MODEL ESTIMATION OF ENERGY FLOW IN OREGON COASTAL SEABIRD POPULATIONS

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Birds are a conspicuous element of marine ecosystems, especially during the breeding season when they aggregate in dense colonies on oceanic islands or along rocky shorelines. Although their populations may number in the millions in areas of coastal upwelling, little effort has been made to assess their importance in energy transfer or nutrient cycling in these systems. Several studies (e.g., Ashmole and Ashmole 1967, Sanger 1972) have considered seabird dynamics in open ocean regions. Swartz (1966) attempted to analyze biomass flux in the food web of a coastal system in Alaska, but documentation of the caloric and chemical impacts of the birds was thwarted by a lack of information on energy balances. Information on the bioenergetics of free-ranging marine birds is virtually impossible to obtain directly, but it can be approximated indirectly. For example, a simulation model which estimates energy demands of populations from basic avian life history information may be used (Wiens and Innis 1974). Here we employ this modeling approach to explore the bioenergetics and patterns of prey consumption of four species of marine birds along the Oregon coast. The species considered are the Sooty Shearwater (*Puffinus griseus*), Leach's Storm-Petrel (*Oceanodroma leucorhoa*), Brandt's Cormorant (*Phalacrocorax penicillatus*), and Common Murre (*Uria aalge*).

METHODS AND DATA BASE

GENERAL BIOLOGY

Of the four species considered here, the Brandt's Cormorant and Common Murre commonly breed in suitable locations along the Oregon coast and winter at varying distances from the shore. Leach's Storm-Petrels breed along the coast, but forage well offshore and disperse far offshore and south in winter. Sooty Shearwaters occur primarily as spring and fall migrants, breeding in the southern hemisphere (Gabrielson and Jewett 1940, Palmer 1962). Several other species (Tufted Puffin, *Lunda cirrhata*; Pigeon Guillemot, *Cepphus columba*; Pelagic Cormorant, *Phalacrocorax pelagicus*; and several gulls, *Larus* spp.) are also members of the same general foraging "guild" (Root 1967) in some locations (Scott 1973). They are not considered here either because of their generally low abundance or because estimates of their population densities were not available.

The three breeding species nest on offshore stacks or steep cliff faces. The occurrence of breeding birds at sea along the Oregon coast during the summer is dictated largely by the availability of suitable nesting sites and the distance which individuals range from a nesting area during the day. During winter, when they no longer are tied to the nesting rocks, the birds disperse into areas not occupied during the breeding season. Murres disperse more uniformly along the coast and are found farther offshore and over a larger area than Brandt's Cormorants, which tend to aggregate in protected bays and estuaries during the winter and are observed less frequently offshore than during the summer. These seasonal patterns in species' distributions are diagramed in figure 1. The spring and fall distributions of shearwaters along the coast are similar in area but differ markedly in the numbers of birds involved (see below).

The biological features of these four species which we used as input variables for our model are listed in table 1. Our analysis considered seabird dynamics over the entire Oregon coast, from the mouth of the Columbia River to the California border. While many of the values in table 1 were obtained from studies of more limited geographic scope (Scott 1973, unpubl. data), the estimates of breeding population density were made for the entire region. During the 1964–1973 breeding seasons, personnel of the U.S. Fish and Wildlife Service conducted aerial counts of individuals in all known breeding colonies along the Oregon coast. The density estimates of breeding storm-petrels were based in addition on data taken during visits to selected island sites by Gabrielson and Jewett (1940), Browning and English (1972), and Scott (unpubl. data). To derive the population density estimates of table 1, we converted these statewide totals into individuals/km^2 using the distributional information depicted in figure 1. Densities of wintering populations and of shearwaters were determined from regular censuses of the oceanic area off Newport, Oregon, conducted from 1969–1972 (Scott 1973, unpubl. data). The remaining variables listed in table 1 deal with breeding phenology, body weights, and natality/mortality characteristics. Details for most aspects of breeding biology are presented elsewhere (Scott 1973, and the references cited in table 1).

MODELING PROCEDURE

The simulation model used in our analysis was developed originally by Wiens and Innis (1974) as part of the US/IBP Grassland Biome Studies and was applied

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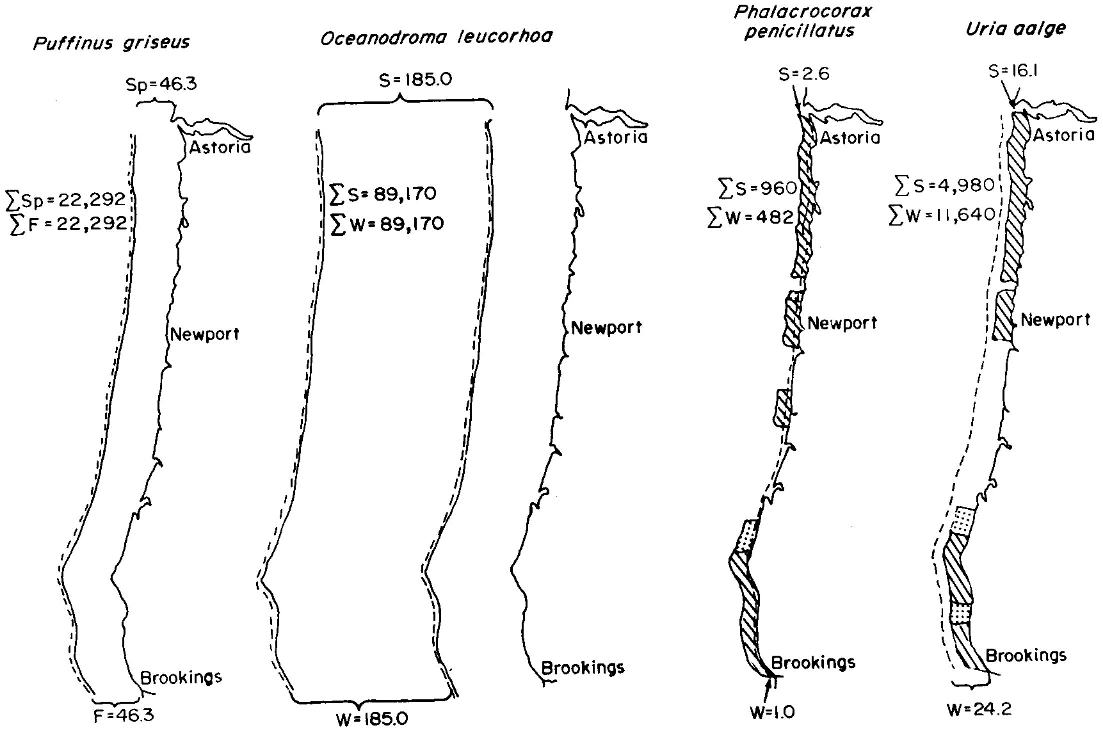

FIGURE 1. Seasonal distributions of the four seabird species along the Oregon coast. The dotted line and the value given for W or F at the bottom of the figure indicate the width (km) of the coastal zone occupied in winter or fall. For shearwaters and petrels, the solid line paralleling the coast and the values given for Sp or S at the top of the figure indicate the width of offshore distribution in spring or summer. The seaward distribution of the petrels was limited arbitrarily to a distance 268 km offshore. Leach's Storm Petrels do occur further offshore (Sanger 1972, Scott, unpubl. data), but the breeding status of these birds is unknown. Summer (breeding) distribution of cormorants and murres along the coast is discontinuous: cross-hatched areas are occupied by two or more colonies; stippled areas are used by birds from a single colony; blank areas are not utilized. For each species, the total areas (km²) of the zones of seasonal occupancy are indicated (from Scott 1973, unpubl. data).

initially to the seabird populations to test its robustness and generality. The details of the structure and assumptions of the model are given in their paper and will be summarized only briefly here.

