

FOOD WEBS IN THE OCEAN: WHO EATS WHOM AND HOW MUCH?

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ABSTRACT

Over 100 food webs have been published for marine ecosystems to describe the transfer of food energy from its source in plants, through herbivores, to carnivores and higher-order predators. The webs suggest that the lengths of the chains that form food webs are typically short (3-4 links), and that few species feed at more than one trophic level. The webs also suggest that ecosystems with long food chains may be less stable than those with shorter food chains.

Stomach contents have been the primary means for determining what marine organisms eat. More recently developed techniques include faecal analysis and fatty acid signatures from blood or fat samples. Consumption has been estimated from the volume of food found in stomachs, from the feeding rates of captive individuals, and from bio-energetic modelling. Consumption of marine organisms, expressed as a percentage of an individual's body weight per day, ranges from about 20-30% for zooplankton, to 10% for cephalopods, 1-4% for fish, 4-8% for marine mammals, and 15-20% for sea birds. Immature age classes consume about twice as much (per unit of body weight) as do mature individuals. Furthermore, consumption is not constant throughout the year, but varies seasonally with periods of growth and reproduction. Most groups of species consume 3-10 times more than they produce, and export or pass up the food web about 70-95% of their production. Marine organisms tend to be larger at successive trophic levels and are limited in the sizes of food they can consume. Humans are one of the few species that can prey upon almost any level of the food chain and any size of prey.

INTRODUCTION

[1] Understanding predator-prey relationships within marine food webs has increased enormously since the first simple food web was drawn for herring in the North Sea (Hardy, 1924). What were once simple qualitative depictions of the interrelationships between species are being increasingly replaced with quantitative descriptions of entire ecosystems. This in turn is allowing fisheries biologists to better estimate the amount of food consumed by various species, and to make predictions about the effects of fisheries on predator-prey relationships, and of the effect of food web dynamics on fisheries.

[2] The following provides an overview of marine food webs and the amounts of food that marine organisms consume. Emphasis is placed on apparent patterns that a number of biologists have noted in comparing food webs among different ecosystems regarding ecosystem stability, food chain lengths, and food web complexity. The efficiency of energy transfer between trophic

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levels is also discussed in the context of digestion and assimilation efficiencies of marine organisms; and the interplay between food webs and consumption is highlighted with a case study from the eastern Bering Sea.

FOOD WEBS

[3] A food chain delineates one possible pathway for the transfer of energy from plants to herbivores to carnivores and top predators. Myriads of food chains within an ecosystem form a food web, which biologists have typically drawn as a series of interconnected species joined by lines showing the presence or absence of interactions (e.g. Figure 1). This is simplest depiction of who eats whom. Species may be individually identified or may be grouped into functional categories (e.g., groundfish or benthic invertebrates) based on similar life history characteristics or other traits.

