$$

$$F_i = \frac{H_i}{B_i} \quad (4)$$

where H_i is harvest on group i ,

$$M0_i = (1 - \text{EE}_i)Z_i. \quad (5)$$

Moreover, for each group, $M2$ is further partitioned among all predators that feed on it, in proportion to the quantity consumed (Christensen et al. 2000).

In this application, Eq. 2 is solved for EE , and the input parameters for each trophic group included in the food web are P/B (yr^{-1}), Q/B (yr^{-1}), B (Mg/km^2), and diet composition (DC) expressed as weight fractions. If group production does not exceed the amount predated upon or removed, then the EE will be less than or equal to 1. However, if production is lower than predation or removal, then the EE will be higher than 1, in proportion to the amount needed to fulfill the excess that is lost.

Trophic groups and parameters of the food web model

This analysis focused on the decade 1990–2000. A total of 39 trophic groups plus two detritus pools (benthic and pelagic) were included in the ECOPATH representation of the Pribilof Islands food web (Table 1). The characterization of a trophic group was based on different criteria, including the relative abundance, similarities in physiology, and diet among species. Trophic groups that can potentially follow a CPF feeding strategy were fur seals, Steller sea lions, Common and Thick-billed Murres, Red- and Black-legged Kittiwakes, Horned and Tufted Puffins, and Red-faced Cormorants. A detailed description of the parameterization of each trophic group (i.e., determination of biomass, P/B and Q/B , and diet) is presented in the Appendix.

Food web simulations

We estimated the energetic balance of three trophic webs, each representative of a species assemblage at increasing distances from the Pribilof Islands. The shape of each simulated area was assumed to be a circle, with radii of 50 nautical miles (NM) (92.6 km; 50-NM system), 100 NM (185.2 km; 100-NM system), and 150 NM (277.8 km; 150-NM system) from a point located at approximately the center of the Pribilof Archipelago ($57^{\circ}00.00'$ N, $170^{\circ}00.00'$ W; Fig. 1). For each trophic group, the balance between predator demand and prey availability was measured by the EE of the prey (i.e., $\text{EE} > 1$ indicated that more prey biomass was removed than produced). The total mortality rate (Z) of groups with $\text{EE} > 1$ (henceforth overtaxed groups) was partitioned among its component $M2$, F , and $M0$, using Eqs. 3, 4, and 5, respectively. Moreover,

⁶ URL: www.ecopath.org

TABLE 1. List of trophic groups included in food web analysis, with respective trophic level (TL), production to biomass rate (P/B , yr^{-1}), consumption to biomass rate (Q/B , yr^{-1}), and biomass (B , Mg/km^2).