The model has two major submodels (fig. 2). In the population submodel, the adult breeding population of a species changes through time as a result of immigration and emigration and mortality. The reproductive output of this adult population is, of course, contributed by the breeding females, which comprise a specified portion of the total adult population. With a timing specified by phenological inputs to the model (see below), and in accordance with individual clutch sizes, the breeding females produce an egg population. The flow of individuals from this egg population is either to nestlings or to the mortality sink as dictated by the value of hatching success. The flow from the nestling population to the fledgling population is controlled by fledging success and that from fledgling to juvenile by post-fledging survival. Collectively, this submodel generates estimates of the density of each age class of each species considered at any given time.

The energy submodel is driven by ambient temperature which is specified as input. It is difficult to determine precisely the actual temperature regimes to which the birds are exposed. A storm-petrel, for example, may feed in warm offshore waters, travel through cool upwelling zones, and spend the daylight hours inside a cool burrow. We have used mean air temperatures from Newport, Oregon, as approximations of the "effective" ambient temperature encountered by the birds.

Body weights of adults are specified as input to the model, while weights of nestlings and fledglings are approximated by a logistic function (Ricklefs 1968, 1972). Given these values, the existence energy requirements (i.e., the energy, M, expended in standard metabolism, specific dynamic action, and limited locomotor activity) of adult, juvenile, nestling and fledgling age classes are calculated for each species according to the equations of Kendeigh (1970) for adult nonpasserines:

$$M_0 = 4.337\ W^{0.53} \text{ at } 0°\text{C}$$
$$M_{30} = 0.540\ W^{0.75} \text{ at } 30°\text{C}$$

where W = body weight (in g). Existence energy requirements (kcal bird^{-1} day^{-1}) are extrapolated linearly through the 30°C and 0°C values, and thus for the ambient temperature on any given date the metabolic energy demands of an individual of body weight W can be calculated. These estimates, however, must be modified to account for the demands of other functions. The cost of producing a clutch of eggs (EC), for example, is obtained from:

$$EC = EW(CS)\ (1.23)\ (1.37) \text{ kcal}$$

where EW = egg weight (determined as a function

TABLE 1. Values for input variables used in the simulation analysis for the four species of Oregon seabirds. Codes refer to those listed in figures 2 and 3.

		Input values				
		Puffinus griseus				
Input variable and code	Units	Spring	Fall	*Oceanodroma leucorhoa*	*Phalacrocorax penicillatus*	*Uria aalge*
Popul. at start of immigra. (PS)[a]	Indiv./km^2	0.05	0.10	0.12	3.86	20.70
Popul. breeding density (PBD)[a]	Indiv./km^2	38.61	128.70	14.25	17.77	48.20
Popul. at completion of emigra. (PE)[a]	Indiv./km^2	0.10	0.05	0.12	3.86	20.70
Immigra. onset (TS)[a, b]	days since 1 Jan.	92	192	100	1	1
Immigra. complete (TIN)[a, b]	days since 1 Jan.	122	219	121	121	106
Ad. emigra. begins (TD)[a, b]	days since 1 Jan.	121	245	245	247	197
Ad. emigra. ends (TE)[a, b]	days since 1 Jan.	136	275	282	275	275
Juv. emigra. begins (TJD)[a, b]	days since 1 Jan.	121	245	245	239	197
Juv. emigra. ends (TJE)[a, b]	days since 1 Jan.	136	275	282	269	275
Onset incuba. (DOI 1)	days since 1 Jan.	—	—	153[b, c]	139[a, d]	130[a, d]
Incuba. of last clutch started (DCI 1)	days since 1 Jan.	—	—	162[b, c]	160[a, d]	158[a, d]
Incuba. period (PI)	length days	—	—	41[c]	30[c]	33[d]
Nestling period (PN)	length days	—	—	40[c]	39[c]	21[d]
Fledgling period (PF)	length days	—	—	23[j]	31[c]	28[g]
Propor. popul. breeding ♀♀ (PPBF)[j]	% total popul.	—	—	0.42	0.42	0.42
Clutch size (CS1)	number	—	—	1.0[c]	4.0[b, c]	1.0[d]
Hatching success (HS)	% eggs laid	—	—	0.80[e]	0.70[j]	0.61[f]
Fledging success (FS)	% egg nestlings fledged	—	—	0.90[e]	0.60[j]	0.67[f]
Post-fledging survival (PFS)	% indiv. fledged	—	—	0.60[j]	0.80[j]	0.80[f]
Ad. $\bar{x}$ body wt. (AMW)	g	787.0[a]	787.0[a]	48.0[c]	2459.0[a]	1022.0[a]
Hatching wt. (HMW)	g	—	—	6.4[e]	32.0[c, j]	80.0[g]
Fledging wt. (FW)	g	—	—	67.0[e]	2400.0[c, j]	200.0[d]
Growth rate (AK)[i]	—	—	—	0.117	0.186	0.110
Winter mortality (WM)[i]	% indiv. dying	—	—	0.10	0.10	0.10
Onset of molt (DOM 1)	day since 1 Jan.	—	—	222[c]	230[c]	180[h]
Duration of molt (PM 1)	length days	—	—	20[c]	15[c]	20[h]

[a] Scott (unpubl. data).
[b] Gabrielson and Jewett (1940).
[c] Palmer (1962).
[d] Scott (1973).
[e] Gross (1966).
[f] Leslie (1966).
[g] Belopolski (1957).
[h] Storer (1952).
[i] Ricklefs (1968, 1972).
[j] Estimated.

of adult body weight, from the data of Lack 1968 and Huxley 1927 for alcids), CS = mean clutch size, 1.23 = the caloric value of a gram of egg, and 1.37 is an adjustment for the efficiency of egg production (73%). The additional cost above existence level incurred by normal activity (primarily flight and diving in the species considered here) is estimated to be 40% of existence energy demands. Nestlings are not especially active during their growth period and therefore are not charged this activity cost. Their growth, however, does increase energy demands, and to account for this we elevate existence demands during the nestling period by 20%. Fledglings are moderately active, and we elevate existence energy demands by 10% to account for this activity. Growth of fledglings, on the other hand, is much less rapid than that of nestlings, and we therefore assume that growth increases existence metabolism by only 5%.