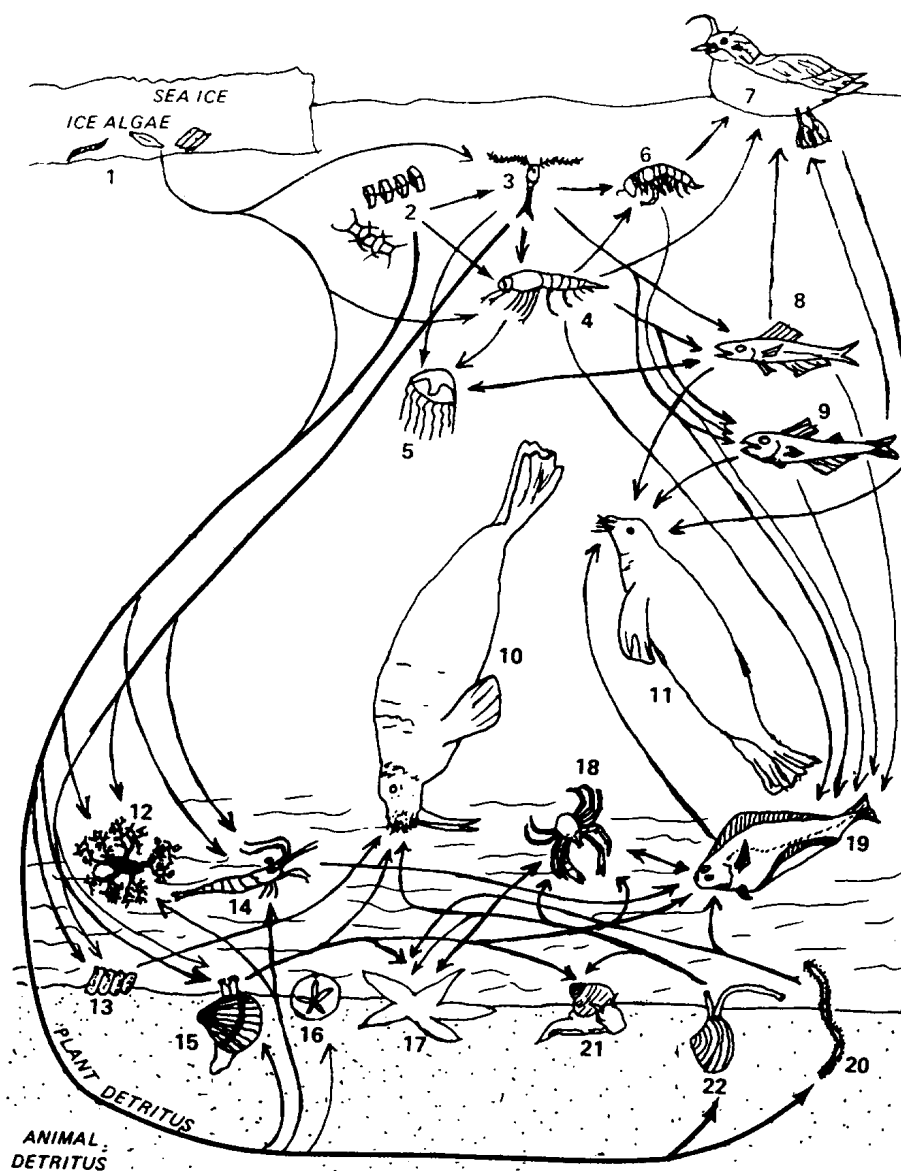


Figure 1. A simplified depiction of the Bering Sea food web: (1) ice algae; (2) phytoplankton; (3) copepods; (4) mysids and euphausiids; (5) medusae; (6) hyperiid amphipods; (7) seabirds; (8, 9) pelagic fishes; (10) walrus; (11) seals; (12) basket stars; (13) ascideans; (14) shrimps; (15) filter-feeding bivalves; (16) sand dollars; (17) sea stars; (18) crabs; (19) bottom feeding fishes; (20) polychaetes; (21) predatory gastropods; (22) deposit feeding bivalves (from McConnaughey and McRoy, 1976).

[4] A more refined depiction of food webs (energy flow food webs) highlights the trophic level of each species and the relative strength of the interactions (based on the amount of energy flowing from producers and consumers (e.g., Figure 2). Here species or groups of species are placed according to their trophic level (calculated as 1.0 plus the mean trophic level of the species that they consume), and the size of each box is relative to the biomass of the species.

[5] Energy flow food webs convey considerably more information about the ecosystem than do topological food web drawings. However, both fail to convey which interactions are critical to maintaining the ecosystem in its normal state. For example, regardless of the amount of energy consumed or produced in a near-shore marine ecosystem, removing limpets would have little effect compared to removing urchins, because urchins dramatically alter the physical structure of the ecosystem by consuming kelp. Functional food webs thus differ from the other two depictions of food webs by highlighting the linkages that are most important to community structure (Paine, 1980; Huxham *et al.*, 1995). However, functional relationships are not yet well enough understood to make this a practical depiction of food webs.

[6] Food webs are built by knowing which producers are eaten, and in what proportion consumers eat them. Stomach contents have been the principal source of dietary data and continue to be the main tool for identifying the numbers, sizes and types of species consumed by fish (e.g. Christensen 1995). Seabird and marine mammal diets are determined in a similar manner (e.g. Pauly *et al.*, 1998; Santos *et al.*, 2001), although attempts are being made to determine diet from alternative means. Fatty acid signatures are one of the newer means of identifying prey of whales and seals from milk samples, blood samples and blubber biopsies (e.g. Grahl-Nielsen and Mjaavatten, 1991; Iverson *et al.*, 1997; Kirsch *et al.*, 1998). Seal diets are more commonly being determined now from the hard parts (bones, eye lenses and beaks) found in stomachs or faecal remains collected from sites where animals haul out and rest (e.g. Tollit *et al.*, 1997; Kirkman *et al.*, 2000; Cottrell and Trites *in press*). Stable isotope analysis is yet another recently developed technique for determining diet (e.g. Wada *et al.*, 1991; Kaelher *et al.*, 2000; Kelly, 2000).

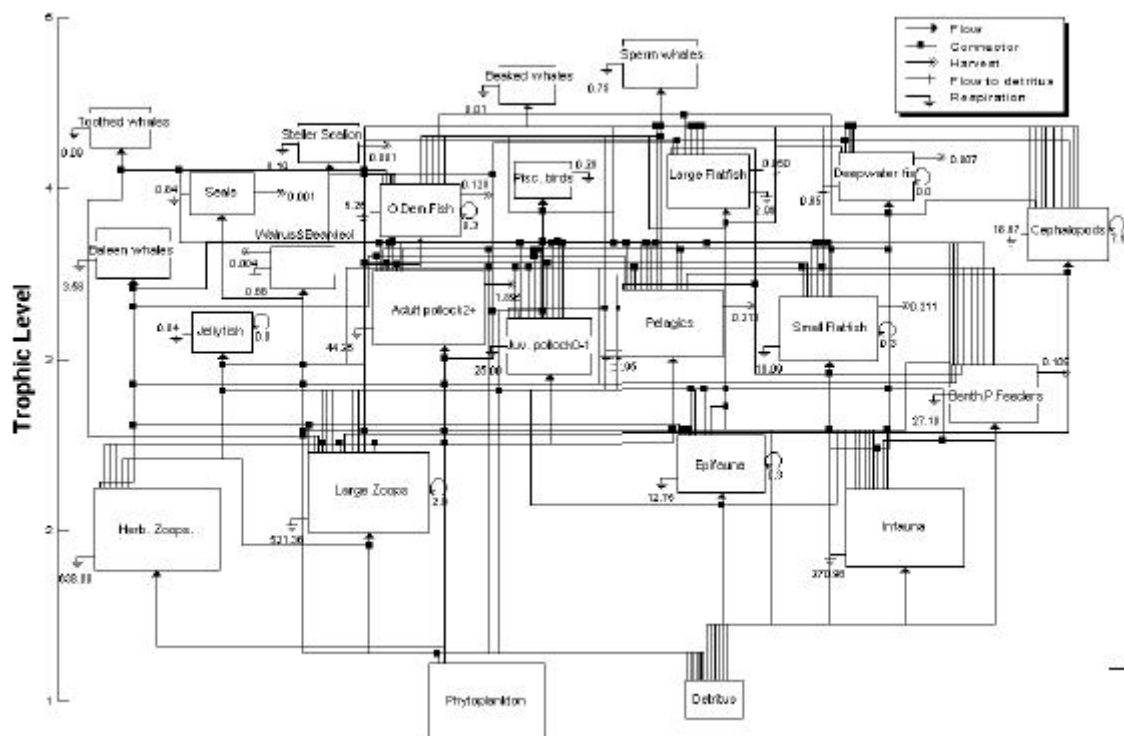


Figure 2. Flowchart of trophic interactions in the eastern Bering Sea during the 1980s. All flows are in t/km²/yr. Minor flows are omitted, as are all backflows to the detritus. The size of each box is roughly proportional to the biomass therein (from Trites *et al.*, 1999).