Trophic group	Description	TL	P/B	Q/B	Biomass (Mg/km^2)		
					50 NM	100 NM	150 NM
Phytoplankton	diatoms: <i>Thalassiosira</i> spp., <i>Chaetoceros</i> spp.	1	148.10	...	36.22	36.22	36.22
Pelagic detritus		1
Benthic detritus		1
Protozoa	phytoflagellates, semi-autotrophic	1.5	72.00	144.00	10.00	10.00	10.00
Bacterioplankton		2	150.00	300.00	11.08	11.08	11.08
Crabs	<i>Chionoecetes opilio</i> , <i>Paralithodes</i> spp.	2	1.16	5.09	1.78	1.48	1.27
Infauna	bivalves, polychaetes, benthic amphipods	2	1.97	12.00	22.45	17.99	13.83
Mesozooplankton	copepods: <i>Calanus marshallae</i> , <i>Neocalanus</i> spp.	2.2	9.00	27.00	25.74	25.74	25.74
Microzooplankton	ciliates, nauplii, trocophores, veligers	2.2	9.00	27.00	13.26	13.26	13.26
Macrozooplankton	euphausiids: <i>Thysanoessa</i> spp., <i>Euphausia pacifica</i>	2.4	2.70	9.00	16.60	16.60	16.60
Epibenthic	seastars, sponges, pagurids	2.6	1.57	5.78	6.99	5.81	4.39
Small jellies	hydromedusae, larvaceans: <i>Oikopleura</i>	2.6	7.00	23.00	50.00	50.00	50.00
Agonidae	<i>Podothecus acipenserinus</i> , <i>Sarritor frenatus</i>	3.1	0.40	2.56	0.13	0.07	0.05
Small flatfishes	<i>Lepidosepta polyxystra</i> , <i>Limanda aspera</i>	3.1	0.40	2.97	8.12	7.05	5.47
Chaetognaths	<i>Sagitta elegans</i>	3.2	1.35	3.87	25.05	25.05	25.05
Forage fishes	<i>Clupea pallasii</i> , <i>Mallotus villosus</i>	3.3	1.00	7.00	0.01	5.00	10.00
Liparidae	<i>Careproctus</i> spp.	3.4	0.60	2.49	<0.01	0.01	0.02
Mesopelagic fishes	<i>Bathylagus</i> , <i>Leuroglossus</i> , <i>Stenobranchius</i>	3.4	1.57	7.83	<0.01	1.48	2.20
Zoarcidae	<i>Bothrocara brunneum</i> , <i>Lycodes</i> spp.	3.4	0.60	2.49	0.06	0.23	0.28
Juvenile gadids	<i>Theragra chalcogramma</i> , <i>Gadus macrocephalus</i>	3.5	6.97	20.23	1.37	1.40	1.34
Rockfishes	<i>Sebastes alutus</i> , <i>S. borealis</i> , <i>S. alascanus</i>	3.5	0.16	3.10	0.08	1.24	2.77
Grenadiers	<i>Albatrossia pectoralis</i> , <i>Coryphaenoides cinereus</i>	3.6	0.40	2.49	<0.01	12.87	13.83
Adult pollock	<i>Theragra chalcogramma</i>	3.7	0.50	4.16	15.60	11.66	8.56
Large jellies	<i>Chrysaora melanaster</i>	3.8	1.50	3.00	15.00	16.00	19.00
Sculpins	<i>Hemilepidotus</i> spp., <i>Hemitripterus bolini</i>	3.8	0.40	2.56	0.98	0.61	0.48
Squids	<i>Berryteuthis magister</i> and <i>Gonatus</i> spp.	3.8	3.20	10.67	1.00	2.00	3.50
Skates	<i>Bathyraja</i> spp.	3.9	0.40	2.56	1.04	1.03	1.11
Thick-billed Murres	<i>Uria lomvia</i>	3.9	0.97	33.31	0.05	0.01	0.01
Adult cod	<i>Gadus macrocephalus</i>	4	0.50	4.16	2.42	1.86	1.43
Large flatfishes	<i>Atherestes stomias</i> , <i>Hippoglossus stenolepis</i>	4.1	0.40	2.92	2.83	2.99	3.03
Black-legged Kittiwakes	<i>Rissa tridactyla</i>	4.2	0.80	32.15	<0.01	<0.01	<0.01
Steller sea lions	<i>Eumetopias jubatus</i>	4.2	0.06	27.04	<0.01	<0.01	<0.01
Puffins	<i>Fratercula</i> spp.	4.3	0.80	23.50	<0.01	<0.01	<0.01
Red-legged Kittiwakes	<i>Rissa brevirostris</i>	4.3	0.80	20.72	<0.01	<0.01	<0.01
Sablefish	<i>Anoplopoma fimbria</i>	4.3	0.40	2.49	<0.01	0.13	0.20
Common Murre	<i>Uria aalge</i>	4.4	1.09	29.14	0.02	<0.01	<0.01
Harbor seals	<i>Phoca vitulina richardsi</i>	4.4	0.06	19.44	<0.01	<0.01	<0.01
Red-faced Cormorant	<i>Phalacrocorax urile</i>	4.4	0.80	18.89	<0.01	<0.01	<0.01
Dall porpoises	<i>Phocoenoides dalli</i>	4.5	0.40	2.56	<0.01	0.07	0.17
Fur seals	<i>Callorhinus ursinus</i>	4.6	0.06	19.96	1.30	0.32	0.14
Sleeper sharks	<i>Somniosus pacificus</i>	4.6	0.06	28.01	<0.01	<0.01	<0.01

Notes: The biomass is shown for each system (50 NM, 100 NM, 150 NM) simulated (NM = nautical miles; 1 NM = 1.852 km).

to evaluate the deficit of production of the overtaxed group, we calculated the amount of biomass needed to balance the predator-prey trophic link: $P_{\text{req}} = EE \times B \times (P/B)$. The difference between the realized (P) and

the required production (P_{req}) is indicative of the amount of extra biomass that is needed from outside the system, in order to balance the food web (i.e., the biomass import).

TABLE 2. Factors used to determine the parameter distribution to estimate EB error.