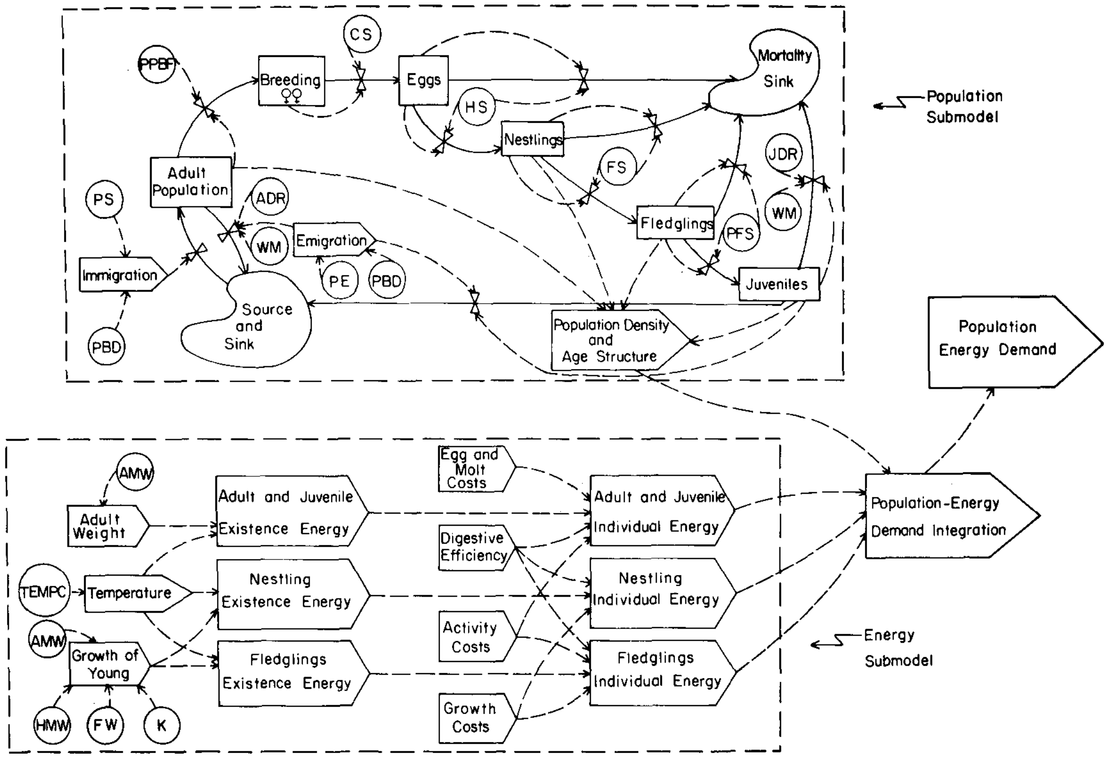

FIGURE 2. A Forrester (1961) compartmental diagram of the simulation model structure. Rectangles indicate state variables; pentagons, computational controls; circles, input variables (see table 1). Solid arrows indicate flows of materials or energy or changes of state; dashed arrows indicate controls or computational transfers (from Wiens and Innis 1974).

In the present analyses, molt was considered to increase existence energy demands by 12% during the molting period.

Unfortunately, most of these model constants have been derived from studies on passerines (see Wiens and Innis 1974) and are only rough approximations at best. Appropriate values for marine birds generally are lacking. Such adaptations as the lower body temperature and metabolic rate of procellarids (Warham 1971) undoubtedly would modify these relationships. The estimation errors in some of the calculations (e.g., activity costs, temperature-dependency of existence energy) are likely of opposite sign and thus at least partially canceling. In addition, the most suspicious constants are those applied to the nestling phase which in most cases discussed here contributes relatively little to the total estimates of population density or energy flux (see below).

The daily energy requirement, as modified by these various factors for each age class of each species, is then adjusted for digestive or assimilation efficiency. Assuming a digestive efficiency of 70% (Kendeigh, unpubl. data), the calculated energy requirement is multiplied by 1.43 to estimate daily energy demands (kcal bird^{-1} day^{-1}) for each age class. Integrating these estimates with those of the population density and age structure produced for a particular date by the population submodel allows estimation of the energy demand

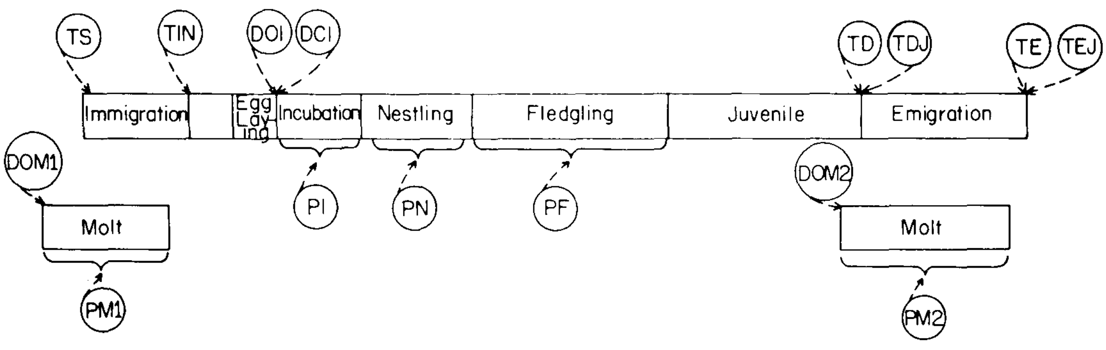

FIGURE 3. Diagram of the phenological stages for a bird population considered in the simulation model. Circled abbreviations indicate required data input (table 1).

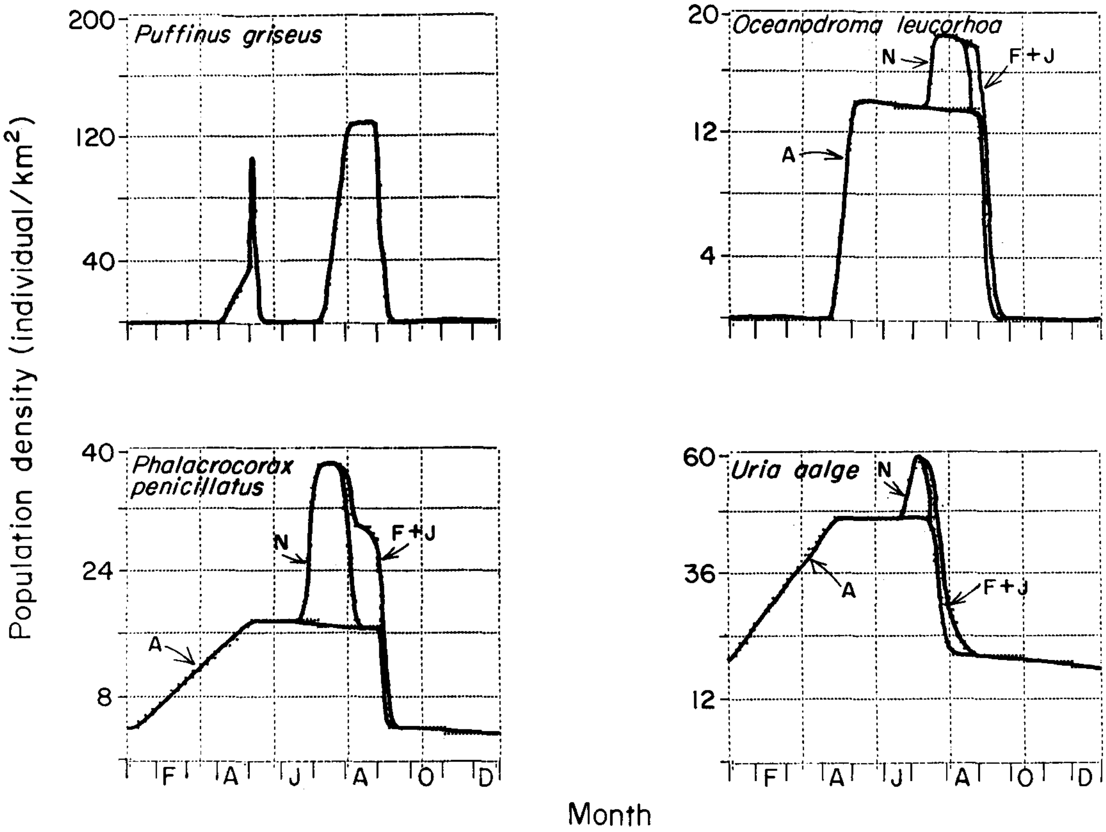

FIGURE 4. Simulation model output estimates of population densities of the four seabird species through the year. A = adults, N = nestlings, F + J = fledglings and juveniles.

of the entire population of each species on any given day.

Various processes or flows within the population submodel are phased in time according to a set of phenological parameters (fig. 3). These relationships, which are largely self-explanatory, are discussed in more detail in Wiens and Innis (1974).

