A Forage Fish Is What? Summary of the Symposium

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Introduction

And well you might ask what a forage fish really is. "Forage fish" is a concept that many people have come to understand because of the context it is used in, but for which we lack a concrete definition. The term embodies a peculiar combination of ambiguity and precision. It lacks clear taxonomic classification, and it lacks sound ecological distinction because it excludes animals, notably squids, that have the same functional role. The answer, in the strict sense, must be any fish in the sea that becomes the meal of a predator. However, this would include, in all probability, all species at some stage of their life cycle. But the forage fishes do not include all the species, only a small subset. In the words of the organizing committee for this conference, "Forage fishes are abundant, schooling fishes preyed upon by many species of seabirds, marine mammals, and other fish species. They provide important ecosystem functions by transferring energy from primary or secondary producers to higher trophic levels."

How small a subset? Very small, but the actual number is a little vague. For example, there are about 290 species of fishes in the Gulf of Alaska (OCSEAP Staff 1986), of which perhaps 6-8, just 2-3%, satisfy this definition of forage fishes. Or, as another example, at least 47 species of fishes have been identified as prey of California sea lions (*Zalophus californianus*) (Lowry et al. 1990). However, 41 species each constituted less that 0.5% of the total number of prey, while one species, northern anchovy (*Engraulis mordax*), constituted 54%. On this basis, the anchovy would be considered a proper forage fish, while the uncommon 41 species likely would not. The remaining 5 species contributed between 3% and 12% of total numbers, and thus might or might not be considered forage fishes.

Note: In this summay, literature references with dates are listed in the References section at the end of the paper. References without dates appear in this proceedings.

What are some others? Well, sand lance (*Ammodytes* spp.)—sand lance is a quintessential forage fish. As a group of very closely related species, it is possibly the single-most important taxon of forage fish in the Northern Hemisphere. *Ammodytes* is the prey of a wide variety of marine fishes, birds, and mammals composing a huge biomass (e.g., Furness 1990), and as a consumer of zooplankton, it has added importance to ecosystem structure (Sherman et al. 1981, Payne et al. 1990). Populations of sand lance wax and wane, and when they do there are usually very noticeable effects at other trophic levels (e.g., Monaghan et al. 1989).

Pacific sand lance (*A. hexapterus*) is one of the classic forage fishes in the Gulf of Alaska. Others are capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), herring (*Clupea pallasi*), juvenile walleye pollock (*Theragra chalcogramma*), lanternfishes (Myctophidae, especially *Stenobrachius leucopsarus*), and Pacific salmon (*Oncorhynchus* spp.). Most of the same, or closely related, species also are important forage fishes in other regions of the North Pacific and North Atlantic (e.g., NMML 1981, Piatt et al. 1989, Sobolebskiy et al. 1989, Vader et al. 1990, Livingston 1993, Springer et al. 1996a). In Arctic seas, Arctic cod (*Boreogadus saida*) is an important forage fish (Bradstreet et al. 1986), while in temperate and tropical regions, the sardines, pilchards, anchovies, and flying fishes (Clupeidae, Engraulidae, and Exocoetidae) also satisfy this definition (Ashmole and Ashmole 1967, Schaefer 1970, Anderson et al. 1980, Furness and Cooper 1982). Species that were considered to be forage fishes by participants at this conference are listed in Table 1.

The primary objective of the conference was "to provide findings to assist in the multispecies management of Alaska marine ecosystems, especially those of the Bering Sea and Gulf of Alaska including the *Exxon Valdez* oil spill region." Why do we particularly care about forage fishes in Alaska? Probably the biggest reason is the dramatic, unexplained decline in the past 15-20 years of Steller sea lions (*Eumetopias jubatus*) throughout much of their range in the Gulf of Alaska and Aleutian Islands and concurrent declines of harbor seals (*Phoca vitulina*) in the Gulf of Alaska, fur seals (*Callorhinus ursinus*) in the Bering Sea, and several species of seabirds in both the Gulf of Alaska and the Bering Sea. A variety of evidence points to lack of food as the likely cause of the declines (Anonymous 1993, NRC 1996). All of the species of concern depend on a similar suite of forage fishes, including walleye pollock, the target of a major commercial fishery.

Additional, pivotal motivation for learning more about forage fishes was provided by the wreck of the oil tanker *Exxon Valdez* in 1989. Although a lack of knowledge about conditions prior to the spill hampered an assessment of its effect on resources in Prince William Sound and downstream in the central Gulf of Alaska, a lack of forage fishes is limiting the recovery of seabirds and marine mammals from direct effects of the oil or from other factors that predated the spill (Piatt and Anderson 1996).