Group	Parameter range			
	Biomass	P/B	Q/B	Diet
Phytoplankton	0.1	0.1
Pelagic detritus
Benthic detritus
Protozoa	0.5	0.3	0.3	0.3
Bacterioplankton	0.5	0.3	0.3	0.3
Crabs	0.1	0.4	0.4	0.3
Infauna	0.8	0.5	0.6	0.3
Mesozooplankton	0.1	0.2	0.2	0.3
Microzooplankton	0.8	0.3	0.3	0.3
Macrozooplankton	0.5	0.2	0.2	0.3
Epibenthic	0.1	0.4	0.4	0.3
Small jellies	0.5	0.4	0.4	0.3
Agonidae	0.1	0.4	0.4	0.3
Small flatfishes	0.1	0.4	0.4	0.3
Chaetognaths	0.1	0.2	0.2	0.3
Forage fishes	0.8	0.4	0.4	0.3
Liparidae	0.1	0.4	0.4	0.3
Mesopelagic fishes	0.8	0.4	0.4	0.3
Zoarcidae	0.8	0.4	0.4	0.3
Juvenile gadids	0.1	0.2	0.2	0.1
Rockfishes	0.1	0.4	0.4	0.3
Grenadiers	0.1	0.4	0.4	0.3
Adult pollock	0.1	0.2	0.2	0.3
Large jellies	0.1	0.4	0.4	0.3
Sculpins	0.1	0.4	0.4	0.3
Squids	0.8	0.5	0.6	0.3
Skates	0.1	0.4	0.4	0.3
Thick-billed Murres	0.1	0.4	0.4	0.3
Adult cod	0.1	0.4	0.4	0.3
Large flatfishes	0.1	0.4	0.4	0.3
Black-legged Kittiwakes	0.1	0.4	0.4	0.3
Steller sea lions	0.1	0.4	0.4	0.3
Puffins	0.1	0.4	0.4	0.3
Red-legged Kittiwakes	0.1	0.4	0.4	0.3
Sablefish	0.1	0.4	0.4	0.3
Common Murre	0.1	0.4	0.4	0.3
Harbor seals	0.1	0.4	0.4	0.3
Red-faced Cormorant	0.1	0.4	0.4	0.3
Dall porpoises	0.1	0.4	0.4	0.3
Fur seals	0.1	0.4	0.4	0.3
Sleeper sharks	0.1	0.4	0.4	0.3

Note: The sampling range around each parameter is drawn from a uniform distribution whose upper and lower extremes are specified by the initial parameter estimate multiplied by the factors listed in the table.

To evaluate the degree of energy balance at an overall ecosystem level, we defined a unique metric, EB, from the sum of the EEs of the overtaxed groups only:

$$EB = \sum_{k=1}^m EE_k \quad (6)$$

where m is the number of overtaxed groups within a simulated system. Using a Monte Carlo resampling approach, we assessed the error of EB estimates from 1000 model runs generated by random combinations of input parameters sampled from prespecified uniform distributions (Table 2). The parameter distributions used in the error analysis were representative of the uncertainty in the initial parameter estimate. In estimating the error around EB, the EE of fishes in the family Zoarcidae was set to 0.9 under the assumption

that the unbalance of this trophic group was the result of low catchability rather than excess predation or removal (see *Discussion*). Differences between estimated EB were statistically tested by ANOVA on log-transformed data (EB were not normally distributed). If the main factor effect was found significant at 95% confidence, we proceeded to detect group mean differences using Bonferroni-adjusted pairwise comparisons.

RESULTS

Groups that had the greatest change in biomass as the boundary was increased from the 50- to the 150-NM system were the CPF assemblage; the species typically found along the slope community and the forage fish assemblage. CPF biomass, primarily driven by fur seals, decreased by approximately one order of magnitude, corresponding to the increase in area between the 50- and the 150-NM system (Table 1). In contrast, taxa generally associated with the slope community increased in biomass by several orders of magnitude, which would be expected since the slope area was excluded from the 50-NM system. The dominant slope groups were grenadiers and mesopelagic fishes, with a lower contribution by sleeper sharks, liparids, sablefish and rockfish (Table 1). Forage fish also increased in biomass over larger boundaries, but their center of distribution was to the north and east of the Pribilof Islands rather than along the slope.