SIMULATION RESULTS

POPULATION DYNAMICS

Graphical simulation output of seasonal changes in population densities of the four species is reproduced in figure 4. Here density is measured as individuals/km^2 over the areas actually occupied by the species; differences in the sizes of occupied areas (fig. 1) are not considered. The seasonal patterns are apparent. Shearwaters are present during spring and fall migration, with the fall passage lasting longer than that of spring, and involving greater densities. Storm-petrels are present in the offshore area through the winter but in extremely low numbers. The population rapidly increases in mid-April and decreases in September as birds disperse through and from the area. Clutches consist of one egg, and only slightly more than 40% of the females produce a clutch (table 1). Thus, recruitment of nestlings and fledglings is relatively low. The breeding population density of Brandt's Cormorants is only slightly greater than that of the storm-petrels, but given their greater clutch size, production of offspring per unit area is substantially greater. Cormorant density increases early in the year, and diminishes rapidly in late August after breeding. At this time the birds move north, dispersing more evenly along the coast (fig. 1); many individuals assume winter residency in estuaries (Van Tets 1959, Scott 1973). Murres exhibit a similar pattern of population flux, but recruitment is quite low, reflecting the one-egg clutch and relatively low hatching and fledging successes (table 1). When the young fledge, murres, like the cormorants, disperse into coastal areas apart from the breeding colonies, but their offshore distribution expands rather than contracts (fig. 1). In all three breeding species, peak population densities in occupied areas generally coincide in time (fig. 4). However, cormorant and murre densities decrease prior to the fall passage of shearwaters as a result of dispersal away from breeding sites.

The forms and magnitudes of the changes

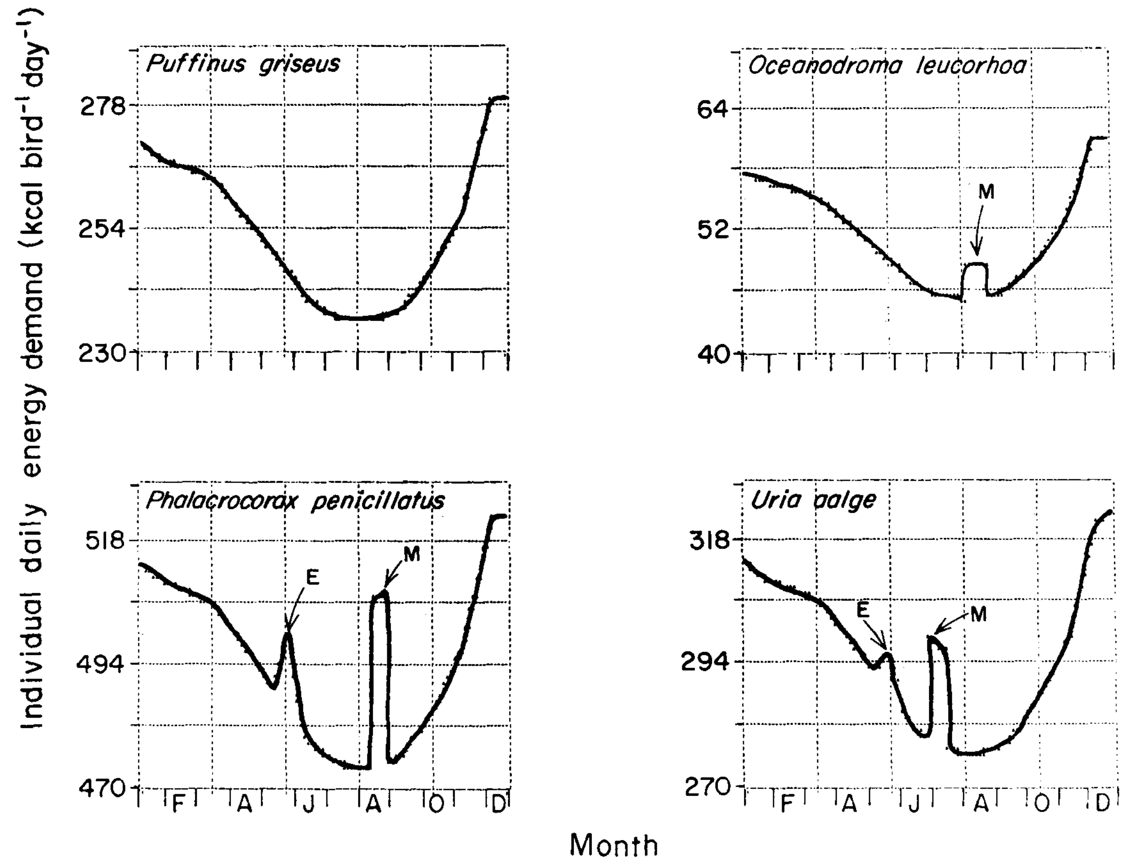

FIGURE 5. Simulation model output estimates of daily energy demands of adult individuals of the four seabird species through the year. E = increase in demands due to egg production; M = increase due to molt.

in population density projected by the model simulations are of course entirely dependent upon the specifications of the data input. Most of the input used was derived from detailed field studies conducted in Oregon by Scott (1973, unpubl. data, see table 1), and thus we have some confidence that these projections are reasonably accurate. Previous sensitivity tests of the simulation model (Wiens and Innis 1974) showed that population density has important effects on model estimates of energy demands, so an accurate estimate of population density flux is critical. Seabird colonies, however, do not lend themselves to censusing, and when the birds leave the breeding colonies, density determinations become even more difficult. Sanger (1972) indicated lower winter population levels of large alcids in the entire coastal domain (the California-Oregon border north to the Aleutians) than we indicate for murres alone in a much smaller area. His summer value for all storm-petrels was less than our figure for Leach's Storm-Petrel alone, and his value for all large alcids was less than twice that of our estimate for murres. The summer values of Sanger seem quite low in view of the large colonies of both large alcids and of Leach's and Fork-tailed (*Oceanodroma furcata*) Storm-Petrels in Alaska and elsewhere (Gabrielson and Lincoln 1959). We believe the differences in population estimates are due to the fact that Sanger ignored birds at breeding colonies, and did not cruise inshore waters (0 to 18 km from shore) where the majority of birds other than storm-petrels occur (Scott, unpubl. data). Until additional field studies supply more detailed population density values, we feel justified in using the model estimates derived from the field censuses (table 1) as a basis for determining population energy demands.

ENERGY DEMANDS

In the model calculations, estimates of population energy demands are derived from determinations of individual requirements. These in turn are functions of ambient temperature, body weight, and the various energy-demanding activities noted above. Model output graphs of daily energy demands of adult individuals (fig. 5) demonstrate the large differences in caloric requirements associated with the wide range of body sizes of the four species (48 to 2, 459 g; table 1). Also apparent is the inverse relationship between ambient temperature and metabolic demand, with peak demands for all species occurring in December–January. Molt by shearwaters during their transit of Oregon coastal waters is not considered here (table 1) even though the birds do molt during their passage through the northern hemisphere (Palmer 1962). Our model estimates of energy demand thus will be slightly low to the extent that molt occurs during shearwaters' occupancy of Oregon coastal waters. For the remaining species the elevation of energy demands for molting range from small in the Leach's Storm-Petrel to large in Brandt's Cormorants. Recently Ainley et al. (in press) have indicated that molt in Leach's Storm-Petrel may occur over a 274-day period; our estimate of the duration of molt in Brandt's Cormorant (table 1) is probably too short also. Adjustment of model input to reflect a longer molt increases the total annual energy demands only slightly in both species. The initial inaccuracy is testimony to the need for more extensive, precise information on the natural history of these species. Individual costs associated with egg production also are significant for cormorants and murres but have no apparent effect on storm-petrel energy demands.

Of greater interest are the patterns of population energy demands. Considering energy requirements per m^2 of sea surface and disregarding differences in the total area occupied by the species, the dominance of energy flow through this four-species "community" by shearwaters during their tenure in coastal waters is at once evident (fig. 6). At the peak of energy demand during the fall passage, the shearwater population consumes more than twice as much energy per m^2 per day as any of the other species during their peak energy consumption. Over the entire year, however, the shearwater and murre populations place roughly equivalent energy demands on the system. Murres and cormorants exhibit similar peak demands although that of the cormorants occurs after that of the murres has begun to diminish. On a m^2 basis, the storm-petrel population apparently plays a minor role in the total energy flow through this "community."