The conference was organized around a number of themes that emerged as papers concerning one or more of the interrelated issues of forage fish basic biology, their role as predators and prey, causes of population fluctuations, assessment methodologies, and management considerations. The papers in this volume are grouped according to subject, but many of them contain information on a variety of aspects of forage fish biology and ecology that can only be discovered by examining them all.

Feeding and effects on prey populations

Diets of forage fishes in general vary according to the size of the fish. Small fishes, whether young age classes of species that grow to large sizes, such as gadoids (cods), or species that never do get very large, such as sand lances, are generally planktivorous. As they grow to larger juveniles and, for some, to adults, their diets change from very small items, like diatoms and copepod eggs and nauplii, to larger copepods, euphausiids, and other mesozooplankton (Ciannelli, this volume; Ciannelli and Brodeur, this volume; Orlov, p. 209 and 323 this volume; Paul et al., p. 633 this volume). As individuals of larger species grow, their diets typically contain progressively more fishes, including occasionally large numbers of their own young. In areas where two or more forage species occur, diet diversity can reduce interspecific competition for prey (Willette et al., this volume). Intraspecific competition is reduced by mechanisms such as behavioral differences between sexes (Orlov, p. 209 and 323 this volume) and size classes (Paul and Willette, this volume).

There is some evidence and conjecture that forage fishes can have substantial positive and negative effects on prey populations. On one hand, copepod eggs passed through the guts of herring in the Baltic Sea have a high likelihood of hatching, and of hatching into a water column that has been cleared of adults (Pers. comm., J. Flinkman, Univ. of Helsinki, Hanko, Finland, Nov. 1996). The purported benefit is that total copepod production is enhanced because the abundant juvenile copepods have to compete with many fewer adults which are more efficient grazers. On the other hand, it is estimated that feeding by young-of-year Atlantic herring in the coastal Baltic Sea accounts for 35-60% of the zooplankton consumption. A variety of top-down controls by herring are thought to be important in the dynamics of zooplankton populations, namely selective predation on particular taxa, effects on the vertical distribution of migrating copepods, and high consumption of the annual production (Arrhenius, this volume). Other examples of apparent depressing effects of fish on prey populations are: (1) changes in abundance of planktivorous whales in the northwestern Atlantic in relation to changes in abundance of sand lance, their chief competitor for zooplankton (Payne et al. 1990); (2) lower provisioning and depressed growth rates of least auklet chicks (*Aethia pusilla*) in the Bering Sea in years of abundant juvenile pollock, the chief competitor of auklets for calanoid copepods (Springer et al. 1986); and (3) special cases of cannibalism that are thought to be important to population dynamics of some populations, such as walleye pollock in the Bering Sea (e.g., Livingston 1989.)

In other cases, no effect of fish on prey populations has been found. In the southeastern Bering Sea, Dagg et al. (1984) estimated that pollock larvae consumed only a small fraction of their chief prey, copepod nauplii. The same conclusion was reached concerning the lack of a significant effect of larval pollock on nauplii prey in the Gulf of Alaska (Kendall et al. 1987). Juvenile wild and ocean-ranched Pacific salmon in Prince William Sound (Gulf of Alaska), totaling some 1.2×10^9 individuals entering the sound annually, consume only about 1-3% of the total production of herbivorous zooplankton and about 3-10% of the mesozooplankton production (Cooney 1993). Such a level of consumption is small at the spatial scale of Prince William Sound. It is perhaps misleading, however, in terms of impacts at smaller spatial scales. Juvenile salmon do not spread out uniformly across the sound, but feed near shore. They appear to aggregate in areas of abundant prey, but move on when prey is not abundant or has been depleted. Thus, in this case and probably most others, the question of whether forage fish have an effect on prey populations must be considered in particular spatial contexts.

Predators on forage fishes

Among all of the predators of forage fishes, besides humans, the most consequential are other fishes: certain species of forage fishes, for example, walleye pollock, consume more of themselves than do any other species (e.g., Dwyer et al. 1987; Livingston 1989, 1993). Specific predators discussed at the conference are shown in Table 2. A comprehensive list would include the majority of piscivorous species in the ocean. But for perspective, in addition to this rather short list, in the North Pacific, for example, there are numerous cetaceans, including particularly fin, minke, and humpback whales (*Balaenoptera physalus, B. acutorostrata,* and *Megaptera novaeangliae*) and harbor porpoises (*Phocoena phocoena*) (e.g., Lowry et al. 1982). Seabird predators of forage fishes not listed in Table 2 are nearly all of the other piscivorous species. A few notable examples are ivory gulls (*Pagophila eburnea*) and Ross' gulls (*Rhodostethia rosea*) that feed on Arctic cod (Divoky 1976) and northern gannets (*Sula bassanus*) that feed on mackerel (*Scomber scombrus*), herring, and capelin (Montevecchi et al. 1988).