Based on their diet, fur seals and sleeper sharks had the highest trophic level (TL = 4.6) of all the groups simulated. Within the 50-NM system, fur seals largely dominated the biomass and total food consumption of CPF; seabird consumption summed to $2.26 \text{ Mg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$, consumption by other marine mammals summed to $0.08 \text{ Mg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ and fur seal consumption was $26.00 \text{ Mg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$. If fur seal consumption was standardized for the loss of energy among trophic levels (transfer efficiency), then it would be the largest of all

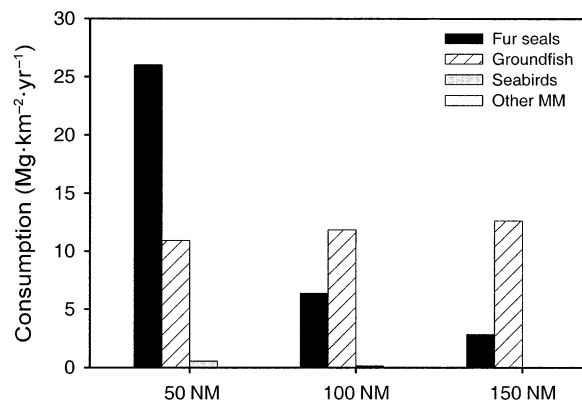


FIG. 2. Food consumption ($\text{Mg}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$) of all groups with trophic level > 4, resulting from a food web analysis for each of the three simulated systems (50 NM, 100 NM, and 150 NM). "Other MM" refers to marine mammals other than fur seals.

TABLE 3. Results of ecotrophic efficiency (EE) for all trophic groups and ecosystem areas (50 NM, 100 NM, and 150 NM) simulated.

Group name	Ecotrophic efficiency		
	50 NM	100 NM	150 NM
Phytoplankton	0.41	0.41	0.41
Pelagic detritus	0.60	0.60	0.61
Benthic detritus	0.11	0.09	0.08
Protozoa	0.86	0.86	0.86
Bacterioplankton	0.19	0.19	0.19
Crabs	1.24	1.40	1.52
Infauna	0.90	0.90	0.90
Mesozooplankton	0.60	0.74	0.88
Microzooplankton	2.42	2.42	2.42
Macrozooplankton	1.55	1.80	2.14
Epibenthic	0.63	1.42	1.97
Small jellies	0.01	0.01	0.02
Agonidae	3.44	2.11	2.68
Small flatfishes	0.36	0.28	0.46
Chaetognaths	0.14	0.14	0.14
Forage fishes	1387.31	1.14	0.61
Liparidae	0.16	0.16	0.16
Mesopelagic fishes	4198.11	3.67	2.82
Zoarcidae	16.29	44.95	41.14
Juvenile gadids	3.31	3.23	3.68
Rockfishes	0.22	0.02	0.02
Grenadiers	0.62	0.62	0.62
Adult pollock	3.09	2.23	2.45
Large jellies	0.00	0.00	0.00
Sculpins	0.69	0.71	0.70
Squids	4.89	2.23	1.22
Skates	0.04	0.06	0.03
Thick-billed Murres	0.00	0.00	0.00
Adult cod	0.66	0.35	0.27
Large flatfishes	0.84	0.74	0.71
Black-legged Kittiwakes	0.00	0.00	0.00
Steller sea lions	0.00	0.00	0.00
Puffins	0.00	0.00	0.00
Red-legged Kittiwakes	0.00	0.00	0.00
Sablefish	0.00	0.00	0.00
Common Murre	0.00	0.00	0.00
Harbor seals	0.00	0.00	0.00
Red-faced Cormorant	0.00	0.00	0.00
Dall porpoises	0.00	0.00	0.00
Fur seals	0.03	0.03	0.03
Sleeper sharks	0.00	0.00	0.00

Note: Groups with EE > 1 are in boldface. NM = nautical mile. 1 NM = 1.852 km.

groups simulated in the 50-NM system. Within the 50-NM boundary, fur seal consumption also dominated among groups with TL > 4, which besides the CPF included sleeper sharks, large flatfishes, harbor seals, Dall's porpoises, and sablefish (Fig. 2). However, as the area was increased from the 50- to 150-NM system, fur seal and CPF food consumption decreased proportionally and became lower than that of non-CPF groups (Fig. 2).