Comparative analyses

[7] Over the past 80 years, food web research has sought to reduce complexity and identify recurring patterns that might infer underlying mechanisms or represent constraints on ecosystem structure (e.g. Summerhayes and Elton, 1923; Elton, 1927; Cohen, 1977, 1978; Pimm, 1982, 1991; Lawton and Warren, 1988; Lawton, 1989; Cohen *et al.*, 1990; Winemiller, 1990; Christensen and Pauly, 1993; Hall and Raffaelli, 1996; Raffaelli, 2000). Based on comparisons of food webs (mostly terrestrial ecosystems), a number of generalizations have been postulated about the sizes of organisms, the lengths of food chains, and the stability of ecosystems.

[8] Elton (1927) was among the first to remark that animals occupying successively higher trophic levels tended to be larger, and that there were upper and lower limits on the size of food that they can eat. Humans are one of the few species that can consume prey of any size and can feed at more than one trophic level. As noted by Krebs (1996), this is one of the reasons that humans are so biologically successful. Omnivorous species are relatively rare, although there are species of fish that eat their way up the food chain as they grow. Organisms at the base of the food web tend to be more numerous than species at higher trophic levels, and are often represented as a pyramid of numbers and size (total biomass) to assess the relative distribution of biomass among trophic levels within an ecosystem (Figure 3).

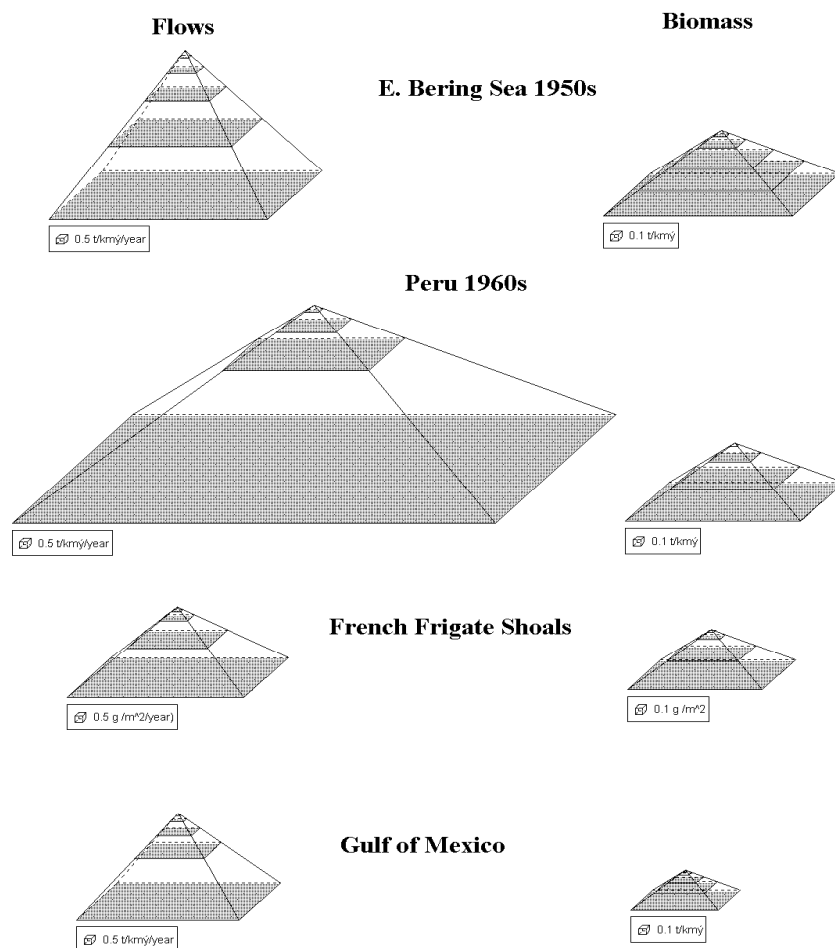


Figure 3. Trophic pyramids representing the distribution of biomass and energy flow in four ecosystems. The pyramids are scaled so that the volume at each trophic level corresponds to the sum of all flows at that level. The top angles are inversely proportional to the transfer efficiency (acute angle = high efficiency) (from Trites *et al.*, 1999).

[9] Overall, system biomass is proportional to primary production (Pimm, 1982), and the proportion of species occupying top, intermediate and basal trophic levels appears to be constant across food webs (Cohen, 1978). There also appears to be a constant ratio of 2-3 species of prey for every predator in an ecosystem (Martinez, 1991).

[10] A number of biologists have noted that food chains are typically short (Elton, 1927; Hutchinson, 1959; Pimm and Lawton, 1977; Pimm, 1982; Ricklefs and Miller, 2000). However, the average number of links appears to be longer in marine ecosystems compared to freshwater communities, grasslands, or wet tropical forest (Briand and Cohen, 1987; Ricklefs and Miller, 2000). Christensen and Pauly (1993) compared 41 aquatic ecosystems and found average path lengths of 2-5 linkages. The longest average path lengths were in tropical estuaries (3.0-5.0), followed by tropical shelves (2.8-4.0) and oceanic upwelling areas (2.2-2.8) (Baird *et al.*, 1991; Christensen and Pauly, 1993). Maximum chain lengths were 8 in tropical shelves, 7 in tropical estuaries and 6 in oceanic upwelling areas (Christensen and Pauly, 1993). This is further supported by a review of 75 aquatic food webs that found only three with maximum food chains longer than 6 (Schoener, 1989).