Stock identification and assessment

Seabird biologists have been saying for years that the most efficient way to monitor the abundance of forage fishes in the broader issue of environmental change is to use the birds themselves (e.g., Cairns 1987, Furness and Greenwood 1993, Montevecchi and Myers 1996). Several papers in this symposium make a strong case for this approach, and for using other easily accessible predators of forage fishes to provide sensitive, low-cost measures of their abundance (Byrd et. al., this volume; Hayes and Kuletz, this volume; Logerwell and Hargreaves, this volume; Roseneau and Byrd, this volume). After all, any scheme for sampling forage fishes provides only an index of abundance, and traditional approaches using boats, nets, and hydroacoustics are vastly more expensive and often less precise because schooling fishes are highly mobile, will avoid boats, are patchily distributed, and often occur in the surface layer that is invisible to hydroacoustic sampling (Montevecchi and Myers 1996).

There is considerable resistance to adopting such an approach by fish scientists, and in defense of traditional sampling, e.g., with nets, predators do not always sample non-forage species and therefore they cannot provide the same level of detail about changes in fish communities that can be derived from traditional methods and that can be important to understanding ecosystem processes (e.g., Anderson et al., but see Montevecchi et al. 1988). Similarly, studies of predators cannot always provide the necessary details of the three-dimensional distribution of fishes that is needed to determine whether fish abundances have changed or only whether their availability to predators with foraging ranges limited by depth or distance. The utility of using predators for population assessment for commercial fishery management is debatable (Anderson et al. 1980, Adams et al. 1992, Montevecchi and Myers 1995).

One comparatively new assessment approach is the use of aircraft with novel ways of imaging fish schools. In Newfoundland, digital imaging spectrometry from aircraft has greatly improved upon aerial photography in detecting and differentiating capelin schools (Nakashima and Borstad). An innovative method being used in Puget Sound is beach surveys for spawn of sand lance and surf smelt (*Hypomesus pretiosus*) (Penttila, this volume).

All of the population assessment methods are hampered by the mobility of forage fishes, and while many are sensitive to changes in the distribution and behavior of fish, there remain questions about how well they measure the abundance of populations at various spatial scales in either absolute or relative terms (Blackburn, this volume; Carscadden and Nakashima, this volume). In the end, the best estimates likely will come from the use of a suite of assessment methods, each providing a particular kind of information on individual populations.

Forage fish stock variability

Although there remains considerable uncertainty about the accuracy and precision of estimates of forage fish abundance, there is little doubt that populations do undergo dramatic fluctuations in abundance in a variety of temporal and spatial scales (Anderson et al., this volume; Bechtol, this volume; Bogstad and Mehl, this volume; Emmett et al., this volume; Gjøsæter and Ushakov, this volume; Wilson, this volume). Populations of many species of forage fishes can increase rapidly because of particular life history strategies they have evolved, namely early maturation and high fecundity. Collapses can occur rapidly as well because of the sensitivity of eggs and larvae to predation and physical environmental impacts. Also, many species are not long-lived and their populations are not buffered against recruitment vagaries by having many age classes.

Causes of fluctuations in abundance

"In conclusion, it appears that 30 years after the onset of the gadoid outburst we are no closer to understanding its causes than at the time of the previous Århus Symposium." Thus John Hislop summed up his view of the current state of knowledge of why certain fish populations fluctuate over decadal time scales in the North Sea, where a daunting amount of work has been undertaken in an attempt to do just that (Daan and Richardson 1996, Hislop 1996). This issue of why populations fluctuate is likely the most intriguing, frustrating, and contentious of any surrounding forage fishes, or any fishes for that matter. A principal reason is the role of commercial fisheries in population dynamics of some species, i.e., an "unnatural" factor, versus the role that "natural" factors, such as climate fluctuations, can have.

The mechanisms by which fishing can affect fish populations are varied. The most obvious is the removal of fish at a rate faster than they are produced (Mackinson et al., this volume). Fishing can also have indirect, and not always deleterious, effects on forage fishes because of functional relationships between forage fishes and their predators. For example, on both sides of the Atlantic in the 1960s and 1970s there was a rapid increase in numbers of small, fast-growing sand lance as herring and mackerel populations declined. The loss of such a large biomass of predators of sand lance appears to have allowed the sand lance populations to proliferate (Sherman et al. 1981).