Within the 50-NM system, many species were in energetic imbalance, as suggested by their high EE (Table 3). Trophic groups with highest EE were mesopelagic fish (EE = 4198.11) and shelf forage fish (EE = 1387.31). Other overtaxed groups were zoarcidae, adult pollock, agonids, juvenile gadids, squids, macrozooplankton, microzooplankton, and crabs (Table 3). Fur seals caused more than 76% and 42% of

the total predation mortality of the mesopelagic and shelf forage fishes, respectively (Fig. 3). Increasing the system boundary from 50 to 100 NM (from 92.6 to 185.2 km) substantially reduced the energetic imbalance of mesopelagic and shelf forage fishes. Their respective EE dropped to 3.67 and 1.14 (Table 3). Other overtaxed groups that had a decrease in EE in the 100-NM system were adult pollock (3.09 to 2.23), squids (4.89 to 2.23), agonids (3.44 to 2.11), and juvenile gadids (3.31 to 3.23). Some overtaxed groups further increased their EE from the 50- to the 100-NM system. These were zoarcids (from 16.29 to 44.95), macrozooplankton (from 1.55 to 1.80), crabs (from 1.24 to 1.40), and epibenthic fauna (from 0.63 to 1.42) (Table 3). A further increase of the system boundary, from the 100- to 150-NM system resulted in a further energetic balance of mesopelagic fishes, forage fishes, and squids, albeit to a much smaller degree than that observed from the 50- to the 100-NM system (Table 3). However, a larger number of trophic groups further increased their EE in the 150-NM simulation with respect to the 100-NM simulation. These were adult pollock, agonids, macrozooplankton, crabs, epibenthic, and juvenile gadids. Zoarcids, which had initially increased their EE from the 50- to the 100-NM systems, decreased in their EE for the 150-NM system (Table 3).

The estimated average EB for each system, resulting from the Monte Carlo model run under parameter uncertainty, was 8349.49 (1 SD = 5252.89) for the 50-NM system, 22.57 (6.42) for the 100-NM system and 25.34 (7.14) for the 150-NM system (Fig. 4). All EB values were significantly different from each other (Bonferroni, $P < 0.001$). It is important to note that none of the simulated areas reached a balance between prey production and predator consumption. From the model simulations it appeared that the 100-NM system required the lowest import in order to reach the balance, while the 150-NM system required the highest (Table 4). The import of zooplankton biomass (including micro- and macro-zooplankton) increased with the increase of the ecosystem boundary, while the import of fish biomass (including pollock, forage, mesopelagic, juvenile gadids, and squids) decreased (Table 4). This pattern indicates that there was an excess of piscivory in the 50-NM system and an excess of zooplanktivory in the 150-NM system.

DISCUSSION

Our analysis clearly showed that within 50 NM (92.6 km) of the center of the Pribilof Islands the predatory demand is unsustainable, given the available prey biomass and production. However, an enlargement of the ecosystem boundary can bring the predator community toward a better energetic balance with their prey. This was indicated by a progressive reduction of the EE of overtaxed groups (Table 3), by a reduction of whole-system EB (Fig. 4), and by a reduction of the required biomass import (Table 4). Key prey species in defining

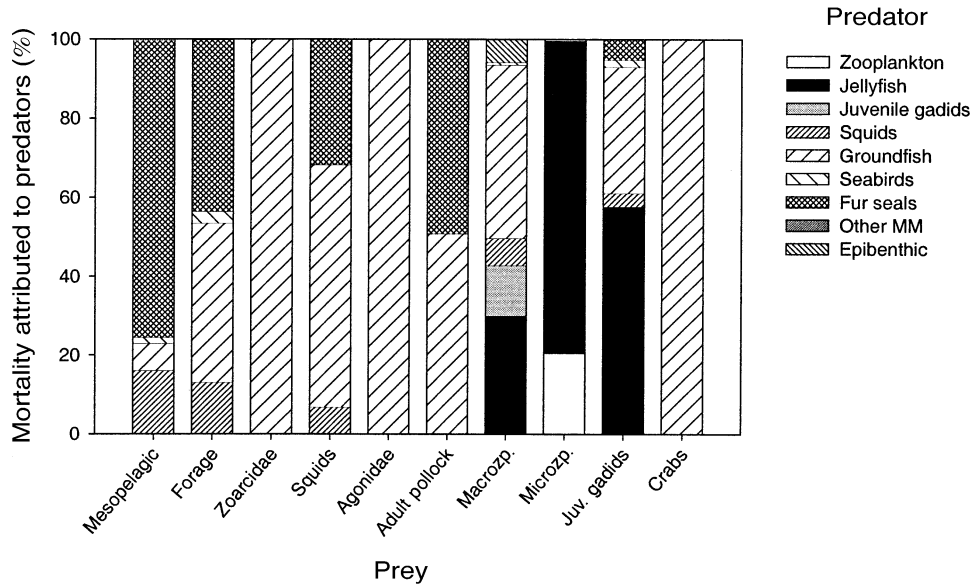


FIG. 3. Partitioning of predation mortality (M_2) of all groups with $EE > 1$ in the 50-NM ecosystem simulation. Prey groups are indicated in the x -axis, and predator groups are identified in the key (zooplankton = micro-, meso-, and macrozooplankton; other MM = marine mammals other than fur seals). Abbreviations for x -axis: macrozop. = macrozooplankton; microzop. = microzooplankton; juv. gadids = juvenile gadids.