To evaluate the significance of these energy demands in the marine ecosystem, we must consider their areal extent. Cormorants, for example, have a relatively high daily demand per m^2 but have a discontinuous distribution in a narrow band along the coast (fig. 1). When their demand is considered in terms of the total occupied area (fig. 6), it is quite small relative to the other species. For the storm-petrel population the reverse is true. The murre population exhibits seasonal shifts in dispersion; thus, in summer when the birds aggregate, the energy demand per m^2 is high relative to other times of year. Considered over the entire area occupied, however, the daily energy demand of the population is remarkably constant through the year, reflecting the relative constancy of total population size. Again the overwhelming dominance of shearwaters emerges from this analysis. Their spring and fall movements through the coastal zone produce sharp peaks in total energy flow through the four-species "community" (fig. 6, upper right), which otherwise exhibits relatively little variation through the year. During their fall passage, the shearwaters consume nearly seven times as much energy as any of the remaining species. Sanger (1972) reported a similar dominance by shearwaters over the North Pacific.

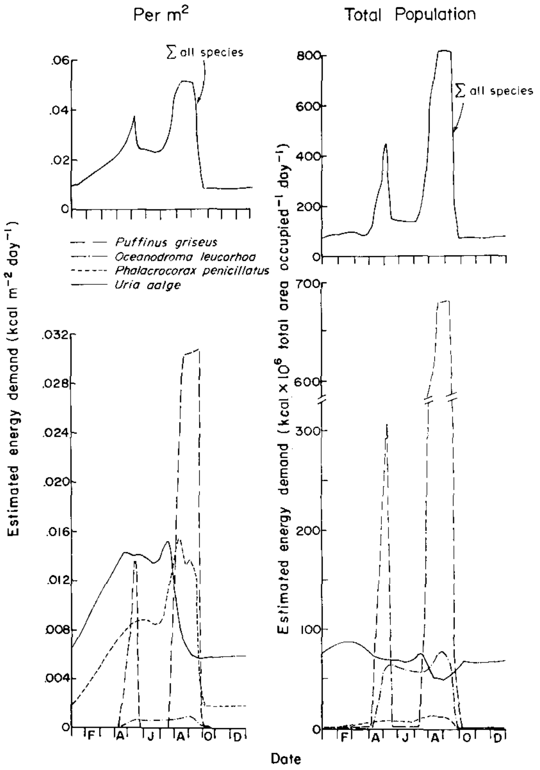

FIGURE 6. Model estimates of total daily energy demands of populations of the four seabird species, based on demand per m^2 in the area occupied (left) and demand over the entire occupied area (right), from figure 1. The upper graphs chart energy demand for the entire four-species "community."

Because of the importance of shearwaters in total community energy flow, we simulated

TABLE 2. Annual and breeding season energy demands of age classes of the four seabird species, from model output.

	Annual energy demand (kcal m^{-2})				Breeding season energy flows (1 May–1 September)				
Species	Adults & juveniles	Nestlings	Fledglings	Σ	Total (kcal m^{-2})	% to egg production	% to nestlings	% to fledglings	% to reproduction
Puffinus griseus	1.653	N[a]	N[a]	1.653	N[a]	N[a]	N[a]	N[a]	N[a]
Oceanodroma leucorhoa	0.096	0.006	0.004	0.106	0.090	0.01	6.67	4.44	11.12
Phalacrocorax penicillatus	1.987	0.171	0.150	2.308	1.367	0.33	12.51	10.97	23.81
Uria aalge	3.440	0.011	0.037	3.488	1.471	0.55	0.75	2.64	3.94

[a] N = Nonbreeding.

two alternative patterns for their movement through Oregon coastal waters (although the values given in table 1 represent our best estimates of the normal patterns). First, it is possible that the birds spend less time than we have estimated along the Oregon coast in the spring as they move north into the Alaskan coastal waters (Sanger 1972, Gabrielson and Lincoln 1959). To examine such a change, we maintained the times of initiation of spring immigration and completion of emigration unchanged (table 1) but shortened the immigration and emigration periods by 16 days. Thus the same number of birds moves through the area, but more rapidly. The effect of this change is to reduce the total population energy consumption over the spring movement period by 44%. Second, in late summer shearwaters may remain longer in coastal waters than we suggested initially (especially during "good" years), perhaps feeding upon the resources produced by coastal upwelling. We thus extended the stay of the population from 2 October to 27 October. This increased total energy demand during the fall phase by 29%. If both alterations are considered together, they effect a 17% increase in the annual energy demand of the shearwaters. Given the importance of this species in the system, the timing and magnitude of these seasonal movements warrant closer study.

One additional consideration of energy flow patterns through the populations of the four species is instructive. In table 2 we give the model estimates of total yearly energy demand (kcal m^{-2}) for age classes of each species. On such an annual basis, murres consume the greatest amount of energy per m^{2}, while storm-petrels consume less than 1/30 of this amount. Energy consumption by nestling and fledgling murres and storm-petrels is relatively low compared to cormorants. These relationships of offspring to adult energy flow may be quantified more readily by restricting our examination to the breeding season (1 May to 1 September). In the three Oregon breeding species, the costs of egg production account for a relatively small proportion of the total energy flow, largely because egg production is quite restricted in time (table 2). Egg production costs are higher in murres, which lay a single, very large egg, than in cormorants, which lay three or four moderately sized eggs. Lack (1968) has suggested that variations in egg size relative to adult body size may be linked to the availability of food for the female or the newly hatched young, with seminidifugous species generally having relatively larger eggs than nidicolous species. Temporal variation in the standing stocks of zooplankton and small nektonic animals, presumed prey, is greater in inshore waters influenced by upwelling than in more predictable offshore waters (Laurs 1967, Pearcy, unpubl. data). Of the three breeding species, storm-petrels have nidicolous young, feed in the relatively stable offshore oceanic waters, and have the smallest proportionate energy commitment to egg production. Brandt's Cormorants, on the other hand, feed in close inshore waters, have nidicolous young, and are intermediate between storm-petrels and murres in the energy allocated to egg production. Murres, which forage at intermediate distances, have precocial, seminidifugous young, and channel a greater proportion of their energy intake into egg production. Other factors, some of which we discuss elsewhere (Wiens and Scott, unpubl. data), also influence such reproductive strategies. Overall, costs associated with reproduction (egg production plus nestling and fledgling energy demands) account for nearly 24% of the total breeding season energy demand of cormorants while comprising less than 4% of the flow through murre populations; storm-petrels are intermediate. These percentages are not, strictly speaking, measures of total energy allocation to reproduction by each species population because costs incurred by adults in feeding offspring are not included. These costs may be large and year-to-year variation great. As prey availability changes, the distances traveled to foraging areas may change by a factor of 10 or more. Of the three Oregon breeding species, Leach's Storm-Petrel travels the greatest minimum distance (straight-line round trip distance from beach to inshore edge of feeding area) to its foraging area (176 km) and Brandt's Cormorant the least (0.2 km). Nonetheless, the degree of interspecific variation evident in table 2 suggests major differences in energy allocation strategies (Gadgil and Solbrig 1972).

TROPHIC DYNAMICS

To determine the relationships of the four species within the coastal marine ecosystem, it is necessary to relate seasonal patterns of energy requirements to various food types. Ideally, such an analysis is based upon detailed assessments of the patterns of prey selection by the birds. Our best estimates of prey selection come from analyses of gut contents of collected specimens (table 3). The values for cormorants (in summer) and murres are based on large samples (Scott 1973), while those for shearwaters and storm-petrels are based on very small samples and literature reports (Gabrielson and Jewett 1940, Palmer 1962). The scarcity of data of the diet of shearwaters during their tenure along the Oregon coast is especially unfortunate.