One thing we do know is that forage fish populations fluctuate in the absence of any form of human involvement (Baumgartner et al. 1992). Concurrent fluctuations in widely separated populations of sardines and salmon in the Pacific Ocean provide strong support for the notion that fish populations are greatly influenced by large-scale oceanographic processes (Mann 1993, Francis and Hare 1994). In recent times, from 1983 to 1986, capelin populations in the Barents Sea crashed dramatically, recovered somewhat, only to crash again from 1992 to 1994. Although they were heavily exploited from the early 1970s to 1983, fishing apparently had only a secondary role in the first collapse and practically no role in the second (Gjøsæter, this volume). Instead, changes in population size are attributed to life history characters of capelin, environmental factors such as changes in climate, and changes in the abundance and geographical distribution of predators in the Barents Sea, particularly herring, that caused nearly complete recruitment failure.

For other species, the evidence for fisheries effects on population change is compelling, as in the collapse of North Sea herring and mackerel populations in the face of intense exploitation (Serchuk et al. 1996). But the question remains of how those populations would have behaved in the absence of exploitation. The Icelandic summer-spawning herring population plummeted from about 10×10^6 t to 3×10^6 t in the decade between the mid-1950s and mid-1960s, well before the beginning of heavy fishing mortality, which then likely contributed to the continued collapse of the population to about 1% of its historic size by the mid-1970s (Rothschild 1995).

There are also strong indications that fishing had a major role in the collapse of Atlantic cod populations in Canadian waters and in the Barents Sea (Mehl 1991, Myers et al. 1997). Yet there remains uncertainty about the relative effects of fishing and climate on the populations—the outburst of gadoids in the North Sea beginning in the early 1960s was an anomaly in this century, and the fact that the populations have now returned to "normal," with or without fishing, is not necessarily surprising.

In the Bering Sea, populations of herring and Pacific ocean perch (*Sebastes alutus*) collapsed in the 1950s and 1960s following the development of major commercial fisheries, yet it is not known if or how they would have changed without the fisheries. Time series of abundances of these species begin with the inception of the fisheries, which developed rapidly and might have had a major impact on the dynamics of the populations. However, in southeastern Alaska and British Columbia, sea surface temperature and upwelling explain a large proportion of the variability in herring recruitment (Zebdi and Collie 1995, Schweigert, this volume). A trophodynamic model of plankton and fish (herring and hake) production in British Columbia indicated that interannual and longer-term variability in fish production is mediated by the efficiency of transfer of material and energy from diatoms to zooplankton (Robinson 1994). Variability in transfer efficiency is caused by the effect of upwelling on diatom production and trophodynamic phasing with zooplankton.

Ultimately, annual primary production sets the upper limit on fish production (Jones 1989), or perhaps more specifically, the amount of nitrate-nitrogen (new nitrogen) incorporated into phytoplankton biomass and transferred through food webs (Iverson 1990). Thus, an apparent long-term decline in the abundance of phytoplankton associated with climate change in the North Sea might have led to declines in, successively, zooplankton, herring, and seabird populations (Aebischer et al. 1990). Likewise, an apparent increase in primary production in the subarctic North Pacific in response to an atmospheric regime shift might have led to increases in secondary production and dramatic increases in several species of Pacific salmon and other fishes (Venrick et al. 1987, Francis and Hare 1994, Trenberth and Hurrell 1994, Brodeur et al. 1996). Hollowed and Wooster (1992) and Beamish and Bouillon (1995) found strong, long-term relationships between fish production in the North Pacific, winter ocean conditions, and the Aleutian Low Pressure Index, and concluded that meteorological conditions and the carrying capacity of the ecosystem fluctuated in parallel.

The environment can play numerous roles in the biology of forage fishes, as suggested by papers at the conference (Carscadden and Nakashima, this volume; Hay et al., this volume; Klyashtorin, this volume) and by earlier publications (e.g., Frank and Leggett 1981a, b). Paul et al. (this volume) described an application of the match-mismatch hypothesis (Hjort 1914, Cushing 1975) to explain differences in pollock recruitment between two years in the Gulf of Alaska.