the community energetic balance were the mesopelagic fishes and shelf forage fishes, and the key predator species were the CPF, in particular, fur seals. Both a dispersion of fur seal predation over a broader area and an inclusion of more forage and mesopelagic fish biomass within the modeled area moved the system toward energetic balance with boundary enlargement. About 32% of the fur seal diet depended on shelf forage and mesopelagic fishes, which were almost completely excluded within the 50-NM boundary system. Mesopelagic fishes tended to be more abundant toward the shelf break (Sinclair et al. 1999, Sinclair and Stabeno 2002). Likewise, shelf-forage species, other than juvenile gad-

ids, were more abundant toward the northern and eastern part of the shelf (Brodeur et al. 1999, Nebenzahl and Goddard 2000).

The achievement of energetic balance between predator demand and prey availability, however, did not progress steadily as the system increased its boundary, as shown by some of the metrics developed in this study. In fact, the system EB and biomass import reached a minimum at the 100-NM area. Also, the type of import switched from primarily fish (50-NM system) to primarily zooplankton (150-NM system), indicating that the 100-NM area was in balance between piscivory (high in the 50-NM system) and zooplanktivory (high in the 150-NM system). Thus, while the Pribilof system gained energetic balance upon an initial boundary enlargement (from 50 to 100 NM), a further enlargement did not result in more stability, but rather brought the

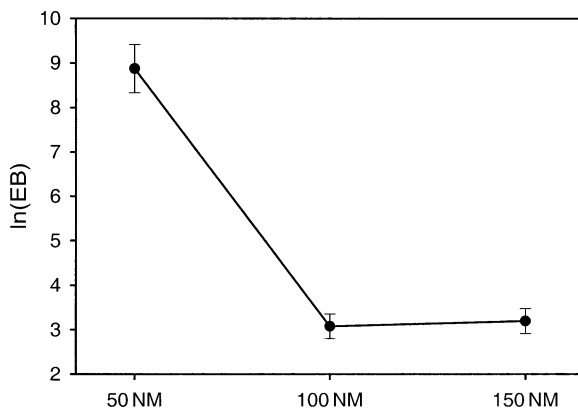


FIG. 4. Natural logarithm of average energy balance (EB) from 1000 model simulations of each system, based on random combinations of input parameters sampled from pre-specified uniform distributions (see Table 2). Error bars are $\pm 1SD$.

TABLE 4. Estimates of biomass import ($Mg \cdot km^{-2} \cdot yr^{-1}$) for each overtaxed trophic group and simulated ecosystem area.

Group name	50 NM	100 NM	150 NM
Adult pollock	16.27	7.19	6.21
Zooplankton	194.40	205.69	220.80
All forage	49.41	36.13	33.73
All epibenthic	0.50	4.62	7.55
Agonidae	0.12	0.03	0.03
Sum	260.69	253.66	268.31

Notes: Zooplankton = micro- and macrozooplankton; all forage = mesopelagic, forage, juvenile gadids, and squids; all epibenthic = epibenthic and crabs. Zoarcidae, although overtaxed, were not included in the calculation of biomass import. NM = nautical mile. 1 NM = 1.852 km.

system toward new imbalances and an excess of zooplanktivory. These results indicate that the Pribilof ecosystem boundary cannot grow indefinitely, further corroborating the assumption of a functional distinction of the Pribilof area from the rest of the Eastern Bering Sea. We therefore conclude that, during the decade 1990–2000, the 100-NM simulation yielded a more realistic representation of a minimum area required for a balanced trophic web than both the 50-NM and the 150-NM simulations.

Within the proposed area of energy balance, however, there were still several energetically unbalanced groups. The majority of them were either planktonic organisms, such as macrozooplankton, microzooplankton and juvenile gadids, or migrating demersal and forage fish, such as age 1+ pollock. One other group that did not fit in either category and yet was unbalanced was zoarcid fishes (i.e., eelpouts), with the highest EE among all groups in the 100-NM system (Table 3). With respect to planktonic or migrating demersal and forage fish, the unbalances could actually reflect a net import of biomass from adjacent areas into the Pribilof ecosystem. Biomass import was not included in our model due to the lack of studies that could support any reasonable estimate of such a quantity. However, we were able to estimate that the amount of import required to balance each simulated food web minimized at the 100-NM area (Table 4). The role of net biomass import in the characterization of open-boundary marine ecosystems is considered in the *Discussion*.