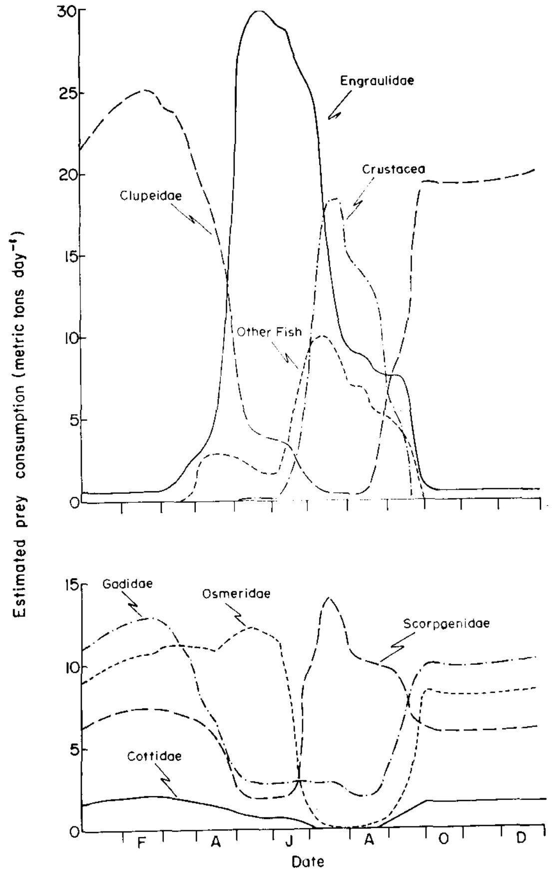

FIGURE 7. Seasonal variations in consumption of prey types by Common Murres, as projected from model estimates of energy demands and information on dietary composition (table 3).

TABLE 3. Dietary composition (% of stomach volume) of the four species considered in this analysis. Shearwater data from Scott (unpubl.) and Gabrielson and Jewett (1940); storm petrel data from Scott and Pearcy (unpubl.); cormorant and murre data from Scott (1973, unpubl.). Caloric values and dry weight:wet weight ratios from Cummins and Wuycheck (1971) and Pearcy (pers. comm.).

Food type	Caloric value (kcal/g dry wt)	Dry wt/ wet wt	*Puffinus griseus*	*Oceanodroma leucorhoa*	*Phalacrocorax penicillatus*		*Uria aalge*		
					Summer	Winter	May–Jun	Jul–Aug	Sep–Apr
Hydrozoa	5.9	0.17[a]	—	0.44	—	—	—	—	—
Crustacea									
Euphausiidae	4.9	0.20[a]	—	0.38	—	—	—	0.13	—
Other	4.5	0.20	—	0.09	—	—	—	0.14	—
Mollusca									
Squid	4.8	0.20	0.08	0.01	—	—	—	—	—
Other	4.8	0.20	—	—	—	—	0.02	—	—
Osteichthyes									
Clupeidae	5.6	0.30	—	—	—	—	0.09	0.01	0.49
Engraulidae	5.5	0.22	0.80	—	0.30	—	0.52	0.21	—
Osmeridae	5.0	0.27	—	—	0.04	0.06	0.23	—	0.16
Gadidae	5.0	0.27	—	—	—	—	0.06	0.05	0.20
Scorpaenidae	5.0	0.27	—	—	0.20	0.28	0.04	0.27	0.12
Cottidae	5.3	0.27	—	—	0.20	0.28	0.01	—	0.03
Other	5.0	0.27	0.12	0.08	0.26	0.38	0.03	0.19	—

[a] Perhaps slight overestimates (Pearcy, pers. comm.).

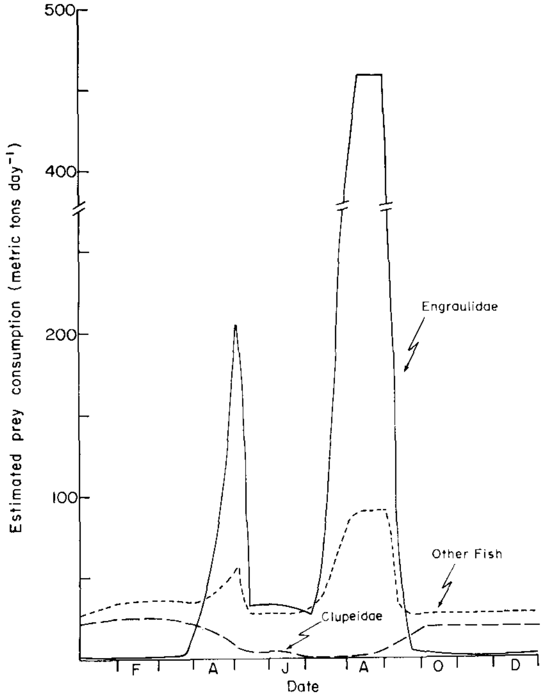

FIGURE 8. Seasonal variations in consumption of herring, anchovy, and other fish taxa by the four-species seabird "community."

With information on dietary preferences of the species and on the caloric values and dry weight:wet weight ratios of prey types (table 3), one can convert the model estimates of caloric energy demands into grams consumption of each food type. Our data perhaps justify an analysis of seasonal variations in prey consumption only in the murres (fig. 7). As murre energy demands over the entire occupied area remain relatively constant through the year (fig. 6), the variations apparent in figure 7 stem largely from seasonal differences in prey selection (table 3). During the nonbreeding season, murres consume relatively large quantities of herring (Clupeidae) with smaller quantities of cod (Gadidae), smelt (Osmeridae), rockfish (Scorpaenidae), and sculpin (Cottidae). Smelt also form an important component of the diet in summer, and rockfishes in early fall. The summer diet, however, is comprised chiefly of northern anchovy (*Engraulis mordax*), while in early fall euphausiids, miscellaneous crustaceans, and a variety of other fishes contribute to the diet.

These seasonal shifts in diet probably are related to changes in offshore dispersion of the birds, availability of prey species, and oceanographic conditions. The northern anchovy prefers warmer water than do other fishes eaten by murres. Baxter (1967) reported that most catches of this species off California and Baja California were in waters between 14.5° to 20°C. Spawning usually occurs at temperatures of 13° to 17.5°C (Ahlstrom 1956). During the summer off Oregon, Richardson (1973) found that anchovy larvae were most abundant in warm (>14°C) Columbia River plume waters rather than cold upwelled waters near the coast or beyond the plume. The low-salinity plume water is heated more rapidly than surrounding waters and therefore often forms a distinct warm-water tongue, especially in early summer (Pearcy 1973, Owen 1968). In spring and early summer this warm, low-salinity plume often intrudes close to the Oregon coast (Pillsbury 1972) where it provides a favorable habitat for spawning anchovies. Thus, the high availability of anchovies to murres immediately before they disperse offshore from their rookeries in May–June may be explained by the nearshore distribution of plume waters. Anchovies likely form dense schools in the frontal zones between cold, highly productive upwelled waters along the coast and the warm plume. During the fall and winter after upwelling subsides, anchovies move offshore and are less available in inshore waters (Baxter 1967).

The importance of anchovies in the overall trophic dynamics of these seabirds is apparent from figure 8. These seasonal patterns are again dominated by the effect of shearwaters which apparently forage predominately upon anchovies during their spring and fall movements along the coast. Herring, which are taken in significant quantities only by murres, account for nearly half the food consumed during the nonbreeding season. It is necessary to point out, however, that these estimates of quantities of particular prey types taken are influenced by our selection of areas for collection of specimens for stomach analysis. Birds of the same species foraging in different areas may be exposed to and capture quite different types of prey (Hubbs et al. 1969, Scott 1973). For example, we did not collect birds inside bays and estuaries. Large numbers of herring and smelt occur in these areas especially during the spring spawning period. Both murres and Brandt's Cormorants are known to feed on these fish (pers. observ., Gabrielson and Jewett 1940). Thus our estimates of herring consumption may be conservative, at least for these two species. On the other hand, our estimates of herring consumption by murres during the winter are based on a small sample and therefore may be somewhat high.