Besides trophodynamic phasing, other variables that can lead to fluctuations in food web production include: onshelf Ekman transport of eggs and larvae of walleye pollock that removes them from predation by cannibalistic adults (Pers. comm., V. Wespestad and L. Fritz, National Marine Fisheries Service, Seattle, WA 98115, Nov. 1996); water temperature effects on zooplankton production and subsequent fish production (Bienfang and Ziemann 1995); water temperature effects on fish production via physiology (Laevastu 1984, Lin and Regier 1995); storms, wind mixing, and food availability to fish larvae in nursery layers (Lasker 1975, Nishiyama et al. 1982); oceanographic fronts and their effect on distributions of fishes and their prey (Brodeur et al.); and currents and the transport of eggs, larvae, and prey of forage fishes (Reed et al. 1989, Tomosada 1989).

Effects on higher trophic levels

Numerous predatory species depend on forage fishes for food, and changes in forage fish populations can have major consequences on the behavior and production of predator populations. For example, the occurrence of capelin in Atlantic cod (*Gadus morhua*) diets in the western Atlantic was proportional to the abundance of capelin: when capelin abundance was high, consumption was high (Methven and Piatt 1989). During the first half of the 1980s in the Barents Sea, the population grew by about 50% at a time when capelin were abundant. But when the capelin population crashed in the mid-1980s it had far-reaching direct and cascading effects. For medium-aged cod that depend most heavily on capelin, the annual consumption was reduced by up to 50%, which severely reduced individual growth rates. Cod switched to other prey, such as redfish (*Sebastes* spp.) and herring, greatly reducing their abundances. Also, cannibalism increased by a factor of 3, which further reduced the cod population that was already suffering from a general lack of food and heavy fishing mortality. The aggregate effect was a reduction of the Barents Sea cod population to a level far below that which was predicted (Mehl 1991).

In British Columbia, however, no statistically significant relationships were detected between herring abundance and the survival, growth, or abundance of its common predators, Pacific salmon, Pacific cod, and halibut (Schweigert, this volume). In that case, the predatory fishes were apparently able to switch to other prey when herring numbers were low, so that environmental effects were greater than predator effects given the availability of alternate prey.

Seabirds appear to be particularly susceptible to fluctuations in forage fish populations. Many species exhibit changes in diet in response to changes in prey populations (Furness and Cooper 1982; Springer et al. 1984; Anker-Nilssen et al., this volume; Hayes and Kuletz, this volume; Kuletz et al., this volume). When prey abundance is low, seabirds may increase foraging effort, suffer reduced chick growth and breeding success, may not breed at all, may emigrate, or may suffer increased mortality (Springer et al. 1986, Cairns 1987, Furness and Barrett 1991, Furness and Nettleship 1991, Hamer et al. 1991, Anker-Nilssen et al., this volume). In Shetland, numbers of breeding pairs of several species, including Arctic terns (*Sterna paradisaea*), great skuas (*Catharacta skua*), black-legged kittiwakes (*Rissa tridactyla*), and parasitic jaegers (*Stercorarius parasiticus*), declined as sand lance populations declined. In addition, terns, Atlantic puffins (*Fratercula arctica*), jaegers, and kittiwakes experienced complete breeding failure in some years when sand lance abundance was low (Furness and Barrett 1991, Furness and Nettleship 1991). During the development of the Peruvian anchovy (*Engraulis ringens*) fishery, seabird numbers decreased by more than an order of magnitude, apparently because birds were unable to rear sufficient chicks to balance the irregular adult mortality caused by periodic oceanographic perturbations (Schaefer 1970).

There are several documented cases in Norwegian waters of both increases and decreases in seabird populations that are correlated with changes in forage fish populations (Anker-Nilssen et al., this volume). The Atlantic puffin population declined from about 1.4 million pairs in 1979 to 500,000-600,000 pairs in recent years, and the decline was attributed to prolonged failure of chick production following the collapse of the Norwegian herring population in the late 1960s. While herring populations were depressed and unavailable in the 1980s, black-legged kittiwakes, common murres (*Uria aalge*), and Atlantic puffins fed their chicks >70% capelin, and had high reproductive success in most years. As herring populations recovered, the proportion of age-1 herring increased in the birds' diets, becoming a very significant component in some years (>90% for kittiwakes in 1993 and 1994). However, there was a clear negative relationship between the reproductive success of kittiwakes and the amount of herring in their diet, and it now appears that as herring replace capelin in the Barents Sea, kittiwake chick production is dropping and the overall kittiwake population in the Barents Sea is decreasing.