[11] It appears that the average number of feeding links per species (linkage density) increases as the size of the web (i.e. number of species) increases. This implies that the number of prey that a predator will eat increases in proportion to the total number of species in that community. However, the number of links relative to all possible links (connectance) decreases as the number of groups in a food web increases (Pimm, 1982; Christensen and Pauly, 1993). Martens (1987) suggested that this might reflect an increase in ecosystem stability. However, Christensen and Pauly (1993) conclude that any interpretation of connectance is ambiguous due to the binary nature of its scoring (i.e. either a link exists or it does not, irrespective of the fraction of diet it represents).

[12] The length of food chains may be a function of the amount of primary production at the base of the food pyramid, and the efficiency with which energy is transferred from one trophic level to the next (Hutchinson, 1959; Slobodkin, 1960). Higher rates of transfer efficiency presumably mean that more energy can be passed up the food chain to support more species. However, Pimm (1991) disputes this explanation, noting that some areas of high ocean productivity have short food chains. He argues instead that longer food chains are associated with stable environments, while shorter food chains are in less predictable environments. Species at the end of long food chains would be at risk of extinction if the abundance of species lower in the food chain fluctuated severely.

[13] In general, it appears that food webs in variable environments have fewer linkages than webs in more constant environments (Briand, 1983). However, it has also been shown experimentally that food chains are longer in more productive environments (Pimm and Kitching, 1987; Jenkins *et al.*, 1992), and that population dynamics are less stable in long food chains than in short ones (Lawler and Morin, 1993). Thus it appears that the length of food chains is a function of both environmental stability and energy transfer efficiency.

Limitations of food webs

[14] Food webs, such as those shown in Figures 1 and 2, are collages of species interactions that sometimes conceal more than they reveal (Paine, 1988; Raffaelli, 2000). For example, some of the interactions may not occur simultaneously, or they may change over seasons or years. They also tend to be over-simplifications. Similarly, some interactions, such as parasite/pathogen host interactions or mutualistic interactions, may be critical to community dynamics but fail to be captured by food web depictions (Cohen, 1993; Paine, 1994; Huxham *et al.*, 1995; Hall and Raffaelli, 1996).

[15] Food web diagrams are useful tools for conceptual understanding of ecosystems despite their shortcomings and the inadequacy of many of the food webs used in comparative analyses

(see critiques by Paine, 1988; Polis, 1991; Hall and Raffaelli, 1993, 1996). With the advent of quantitative ecosystem modelling tools (e.g. Christensen and Pauly, 1992; Jørgensen, 1998), food web analysis is leading towards a better understanding of food web structure and the design of better management strategies for conservation. The structure of food webs has implications for community persistence (Pimm, 1991), and may provide insights into which systems can support additional species, and which are unstable and susceptible to species losses. This is particularly relevant to understanding the effects on food webs of culling (e.g. Yodzis 1998), overfishing (e.g. Christensen, 1998; Hacquebord, 1999; Jackson *et al.*, 2001), or introducing exotic species (e.g. Grosholz *et al.*, 2000). Food web analysis may also help to identify which processes are critical to the ecosystem, and highlight which components need more research (Wooten, 1994).

FOOD CONSUMPTION

[16] Consumption can be expressed as the total amount eaten, or as the rate (i.e., velocity) that energy is ingested. It can also be expressed as a proportion of primary production in the food web. For the purpose of this review, consumption is defined as the amount of food eaten in a fixed period of time (i.e. days or years).

[17] Organisms require energy for growth, reproduction, physical activity, and maintenance of cells and organs – and must ingest sufficient calories to meet these fixed costs of living. However, organisms cannot assimilate all of the energy contained within the food they ingest, due to differences in the nutrient content and digestibility of different types of prey. For example, an organism that ingests excess nitrogen in its diet will excrete it as energy in the form of nitrogen-containing organic waste. Thus, energy that is digested and absorbed (assimilated energy) is a function of digestive physiology and of the make up of the prey (e.g. proportion of bones, scales, exoskeleton, etc.). Digestibility of prey may also vary by season. Generally, foods of animal origin are easier to digest than foods of plant origin, and vertebrates are easier to digest than invertebrates. Thus assimilation efficiency depends on the quality of the diet (particularly the amount of digestion-resistant structural material it contains) and varies from about 15% to 90%.

[18] Assimilated energy can be used by the organism for the synthesis of new biomass (production) through growth and reproduction, which can be consumed by organisms at higher trophic levels. Net production efficiencies are lowest in organisms whose costs of maintenance and activity are greatest, and highest in species with low maintenance and activity costs (e.g. 2-6% production efficiency in mammals, 40-80% in fish, 300% in cephalopods, and 500-600% in zooplankton – from P/B ratios in Trites *et al.*, 1999). Non-assimilated energy – excreted in the form of waste – contributes to detritus and is consumed by species specializing in digesting recalcitrant materials. Within the context of an ecosystem, no energy is wasted energy.

Estimating energy requirements

[19] There are a number of ways to estimate the amount of food consumed by marine organisms. Stomach content analysis is one method of determining daily ration, but involves making a number of assumptions about frequency of feeding and seasonal changes in energy requirements (e.g. Jarre *et al.*, 1991). Another approach is to infer feeding rates from those of captive fed individuals, or to measure the metabolism of free-ranging individuals (e.g. via doubly labelled water) or of captive individuals (via oxygen exchange) (e.g. Winberg, 1956; Mann, 1978; Innes *et al.*, 1987). An alternative, but practically impossible method in aquatic systems, is to derive consumption from estimates of biomass missing from lower trophic levels. A fifth approach is modelling.