With respect to zoarcids, the imbalance in each of the simulated Pribilof areas could reflect a low catchability of the sampling gear for this taxon. In the eastern Bering Sea, there is no direct fishery on zoarcids and consequently there is little incentive to improve their biomass estimates. However, zoarcid fishes play an important role both as predator and prey, especially in communities associated with the shelf edge, where their abundance typically peaks. In the Pribilof ecosystem, for example, zoarcids occurred in the diet of many abundant demersal fish, such as grenadiers, adult pollock, large flatfishes, and skates (Appendix; Brodeur and Livingston 1998), and yet their biomass, estimated from trawl survey, was not sufficient to sustain the predatory demand by at least one order of magnitude. Similar results were obtained for the entire Bering Sea ecosystem (Aydin et al. 2002) and the Northern California Current ecosystem (Field et al. 2001).

The dominant CPF species in the model, northern fur seals, did not limit their foraging to the minimum area required (100 NM) for energetic balance. During foraging trips ($N = 119$) made by lactating fur seals ($N = 97$) in 1995–1996, the median distance from the breeding site to locations recorded at sea was 97.0 NM (179.6 km) on average (range 5.0 to 172.2 NM (9.3 to 318.9 km), $1\text{ SD} = 32.1\text{ NM}$ (59.4 km); Robson 2001). Some of this discrepancy is attributable to the difference between distance measurements made from in-

dividual breeding sites and the central point used for the 50-, 100-, and 150-NM radii (92.6, 185.2, and 277.8 km) in the ECOPATH model. However, the magnitude of this difference was small (mean = 16.7 NM [30.9 km], range = 0.4–29.1 NM [0.7–53.9 km], $1\text{ SD} = 8.8\text{ NM}$ [16.3 km]) relative to the distance females traveled from the islands. Furthermore, the maximum distance recorded for the same foraging trips exceeded 240 NM (444.5 km) with a mean of 130.4 NM (241.5 km) (Robson 2001). Thus, ~50% of the at-sea locations recorded for satellite-tracked females in 1995–1996 were beyond the minimum area of energy balance (100 NM [185.2 km]) estimated in our study. In addition, male fur seals, which constitute ~30% of the non-pup biomass of the Pribilof Island population (Lander 1981), travel further from the breeding islands than lactating fur seals (Loughlin et al. 1999; National Marine Fisheries Service, *unpublished data*). Clearly, additional factors, besides that of reaching an area with sufficient energy balance, motivate the dispersal of fur seals during their foraging trips. Below we list and discuss some of these factors as they can provide important insight into the actual spatial extent required for energetic balance within an ecosystem.

Location, density, and species composition of prey should influence the foraging range of fur seals. The ECOPATH model shows that fur seals exert a massive predatory impact on the Pribilof system. This result is in accordance with predictions made more than 30 years ago by Laevastu et al. (1976) for the Bering Sea. Similarly, Boyd et al. (2002) and Boyd (2002) found that lactating Antarctic fur seals (*Arctocephalus gazella*) likely have a dominant role among top predators foraging in waters surrounding South Georgia. Female Antarctic fur seals consume one-tenth of the mean density of krill on average and could eat almost all of the krill present in regions of intense foraging. Given their large impact, fur seals and other marine predators likely feed on high-density aggregations of prey in order to maximize their net energy gain relative to foraging costs. The ECOPATH model, however, assumes a uniform spatial and temporal distribution of biomass within each modeled area, while, in reality, production is pulsed and prey are patchily distributed (e.g., Swartzman and Hunt 2000). In addition, a greater proportion of high-density patches might be located outside a given area of energy balance in a particular year or season. In a patchy prey environment, an optimal central place foraging strategy may be to travel directly to an area of high prey concentration where predators search randomly for prey, thereby increasing the encounter rate of prey patches per unit of area searched (Orians and Pearson 1979, Schoener 1971). Linear, directed movements away from colonies have been documented in several fur seal species (Boyd et al. 1998, Bonadonna et al. 2001, Robson et al. 2004) and may facilitate the ability of individual animals to return to productive foraging areas. While such directed movements away

from the central place may reduce predator impact due to the effect of geometric spreading, they are also likely to increase the relative dispersal distance if predictable areas of high prey density are located further from the breeding colony in some years.