Dramatic responses of predators to short-term changes in forage fish availability in Norway have also been recorded (Anker-Nilssen et al., this volume). The collapse of the capelin population in 1986-1987 and the lack of suitable alternative prey, herring, precipitated (1) a collapse of 80% in numbers of breeding common murres between the two years at five colonies, (2) an invasion of starving harp seals into Norwegian waters, and (3) a crisis in the traditional Norwegian coastal cod fishery because of a lack of cod that also rely on capelin.

Population responses of marine mammals to changing forage fish populations are not well known, in large measure because the population dynamics of so many species in this century have been driven by direct effects of killing for various reasons and by subsequent recoveries from mass reductions following changes in management practices. However, marine mammals likely are sensitive to prey availability as suggested by changes in populations of several species of cetaceans and pinnipeds in the Southern Ocean following the depletion of the great whales and the increase in the availability of krill (Laws 1985). Additional evidence from the North Pacific is: the decline in growth rates of Steller sea lions and fur seals over time in the Gulf of Alaska and Bering Sea (Calkins and Goodwin 1988, Trites 1996); the relationship between diet diversity and the decline of Steller sea lions in Alaska (Merrick et al. 1997); the decline in pup production and growth rates of California sea lions during El Niño events (DeLong et al. 1991); and the change in seasonal patterns of abundance of California sea lions in response to changes in the abundance of Pacific hake (*Merluccius productus*) following the termination of the commercial fishery in central California (Ainley et al. 1982).

Management considerations

The difficulty of identifying causes of fluctuations in fish populations has important management implications, and the uncertainty of how to proceed with management has led to numerous reviews and hearty debate (e.g., May et al. 1979, Beamish and McFarlane 1989, Koslow 1992, Aron 1993, Ludwig et al. 1993, Mann 1993, Larkin 1996, Roughgarden and Smith 1996). We should not rush to judgment about cause and effect, nor should we necessarily sit back and do nothing, since by definition forage fishes have broad ecosystem importance and in many cases economic importance as well. This is a particularly important part of the social context of the forage fish issue—many people have come to depend on forage fishes, whether they are part of multinational factory fleets, local families who harvest herring and smelt by hand during the annual spawning runs, or aquaculturists far removed from the harvest of forage fishes (Fischer et al., this volume). If there were no social issues, then there would be less argument for intervention on purely ecological grounds.

One conclusion that emerges is that either there are few hard and fast rules governing forage fish populations and their role in ecosystems, or they have yet to be discovered. For example, there are various cases of positive, negative, and no effect of forage fishes on prey populations. At first glance, these contrasting observations are confusing, yet they might all be part of a general rule akin to one suggested by Cushing (1995), that the relationship between fish recruitment and food is parabolic, so that positive, negative, and no apparent relationships could all be found. In a similar vein, pelagic fish recruitment success in Ekman-type upwelling areas might also have a parabolic form (Cury and Roy 1989).

Furthermore, observations of positive, negative, or no relationship between forage fishes and any other variable must be evaluated in the proper spatial context, a point that follows from the views of Iles and Sinclair (1982) and Hay and McCarter of the importance of regional habitat heterogeneity in the maintenance of discrete populations of herring in the North Atlantic and North Pacific. The issue of the effect of habitat variability as a factor controlling population size is a significant one. Forage species, like all the rest, do not occur with equal abundance everywhere, but are usually found in distinct habitats as described by the basin model of MacCall (1990). The spatial heterogeneity of the seascape, as depicted by patterns of distribution, must be considered when estimating productivity and assessing variability of individual species in marine ecosystems, or of the ecosystem as a whole.

Maintaining an appropriate spatial context is required for the proper management of forage species that are targeted by commercial fisheries. The point was nicely made by Furness and Tasker, who showed how in the North Sea the need for sand lance by the fishery and the need by seabirds could be satisfied simultaneously by geographically partitioning harvests. By allowing the commercial fishery to operate in the central portion of the North Sea distant from the foraging areas of coastal-nesting seabirds and by restricting fishing in areas near the colonies, both user groups get their fair share.

Another major area of uncertainty concerning forage fish is the nature of their role in the ecosystem beyond their importance simply as prey. Do they have even bigger roles in ecosystems? What is their interaction strength? Can populations of forage fishes be manipulated to achieve some desired result through food web relationships, or can other members of food webs be manipulated in ways that affect forage fishes and thus other targets because of a cascade of effects?

For example, Hansson et al. (p. 281 this volume) suggested a possible remedy for algal blooms resulting from eutrophication in the coastal Baltic Sea by increasing the abundance of pikeperch (*Stizostedion lucioperca*), a major predator of herring, which are in turn major predators of herbivorous zooplankton. In theory, as pikeperch numbers go up, herring numbers would go down, zooplankton numbers would go up, and phytoplankton numbers would go down.