[20] Models typically synthesize information (either measured or assumed from related species) about the costs of basal metabolism, activity, growth, reproduction, excreted waste and assimilation efficiencies – and range from simple to detailed accountings. The simplest approach estimates food consumption as a function of food conversion efficiency and mean individual

weight (e.g. Kendeigh *et al.*, 1977; Croxall *et al.*, 1984; Pauly, 1986, 1989; Innes *et al.*, 1987; Christensen, 1995; Guinet *et al.*, 1996; Trites *et al.*, 1997; Lourdes *et al.*, 1998). A more detailed approach – but more difficult to parameterize – calculates the costs of *Respiration* (the energy used for work that is degraded to heat), *Production* (energy deposited into tissue growth, fat storage, eggs, sperm, etc.), and *Faeces* and *Urine* (energy excreted from the body) such that

$$\text{Consumption} = (\text{Faeces} + \text{Urine} + \text{Respiration} + \text{Production})$$

for an organism that is in energy balance (e.g. Klekowski and Duncan, 1975; Stenson *et al.*, 1997; Winship *et al.*, *in press*). Multiplying the mean individual consumption by population density yields an estimate of total consumption by a group of organisms.

[21] Energy requirements are a function of body size and assimilation efficiency of different diets. Metabolic needs for maintenance are a function of body weight raised to 0.75, and thus decrease as body size increases (Kleiber, 1975). This means that metabolic rates per unit mass may vary greatly among differentially sized individuals of the same species, with young animals having the highest rates of consumption compared to mature individuals that have finished growing. Thus, estimating consumption requires estimates of animal density, performance and assimilation efficiency, which in turn depend on animal physiology, and on the digestibility and other nutritional properties of the food.

[22] On average, consumption of marine organisms, expressed as a percentage of an individual's body weight per day, ranges from about 20-30% for zooplankton, to 10% for cephalopods, 1-4% for fish, 4-8% for marine mammals, and 15-20% for sea birds (calculated from Q/B ratios in Trites *et al.*, 1999, and Christensen, 1995). However, consumption is not constant throughout the year, but varies with seasonal growth and reproduction (e.g. Paul *et al.*, 1993, 1998; Winship *et al.*, *in press*). Some organisms, such as baleen whales, may only feed for 6 months of the year, while other may fast for periods of days or weeks (Pauly *et al.*, 1998). Finally, the nutritional quality and energy content of prey may also change seasonally (e.g. Paul *et al.*, 1993, 1998).

Transfer efficiencies and residency times

[23] The number of trophic levels in marine ecosystems averages between 4 and 6, and appears to increase from coastal systems to reefs and shelves, and decline for upwelling systems (Christensen and Pauly, 1993). The fraction of energy that enters one trophic level and passes on to the next higher trophic level (ecological efficiency) is typically low – of the order of 5-20% (Lindeman, 1942) – and decreases with higher trophic levels due to increased respiration (Burns, 1989). Thus, productivity is typically only 5-20% of the level below it. Most energy held within a trophic level is dissipated before it can be consumed by organisms feeding at the next higher trophic level.

[24] As a general rule of thumb, production efficiency decreases at higher trophic levels, and ecological efficiency (assimilation or gross production at level n divided by that at level $n-1$) remains constant between trophic levels, at about 10% (Kozlovsky, 1968; Pauly and Christensen, 1995). A comparison of aquatic ecosystems suggests ecological efficiencies of about 10% for herbivores and detritivores, 11% for the next trophic level, and lower efficiencies of 9.0-7.5% at higher levels (Christensen and Pauly, 1993). Ultimately, the amount of energy reaching each trophic level depends on the net primary production at the base of the food chain and on the conversion efficiencies. Thus, high fish catches are associated with high primary productivity and with fishing at lower trophic levels (Christensen, 1996).

[25] The resident time of energy at each trophic level can be calculated by dividing the biomass (total stored energy) by net productivity (the rate at which energy is converted into biomass). This is effectively the time it takes energy to flow through the ecosystem (Ricklefs and Miller, 2000). Average resident times in marine ecosystems range from about 6 days for phytoplankton to 2 months for zooplankton, to 4 months for cephalopods, 8 months for crabs and shrimp, 1.5 years for fish, 15 years for seals and 50 years for whales (calculated from the inverse of the P/B

ratios in Christensen, 1995, and Trites *et al.*, 1999). Upwelling systems generally have shorter residency times than shelves, reefs and estuaries (Christensen and Pauly, 1993). Longer residence times reflect greater accumulations of energy. Residence times for aquatic primary production are extremely short compared to terrestrial systems (Rickleffs and Miller, 2000).

FOOD WEBS AND CONSUMPTION IN THE BERING SEA

[26] A considerable amount of research is currently being focused on the eastern Bering Sea ecosystem, due largely to the decline of Steller sea lions (1977 to present) and their listing by the USA in 1997 as an endangered species (Alverson, 1992; Trites and Larkin, 1996; Loughlin, 1998). The cause of the population decline is not yet known, but may be related to a decline in prey abundance caused by fisheries or natural changes in the ecosystem (Alaska Sea Grant, 1993). Food web analysis and estimates of prey consumption are essential pieces of information needed to resolve this issue.