A more detailed analysis of the total annual consumption of the prey types by the four species over the entire area occupied by each is given in table 4. During their relatively brief stay in coastal waters, shearwaters consume over 24,000 metric tons of anchovies. Storm-petrels, feeding primarily at the water's surface, consume roughly equal quantities of euphausiids and hydrozoans, while cormorants, which feed largely upon bottom-dwelling fish close to shore, consume a relatively small amount of these fish. Over the year murres may consume approximately equal quantities of anchovy, smelt, cod, and rockfish. It is apparent when data for the four species are combined (fig. 9), that these birds eat primarily fish, with euphausiids, other crustaceans, squid, and hydrozoans forming a relatively minor component of the total annual tonnage consumed. Anchovies overwhelmingly dominate the birds' diet, comprising 43% of the 62,500 metric tons of prey consumed annually. Most of the anchovies (86%) are consumed by shearwaters.

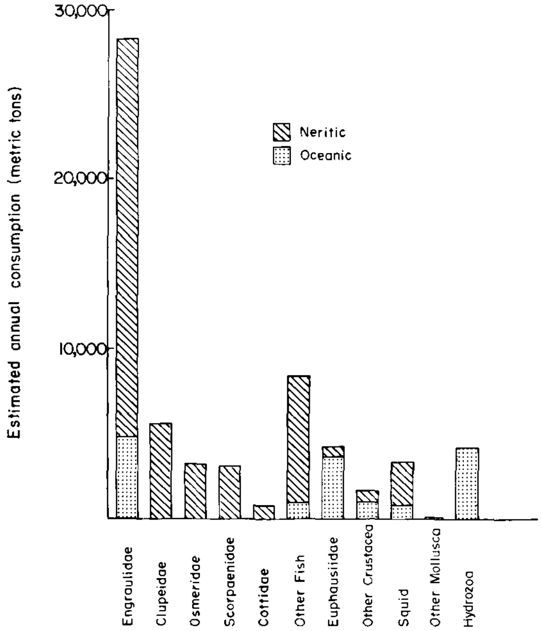

FIGURE 9. Estimated annual consumption of various prey by the four-species seabird community, derived from model estimates of energy demands and information on dietary composition (table 3).

CONCLUDING COMMENTS

These estimates of prey consumption by the four seabird populations are approximations, the accuracy of which depends on the accuracy of the input data required by the model (table 1) and of the dietary information (table 3). Still, such estimates provide an index to the importance of these birds in the marine ecosystem. Ideally, this should be related to knowledge of the standing stocks, population dynamics, and movements of the prey, of which little is known. In the absence of such detailed information, we must use less direct means to make these determinations. Barrett et al. (1972), for example, estimated that the commercial fishery in the northern permit area (from Point Conception north to the Oregon border) took an average of 5920 metric tons of anchovies each year from 1966 to 1971. According to our model estimates, the four seabird populations consume 28,000 metric tons per year, more than four times this

TABLE 4. Estimated annual consumption (metric tons) of prey by the four seabird species.

Food type	*Puffinus griseus*	*Oceanodroma leucorhoa*	*Phalacrocorax penicillatus*	*Uria aalge*	Σ
Hydrozoa	—	4,118	—	—	4,118
Crustacea					
Euphausiidae	—	3,610	—	600	4,210
Other	—	985	—	670	1,655
Mollusca					
Squid	3,075	155	—	—	3,230
Other	—	—	—	50	50
Osteichthyes					
Clupeidae	—	544	—	5,687	5,687
Engraulidae	24,364		336	3,527	28,227
Osmeridae	—		59	3,074	3,133
Gadidae	—		—	3,215	3,215
Scorpaenidae	—		278	2,811	3,089
Cottidae	—		255	478	733
Other	3,278[a]		363	1,030	5,215
Σ	30,717	9,412	1,291	21,142	62,562

[a] Includes some of the other listed families.

amount. At the present time this fishery is limited. However, in view of the relatively large percentage of the neritic fish populations taken by seabirds, it is important that we fully understand the role of these species as predators upon resources which are exploited by man also. The estimated total annual consumption of all fish by the birds (49,000 metric tons) is about nine times the annual troll catch of coho and chinook salmon off Oregon (Verhoeven 1972).

We may obtain a gross estimate of the importance of these birds in the marine food web as follows. Primary production in coastal (neritic) waters off Oregon is about 300 g C m^{-2} yr^{-1} (Small et al. 1972, Anderson 1972). Assuming an ecological efficiency of 10% for each trophic transfer, about 3 g C m^{-2} yr^{-1} of primary carnivores would be produced. Perhaps one-third of this would be in the form of small pelagic fishes like anchovy, herring, and smelt. Assuming a fish composition of 70% protein and 30% lipid, 1 g C converts to 18 kcal. Roughly 20% of the shearwater and all of the petrel populations occur in oceanic rather than neritic waters (from fig. 1, assuming a 37 km wide neritic zone along the Oregon coast). Consumption of pelagic fishes within the neritic zone is 3.9 kcal m^{-2} yr^{-1} (from tables 2 and 4), which represents about one-fifth of the production. Murres, which are the most important resident species in the region, consume roughly 11% of the pelagic fishes produced in the neritic zone.

Relatively few estimates have been made of the magnitude of energy or biomass flow through marine bird populations. Most of these have been calculated from estimates of the proportion of the adult body weight consumed per day. Uspenski (1956), for example, calculated that 2 million murres consumed 25,000 metric tons of food (12,500 g per bird) during the 4-month breeding season at Novaya Zemlya, USSR. Using a similar approach, Swartz (1966) calculated that 157,000 murres at Cape Thompson, Alaska, consumed 4,900 metric tons (31,299 g per bird) during the same period of time. The total breeding population of murres along the Oregon coast is roughly 239,800 individuals. Using Tuck's (1960) suggestion that an adult murre consumes its body weight in food every week, we calculate that during the 1 May to 1 September breeding season, the Oregon population consumes 4,300 metric tons of food, or roughly 17,900 g per bird. From the output of the simulation model for the murre population during the breeding season, we calculate an estimated food consumption of 6400 metric tons, or 26,700 g per adult. This is well within the range of values estimated by less direct and less detailed means.

Swartz (1966) extended his estimates of food biomass consumption to the entire assemblage of breeding seabirds occupying the coastal cliffs at Cape Thompson. His analysis was restricted to species breeding on the sea cliffs (thus excluding migrants such as shearwaters) and assumed that the population remained in the area during the entire 4-month breeding season; thus his results are not directly comparable to ours. He estimated a consumption of 13,100 metric tons of food by the 13 breeding species (421,000 individuals). The Oregon populations totaled 4,395,000 individuals, most of which were shearwaters and storm-petrels. Our model estimates that during the breeding season these birds remove 39,700 metric tons of prey. If shearwaters are excluded from this analysis, the three remaining species consume on the order of 35,800 metric tons of prey during the breeding season. In any event, substantial quantities of prey are removed, attesting to the importance of marine birds in coastal ecosystems.

Tuck (1960) and Murphy (1936) have suggested that seabirds, especially murres, may be a "vital link" in the ecology of this environment in another way. If bird excrement is an important source of nutrients for the production of marine phytoplankton, then murre colonies may be important in recycling and redistributing nutrients. This may be especially true in arctic waters where upwelling does not occur. Because of the high rainfall in these northern hemispheric breeding areas, excrement at nesting sites is washed into the sea and does not accumulate as, for example, on the guano islands off the Peruvian coast. Our model analysis provides a means of estimating the magnitude of the return of energy to the marine system. If we assume a digestive efficiency of 70%, then we may calculate that these bird populations return 2.32×10^{10} kcal over their total distribution (fig. 1), although the return is concentrated around the rookeries. During the breeding season alone, roughly 1.48×10^{10} kcal are returned to the system in excrement. The nutrient content of the excrement is undoubtedly more important than the caloric content, as Tuck (1960) has observed. Our lack of information on the nutritive composition of prey and on the metabolic processing of these nutrients by the seabirds precludes an estimation of the amounts of material redistributed in the system in excrement.