Two variations on this theme of trophic interactions and their role in marine ecosystems involve whales and forage fishes. Payne et al. (1990) suggested that in the western North Atlantic, forage fish, particularly sand lance, structure the ecosystem because of their effects on whale populations. In a given year, more planktivorous fishes means fewer planktivorous whales (right and sei whales, *Eubalaena glacialis* and *Balaenoptera borealis*) but more piscivorous whales (fin and humpback whales). They wonder if the lack of significant recovery of the Atlantic right whale population might be attributable to the increase in ecologically equivalent finfish populations. In another case, Stefansson et al. (1995) concluded that piscivorous minke, humpback, and fin whales have significant direct impacts on cod and capelin populations in Icelandic waters. Moreover, by consuming capelin, the whales had an important indirect effect on cod, which also consume capelin. The management implication is that these trophic interactions complicate predictions of future catches of both cod and capelin, especially as the whale populations recover from very depressed numbers earlier in this century.

However, a cautionary note in this regard has been sounded by Lavigne (1996), who maintains that in general we lack sufficient information to predict with any certainty the consequences of changes in marine mammal populations on prey populations, including commercially exploited fishes. A variety of shortcomings contributes to the situation, notably inadequate empirical data on marine mammals and other members of their food webs and an inadequate theoretical framework for addressing food web interactions in marine ecosystems.

Finally, there is the uncertainty of just what an ecosystem is and thus how to manage anything in an ecosystem context, let alone manage the ecosystem itself (Apollonio 1994). The meaning of ecosystem is as ambiguous as the meaning of forage fish. This is not a minor detail, but there is no need to make it more of a problem than it really is from the standpoint of forage fishes. For example, the specific needs of all users of forage fish resources, which in many cases are reasonably well known, can be taken into account when considering management approaches for fished populations. By explicitly including forage mortality, the other "*F*" in the calculation of total mortality for management purposes, three objectives would be met: (1) the profile of the issue would be raised, (2) the proper context for evaluating forage interactions would be maintained, and (3) a better focus for establishing management objectives would be achieved (Stephenson). Such multispecies considerations likely would improve management of exploited stocks (Bogstad and Mehl, this volume; Tjelmeland, this volume).

Improvements in estimating population abundance and fishing mortality would further buffer fished populations from the effects of efficient, often overcapitalized, fishing fleets. The collapse of Atlantic cod populations in Canada during the 1980s and early 1990s has recently been attributed to overestimates of population abundance and underestimates of fishing mortality because of statistical bias and inappropriate reliance on imprecise catch-per-unit-of-effort data from the commercial fishery and by the discarding of large numbers of juvenile cod (Myers et al. 1997). Similarly, the cod population in the Barents Sea collapsed because of a failure to account for slower growth, hence smaller fish, resulting from the capelin decline when setting harvest quotas. This resulted in many more fish being caught than expected and a large discard rate of small fish (Mehl 1991).

Predators of forage fishes usually are not able to simply switch between prey species as one is depleted or declines and maintain themselves and their populations, because there are few species that satisfy their foraging and nutritional requirements. For consumers it is not simply a matter of having access to some minimum level of fish biomass in the ocean, but of having available a sufficient biomass in sufficient concentrations of a few critical species, often as few as one or two. With the prospect of continued growth in the world demand for protein that is being satisfied by harvesting ever more of the very fishes that are known to be key forage species (Fischer et al., this volume), guidelines must be established for the protection of particular populations.

Relevance to Alaska

So, what was learned at the conference and what else do we know about forage fishes of value to Alaska?

We know which forage fishes appear to be of particular importance to marine birds and mammals, as well as to a variety of piscivorous fishes. They are sand lance, capelin, gadoids (walleye pollock, Arctic cod, and saffron cod, *Eleginus gracilis*), myctophids, and herring—the same or similar species that are important elsewhere in the Northern Hemisphere. We know some things about their basic biology and distribution patterns. We know that their populations here fluctuate widely, as they do elsewhere, and that for most of them commercial fishing likely has had little or no direct effect on their abundance because few species are commercial targets.