Bering Sea food web dynamics

[27] Stomach contents and biomass estimates of fish, invertebrates, birds and mammals were collected by the then Soviet Union during the 1950s, and by the US National Marine Fisheries Service since the 1970s. Food webs constructed for the 1950s and 1980s (before and after the Steller sea lion decline started) suggest that the linkages between species were the same in each era (Figure 2), but that dramatic changes occurred in the biomass of each group and in the amount of energy passing from one group to another (Trites *et al.*, 1999). The mass balance ecosystem models constructed by Trites *et al.* (1999) suggest that most of the top predators (Trophic Level IV) declined from the 1950s to the 1980s, along with a significant number of mid-trophic-level species (i.e. crabs, shrimp and forage fishes such as herring and sandlance – Trophic Level III). Species that increased dramatically during this period (Figure 4) included walleye pollock (Level III) and large flatfish (Level IV). Pollock appear to have contributed over 50% of the energy transferred at the mid-trophic levels during the 1980s compared to only 10% in the 1950s. In contrast, pelagic fishes contributed nearly 50% of the total Bering Sea energy flow in the 1950s.

[28] Stomach contents of Steller sea lions in the Gulf of Alaska suggest changes in their diet that are consistent with stock assessments and model predictions (Table 1). During the 1950s, Steller sea lion stomach samples contained mostly pelagic fishes (herring and sandlance), some gadids (pollock and cod), and no flatfish. From the 1960s to the 1990s, however, the dietary concentration of pelagic fishes fell, while gadids and flatfish became more prevalent (Table 1).

Table 1. Changes in the frequency of occurrence of major prey types in diets of Steller sea lions in the Gulf of Alaska

Period	Gadids	Flatfish	Pelagics
1950-60s	few	none	mostly
1976-78	32%	0%	61%
1985-86	60%	5%	20%
1990-93	85%	13%	18%

SOURCE: from Merrick *et al.*, 1997

[29] Attempts to simulate the effects of commercial fishing on the Bering Sea ecosystem failed to explain the change in ecosystem dynamics between the two eras (Trites *et al.*, 1999). Fishing could not explain the decline of forage fish species (most of which were never fished), nor could it explain the 60% increase in large flatfish or the 400% increase in pollock. Food web interactions could not account for the magnitude of changes that occurred in the eastern Bering Sea. Instead, it appears that the survival of a suite of species was favoured over another by a combination of natural environmental changes in water temperatures and ocean currents. This is commonly referred to as a regime shift (Francis and Hare, 1994; Anderson *et al.*, 1997; Beamish *et al.*, 2000; Benson and Trites, *in review*), and suggests that the Bering Sea can exist in at least two alternative stable states that support suites of species at alternatively high and low population levels (Trites *et al.*, 1999). Ecosystem indices from the models suggest that the Bering Sea was more 'mature' (*sensu* Odum, 1971) in the 1950s than in the 1980s, but is overall relatively resilient and resistant to perturbations (Trites *et al.*, 1999).

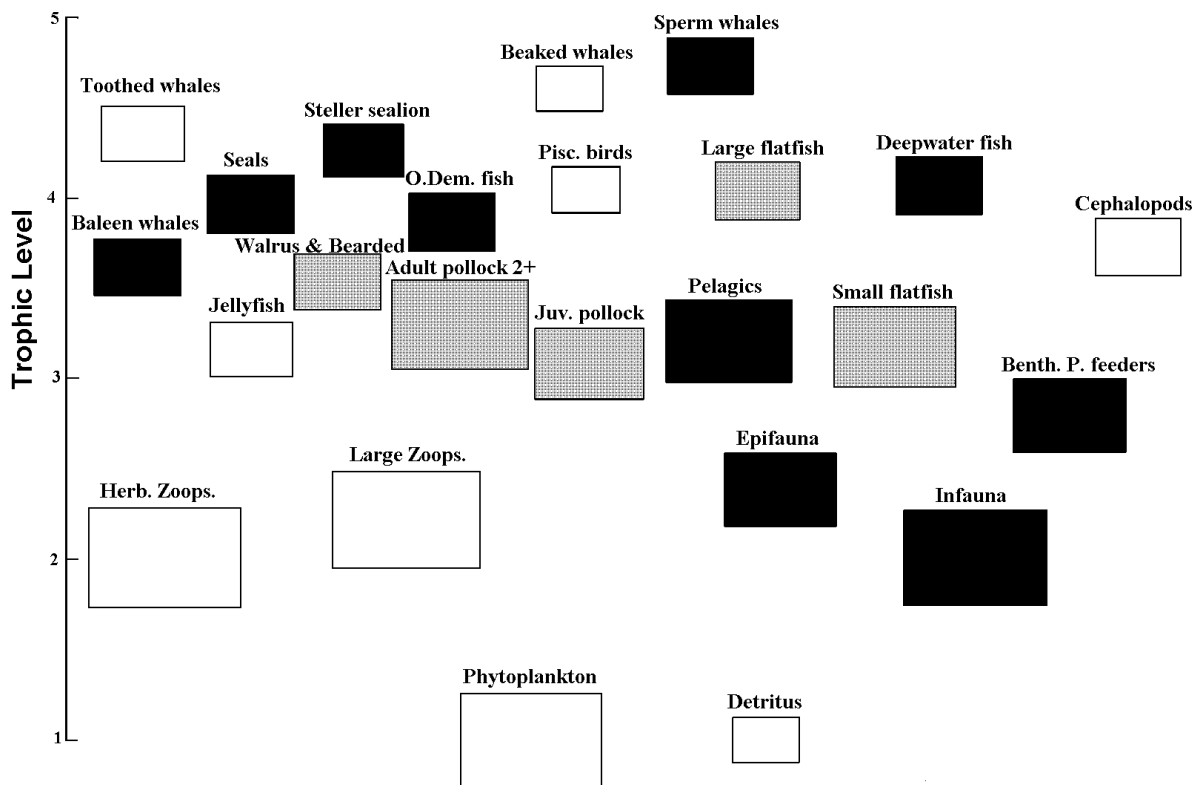


Figure 4. Estimated trophic levels and relative abundance of species in the eastern Bering Sea during the 1980s. Blackened boxes indicate groups that had lower abundance in the 1980s relative to the 1950s, and shaded boxes show species that had higher abundance in the 1980s relative to the 1950s. Major flows of energy between the boxes are shown in Figure 2 (from Trites *et al.*, 1999).