We must stress again that our analysis has provided general approximations rather than precise measurements of what we believe to be reality. One virtue of a modeling approach is that it forces one to examine closely the parameters essential to a given situation. Table 1 suggests that quite a few such parameters are necessary to approximate energy flow through marine bird populations, and while most of these are rather basic life history attributes, our knowledge of many is inadequate. In spite of this, we have used the existing data for some initial analyses rather than waiting until "good" data are available for all parameters. We do not intend to imply that a modeling approach such as this provides an alternative to detailed, precise life history information obtained by field work. It does not. But such a preliminary exploration indicates some of the critical parameters and suggests that seabirds are a significant component of marine ecosystems which require concerted, careful study within a systems perspective.

SUMMARY

A computer simulation model was used to explore the patterns and magnitudes of population density changes and population energy demands in Oregon populations of Sooty Shearwaters, Leach's Storm-Petrels, Brandt's Cormorants, and Common Murres. The species differ in seasonal distribution and abundance, with shearwaters attaining high densities during their migratory movements through Oregon waters, and murres exhibiting the greatest seasonal stability in population numbers. On a unit area basis, annual energy flow is greatest through murre and cormorant populations. However, because shearwaters occupy a larger area during their transit, they dominate the total energy flow through the four-species seabird "community."

Consumption of various prey types is estimated by coupling model output of energy demands with information on dietary habits. This analysis suggests that murres annually consume nearly twice as many herring as any other prey and consume approximately equal quantities of anchovy, smelt, cod, and rockfish. Cormorants consume a relatively small quantity of bottom-dwelling fish, while storm-petrels take roughly equal quantities of euphausiids and hydrozoans. Anchovies account for 43% of the 62,500 metric tons of prey the four species are estimated to consume annually; 86% of this anchovy consumption is by shearwaters. The consumption of pelagic fishes by these four populations within the neritic zone may represent as much as 22% of the annual production of these fish.

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LITERATURE CITED

Ahlstrom, E. H. 1956. Eggs and larvae of anchovy, jack mackerel and Pacific mackerel. California Coop. Oceanic Fish. Invest. Rep. 1:33–42.

Ainley, D. G., T. J. Lewis, and S. Morrell. (In press.) Molt in Leach's and Ashy Storm-Petrels. Wilson Bull.

Anderson, G. C. 1972. Aspects of marine phytoplankton studies near the Columbia River with special reference to a subsurface chlorophyll maximum, p. 219–240. *In* A. T. Prater and D. L. Alverson [eds.] The Columbia River estuary and adjacent ocean waters. Univ. Washington Press, Seattle.

Ashmole, N. P., and M. J. Ashmole. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Mus. Nat. Hist. Yale Univ. Bull. 24:1–131.

Barrett, I., H. Frey, J. Issacs, and M. Sargent. 1972. Review of the pelagic wet fisheries for 1970 and 1971. California Coop. Oceanic Fish. Invest. Rep. 16:15–16.

Baxter, J. L. 1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. California Coop. Oceanic Fish. Invest. Rep. 11:110–116.

Belopolski, L. O. 1957. Ecology of sea colony birds of the Barents Sea. Izd-vo AN SSSR. Moskva-Leningrad (Transl. by IPST, Jerusalem, 1961.)

Browning, M. R., and W. W. English. 1972. Breeding birds of selected Oregon coastal islands. Murrelet 53:1–7.

Cummins, J. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. No. 18.

Forester, J. W. 1961. Industrial dynamics. M.I.T. Press, Cambridge, Mass.

Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Oregon State Monogr., Stud. in Zool. No. 2.

Gabrielson, I. N., and F. C. Lincoln. 1959. The birds of Alaska. Telegraph Press, Harrisburg, Pa.

Gadgil, M., and O. T. Solbrig. 1972. The concept of *r*- and *K*-selection: evidence from wild flowers and some theoretical considerations. Am. Nat. 106:14–31.

GROSS, W. A. 1935. The life history cycle of Leach's Petrel (*Oceanodroma leucorhoa leucorhoa*) on the outer seal islands of the Bay of Fundy. Bird-Banding 18:117-126.

HUBBS, C. L., A. KELLY, AND C. LIMBAUGH. 1970. Diversity in feeding by Brandt's Cormorant near San Diego. California Fish Game 56:156-165.

HUXLEY, J. S. 1927. On the relation between egg-weight and body-weight in birds. J. Linn. Soc. Lond. Zool. 36:457-466.

KENDEIGH, S. C. 1970. Energy requirements for existence in relation to size of bird. Condor 72: 60-65.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LAURS, R. M. 1967. Coastal upwelling and the ecology of lower trophic levels. Ph.D. Diss. Oregon State Univ., Corvallis.

LESLIE, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria aalge* Pont.). J. Anim. Ecol. 35:291-301.

MURPHY, R. C. 1936. Oceanic birds of South America. Vol. 1. Am. Mus. Nat. Hist., New York.

OWEN, R. W., JR. 1968. Oceanographic conditions in the northeast Pacific Ocean and their relation to the albacore fishing. Fish. Bull. 66:503-526.

PALMER, R. S. [ed.]. 1962. Loons through Flamingos. *In* Handbook of North American birds, Vol. 1. Yale Univ. Press, New Haven.

PEARCY, W. G. 1973. Albacore oceanography off Oregon–1970. Fish. Bull. 71:489-504.

PILLSBURY, R. D. 1972. A description of hydrography, winds, and currents during the upwelling season near Newport, Oregon. Ph.D. Diss., Oregon State Univ., Corvallis.

RICHARDSON, S. L. 1973. Abundance and distribution of larval fishes in waters off Oregon, May–October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull. 71:697-711.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110:419-451.

RICKLEFS, R. E. 1972. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177-201.

ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37: 317-350.

SANGER, G. A. 1972. Preliminary standing stock and biomass estimates of seabirds in the subarctic Pacific region, p. 589-611. *In* A. Y. Takenouti [ed.] Biological oceanography of the northern North Pacific Ocean. Idemitsu Shoten, Tokyo.

SCOTT, J. M. 1973. Resource allocation in four syntopic species of marine diving birds. Ph.D. Diss., Oregon State Univ., Corvallis.

SMALL, L. F., H. CURL, JR., AND W. A. GLOOSCHENKO. 1972. Effects of solar radiation and upwelling on daily primary production off Oregon. J. Fish. Res. Board Can. 29:1269-1275.

STORER, R. W. 1952. A comparison of variation, behavior, and evolution in the sea-bird genera *Uria* and *Cepphus*. Univ. California Publ. Zool. 52:121-222.

SWARTZ, L. G. 1966. Sea-cliff birds. *In* N. J. Wilimovsky, and J. N. Wolfe [eds.] Environment of the Cape Thompson region, Alaska. U.S.A.E.C., Div. Tech. Inf., Washington, D.C.

TUCK, L. M. 1960. The murres. Can. Wildl. Serv. No. 1. Queen's Printer, Ottawa.

USPENSKI, S. M. 1956. The bird bazaars of Novaya Zemlya. (Transl. Can. Wildl. Serv.) Transl. Russ. Game Rep. No. 4, Queen's Printer, Ottawa.

VAN TETS, G. F. 1959. A comparative study of the reproductive behavior and natural history of three sympatric species of cormorant (*Phalacrocorax auritus*, *Ph. penicillatus*, *Ph. pelagicus*) at Mandarte Island, B.C. M.A. Diss., Univ. British Columbia, Vancouver.

VERHOEVEN, L. A. [ed.]. 1972. 24th annual report. Pac. Mar. Fish. Comm.

WARHAM, J. 1971. Body temperatures of petrels. Condor 73:214-219.

WIENS, J. A., AND G. S. INNIS. 1974. Estimation of energy flow in bird communities: A population bioenergetics model. Ecology 55:730-746.

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