In addition to prey patchiness, fur seal dispersal may be regulated by a preference for larger or more nutritional forage fishes (e.g., mesopelagic species, herring, capelin, or eulachon), or alternatively by a preference for adult over juvenile pollock. Both the forage species and adult pollock have higher energy and fatty acid content than age-0 pollock (Van Pelt et al. 1997, Cianelli et al. 2002), and are less abundant than age-0 pollock within the 50-NM boundary. Recent stable isotope analyses indicate that during the fall lactating fur seals eat prey at trophic levels equivalent to 2–4-yr-old walleye pollock and small Pacific herring (Kurle and Worthy 2001, 2002). While isotopic ratios did not indicate a diet dominated by juvenile pollock, a combined diet of older pollock mixed with juvenile pollock and other species (e.g., squid) would fall within the range of nitrogen isotope values observed (Kurle and Worthy 2002). These studies, in conjunction with our ECOPATH simulations, support theoretical predictions that larger or more nutritious prey are more likely to be favored as foraging distance increases (Schoener 1971, Orians and Pearson 1979).

In considering the results of this study, it is important to take into account the degree of uncertainty that went into parameterization of the ECOPATH model (Appendix). The relative level of uncertainty of the model parameters is proportional to the coefficients shown in Table 2. In general, the biomass of the forage components, including squids, forage fishes, and mesopelagic fishes, was the most uncertain, unlike those of groundfish and CPF species. Also, the diet of fur seals was influenced by information from scat collections; hence, it might over-represent prey eaten during the last meals of a foraging trip. Although the assumptions made in parameterizing the food model can certainly influence the energy balance of a predator–prey trophic link, the estimated pattern of the EB metric across the three simulated areas, on which we based our assessment of highest energy balance, was robust to a wide range of uncertainty. As more precise data become available for constituent species in the Pribilof ecosystem, examining the sensitivity of energetic balance at a broader range, finer scale of spatial resolution, and different (i.e., not circular) ecosystem shapes could refine our analysis.

Our study and the methodology applied bring to light a number of general issues regarding the spatial characterization of the shape and the extent of open boundary marine ecosystems. The shape of an ecosystem should reflect the distribution of energy production within it. The foraging range of CPF can be an indirect estimate of the ecosystem shape, as typically CPF spend more time foraging in areas of higher prey den-

sity. Around the Pribilof Islands, for example, fur seals forage extensively in the outer shelf and shelf break domain of the Bering Sea (Robson et al. 2004). The primary axis of energy production for the southeastern Bering Sea, also known as the “green belt” (Springer et al. 1996), is oriented in the same direction. Computational convenience forced us to assume food webs with circular shapes, while in reality the shape of the Pribilof ecosystem may resemble an ellipse with the longest axis oriented along the Bering Sea shelf edge. With regard to its spatial extent, an ecosystem should be large enough to reach a balance between energy production and consumption. However, for open boundary marine ecosystems the requirement of energy balance is unattainable without import or export of biomass. Nonetheless, it is important that within the proposed ecosystem area the import is minimized compared to larger or smaller areas, and that the amount of energy imported be considerably less than the total throughput of energy within the system. In our simulations, the biomass import in the 100-NM area was similar to the amount of annual mesozooplankton production, and ~5% of the annual primary production. Mass-balance food web models (e.g., ECOPATH) are useful tools to assess the ecosystem energy budget, provided that one takes into account the limitations of such an analytical approach, the uniform distribution of biomass and the uncertainty of the species parameters being the most important. Because of this limitation, we propose that the area of energy balance, estimated from mass-balance modeling, sets the minimum spatial extent of an ecosystem, while the foraging range of the most distant CPF may indicate the maximum extent.

To our knowledge, this is the first study that attempts to spatially characterize open marine ecosystems. This issue is particularly timely in marine ecology given the importance of managing marine resources at an ecosystem level (Botsford et al. 1997, Mooney 1998, Sinclair and Valdimarsson 2003), particularly those of the Bering Sea, which are heavily utilized by humans (Witherell et al. 2000, Jurado-Molina and Livingston 2002). A practical and immediate application for this study is in setting the boundary of marine protected areas (or special fisheries management areas) to protect CPF and the resources they depend on (Sjöberg and Ball 2000). This is a relevant topic for the Bering Sea and Gulf of Alaska regions where local populations of pinnipeds and seabirds have been declining during the last 20–30 yr (National Research Council 1996, Loughlin and York 2000).

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APPENDIX

An explanation of the calculation of the ECOPATH parameters is presented in ESA's Electronic Data Archive: *Ecological Archives* A014-019-A1.