[30] Pollock and/or Atka mackerel (a hexagramid related to lingcod) currently dominate the diets of Steller sea lions in the declining populations that border the Bering Sea. This is in sharp contrast to the diets of growing sea lion populations in southeast Alaska and British Columbia that contain a more diverse array of prey (i.e. salmon, rockfish, forage fish, gadids and flatfish). Dietary diversity correlates with the rates of sea lion population change (Merrick *et al.*, 1997), and suggests that the recovery of Steller sea lions is linked to consuming a more diverse range of species with higher fat contents than they are currently obtaining.

[31] Recent field observations of foraging Steller sea lions suggest that they preferentially choose herring over pollock (Thomas and Thorne, 2001). This is consistent with predictions of the junk food hypothesis, which proposes that Steller sea lions have declined because they have been consuming too much pollock, which contain fewer calories, and not enough of the fatter, high-energy fishes (Alverson, 1992; Rosen and Trites, 2000b).

Estimating energy requirements

[32] Understanding how a change in diet could affect Steller sea lions comes from laboratory analysis of sea lions (digestive efficiencies and metabolism) and their prey (caloric and nutritional value). For example, bomb calorimetry analysis shows that herring (6-11 kJ g⁻¹) has more energy per unit density than do salmon (5-9 kJ g⁻¹), pollock (3-5 kJ g⁻¹) or squid (4-6 kJ g⁻¹) (from data compiled by Winship and Trites, *in review*). Feeding trials with captive Steller sea lions show that digestive efficiency (90-95% of gross energy intake) increases with prey energy density, while heat increment of feeding (21-13% of gross energy intake) decreases with increasing prey energy density (Rosen and Trites, 1997, 1999, 2000a). Digestive efficiency is the proportion of usable energy within a prey, and heat increment of feeding is the proportion of energy that is burnt during the mechanical and biochemical processes of digesting a prey item. Thus Steller sea lions can digest prey with the higher fat content more easily than they can digest leaner prey. It also

turns out that Steller sea lions have to burn more of the energy contained within larger prey to digest them than they do from smaller meal sizes (Rosen and Trites, 1997). Thus a Steller sea lion would have to eat an average of 56% more pollock than herring to obtain an equivalent amount of energy because pollock are bigger prey, contain fewer calories and require more energy to digest than do herring (Rosen and Trites, 2000b).

[33] Estimating the amount of prey that Steller sea lions require can be determined by incorporating estimates of diet composition, digestive efficiencies, heat increments of feeding, activity budgets, body growth, basal metabolism and population size into bio-energetics models (Winship *et al.*, *in press*, Winship and Trites, *in review*). They indicate that Steller sea lions require more food in winter and spring than they do during summer and fall (about 40-55% more), and that the average sea lion requires about 17 kg of prey per day, or 6 000 kg per year. Within different regions of Alaska, per caput food requirements differ by as much as 23%, depending upon the relative amounts of energy-poor prey (gadids) versus energy-rich prey (e.g. forage fish and salmon) is consumed (Figure 5; Winship and Trites *in review*).

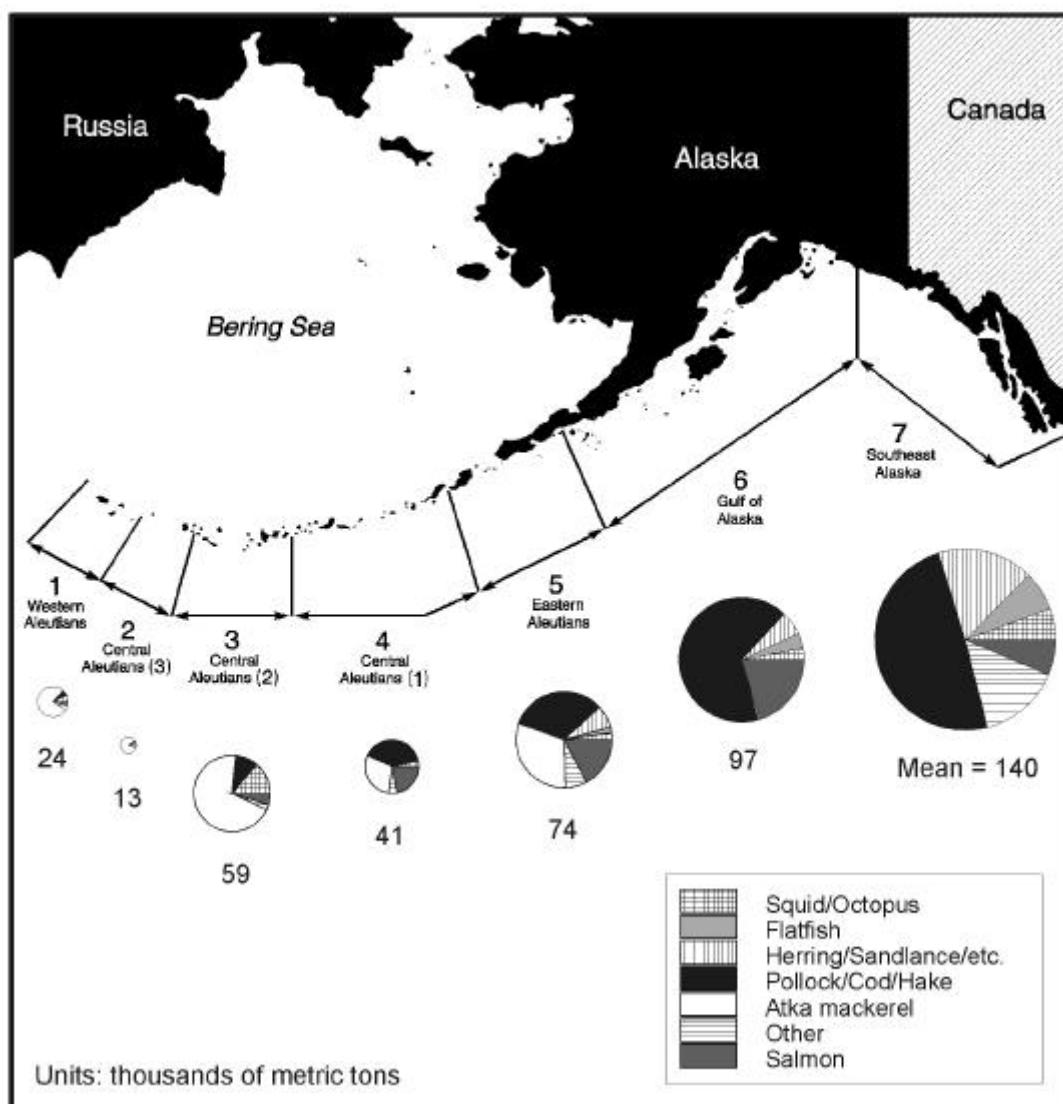


Figure 5. Estimated annual food biomass requirements (thousands of metric tons) for Steller sea lions in 1998 in seven study areas of Alaska, assuming that the summer diet was consumed all year long. Pie charts represent the proportions of diet biomass represented by each prey species category. Diameters of the pie charts are proportional to their respective mean food requirement estimates. Food requirements were calculated assuming digestive efficiency and the heat increment of feeding for maintenance did not vary with prey energetic density.

[34] In 1998, the biomass of pollock and cod in Alaska was estimated at 9.50 million t (7.37 million t pollock, 2.13 million t cod), with an annual natural mortality of 3.29 million t (2.61 million t pollock, 0.67 million t cod), and a total commercial catch of 1.52 million t (1.25 million t pollock, 0.27 million t cod) (see Winship and Trites, *in review*). Total annual gadid consumption by Steller sea lions for all regions of Alaska was 0.18 million t (Winship and Trites, *in review*). Thus, consumption of gadids by Steller sea lions represented about 2% of the stock, or 5% of natural mortality, or 12% of commercial landings). Gadid consumption by Steller sea lions appears to be small relative to total gadid natural mortality and stock size, which is consistent with conclusions drawn by Livingston (1993).

[35] Differences in the quality of prey available to Steller sea lions have consequences on the individual, and ultimately the population. One strategy an animal can invoke when faced with an energy shortage is to reduce the amount of prey they require by reducing their energy expenditures. Captive experiments have shown that Steller sea lions can reduce their metabolism by an average of 31% when food is withheld from them, which is typical of a fasting response (Rosen and Trites, *in review*). However sea lions do not appear to reduce their metabolism when on a low-fat diet, despite losing body mass (Rosen and Trites, *in review*). Instead, they exhibit a hunger response, which might lead them to increase their foraging effort in the wild. However, increased foraging effort has an increased energetic cost, as well as an increased risk of exposure to predation by sharks or killer whales.

[36] Recently weaned young are the segment of the population most likely to incur the greatest cost of reduced caloric intake. Energetically, a 1-year-old female must consume about twice the relative quantity of prey compared to a mature female (14% of her body weight per day eating a mixed diet, compared to 7% for a mature female – Winship *et al.*, *in press*). This same yearling female would require 11% of her body mass per day if she ate only small schooling fish, or 19% if she ate only gadids (Winship and Trites, *in review*). These energy requirements could well be twice these values (i.e. 22-38% of body mass), considering that Steller sea lions do not eat every day, but typically fast for a day between their one- or two-day feeding trips (Trites and Porter, *in press*).

Synthesis

[37] Combining the individual energy requirements with information about the changes that occurred in the Bering Sea energy food web suggests that the population decline of Steller sea lions in Alaska is probably related to the inability of young animals to acquire sufficient energy from the low-quality prey available to them. There is no indication of there being a shortage of low quality prey. However, the energetic modelling and captive feeding studies suggest it may not be physically possible for young Steller sea lions to consume enough of them to meet their daily energetic needs. Consuming fewer calories can stunt growth and cause reproductive failure (i.e. abortions) – symptoms that have been observed in Alaska over the time that Steller sea lions have declined (Calkins *et al.*, 1998; Pitcher *et al.*, 1998). A lower nutritional plane may also increase the susceptibility of sea lions to disease, and increase their risk of being killed by predators – a factor that may account for the apparent high mortality of juvenile sea lions (York, 1994). Mathematical modelling suggests that killer whales could have been a significant contributing factor in the decline of Steller sea lions, and may now be preventing the population from recovering (Barrett-Lennard *et al.*, 1995).

CONCLUSIONS

[38] The Bering Sea case study is an example of the importance of constructing food webs and estimating the energy requirements of marine organisms to understand ecosystem dynamics. This can only be achieved through a combination of fieldwork, captive studies and mathematical models – all of which are essential tools for the responsible management of fisheries and ecosystems. Food webs and energetic modelling shed light on the consequences of removing or

adding one organism, and on the role that humans play in shaping the dynamics of marine ecosystems. More importantly, they are essential techniques for recognizing what our marine ecosystems once were, what they are currently, and what they might be in the future.

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