We know that all forage fishes are not equal in satisfying the metabolic requirements of predators. This issue, commonly referred to as the "junk food hypothesis," has been considered for several years, but it is only recently that direct evidence has confirmed the importance of particular fishes to the maintenance of consumers. Several studies have found large differences in energy density among species of forage fishes. The highest-quality species include myctophids, sand lance, capelin, and herring and the lowest-quality species include pollock (e.g., Payne and Johnson, this volume; Anthony and Roby, this volume). And, it does appear to matter. Seabirds in Prince William Sound fare better on a diet of fatty fishes (sand lance, capelin, and herring) than do birds without access to them and which must feed on pollock or other low-quality species (Anthony and Roby, this volume). Furthermore, preliminary feeding trials of Steller sea lions fed ad libitum on pollock in captivity indicate that they cannot maintain a positive energy balance and lose weight. When pollock are replaced by herring, the animals recover their condition easily (Pers. comm., D. Rosen and A. Trites, Univ. of British Columbia, Vancouver, B.C., Canada V6T 1Z4, Jan. 1997).

We are no better off than others in our understanding of why forage fish populations change between years or between decades. There has been no commercial exploitation for several species in Alaska, notably sand lance and capelin, yet populations have fluctuated widely, providing strong evidence of environmental control. For example, in the northern Bering Sea and eastern Chukchi Sea, where water temperatures are very unstable within and between years, there are strong correlations between temperature, zooplankton abundance, the abundance and growth of sand lance, capelin, Arctic cod, and saffron cod, and the productivity of regional seabird populations (Springer et al. 1984, 1987). In the Gulf of Alaska, capelin crashed in the late 1970s during a period of annual warming and remained at low levels throughout an extended interval of above-average water temperatures, a change that was reflected in the diets, productivity, and abundance of seabirds (Anderson et al., this volume; Kuletz et al., this volume; Piatt and Anderson 1996). At the same time, other species of fishes and invertebrates variously increased or decreased in concert. The role that water temperature played in the changes is not known, but it might be only an indicator of other changes in the physical environment that were more significant to patterns of material production and transfer through forage fish food webs (Brodeur et al., this volume).

In Alaska, as elsewhere, considerations of spatial scale are essential. Iverson et al. (1997) have shown compelling evidence of very localized use of forage fishes by harbor seals in Prince William Sound. The observations have important implications on the importance of local processes and production, and demonstrate a need for considering appropriate spatial scales when characterizing trophic dependencies of predators.

At a larger spatial scale, there is the evidence discussed above of an increase in the carrying capacity of the subarctic North Pacific following the shift in the mid-1970s of the meteorological regime. In the Bering Sea, however, there is growing evidence of a decline in carrying capacity in the past 30 years, beginning at the base of the food web with an apparent decline in primary and secondary production (Sugimoto and Tadokoro 1997; Pers. comm., D. Schell, Univ. of Alaska Fairbanks, Fairbanks, AK 99775, Mar. 1997). At higher trophic levels, kittiwakes on the Pribilof Islands remain about half as abundant as in the mid-1970s (Dragoo and Dragoo 1996); mortality of black guillemots (*Cepphus grylle*) wintering in the Bering Sea has increased (Pers. comm., G. Divoky, Univ. of Alaska Fairbanks, Fairbanks, AK 99775, Mar. 1997); pup production and growth rates of juvenile fur seals on the Pribilof Islands declined for unknown reasons and have failed to recover (York and Kozloff 1987; Trites 1992, 1996); and the ominous decline of Steller sea lions began in the mid-1970s as well.

Yet, during this same time in the western Aleutian Islands, murre and kittiwake populations, at least, were burgeoning, suggesting the opposite conclusion about carrying capacity. A number of characteristics of the marine habitats of the continental shelf differ substantially from those of oceanic habitats in the Aleutian Islands, however, and consequently so do the species of forage fishes available as prey to marine birds (e.g., Springer et al. 1996a). Just as calculations of the productivity of the greater Bering Sea ecosystem have been based on such a view of habitats (Walsh and McRoy 1986, Springer et al. 1996b), interpretations of variability in productivity of the ecosystem or of individual species of forage fishes and their predators must also be framed in the context of a seascape mosaic.

Unfortunately, overlying this convenient view of bottom-up control of ecosystem production and its expression in populations at high trophic levels is the specter of top-down control through direct and cascading effects of the harvesting of fishes and whales (NRC 1996). Although commercial fisheries exploit few forage species important to seabirds and marine mammals, walleye pollock is a major target of many fisheries. Pollock is an important forage species, plays a decisive role in its own population dynamics, has undergone large changes in abundance since the inception of the fishery in the early 1960s, and likely influences patterns of energy flow in pelagic food webs because of its great biomass (Springer 1992, Brodeur et al. 1996). In addition, the decimation of the great whales in the North Pacific in the 1950s-1970s and the collapse of rockfish and herring populations in the face of intense exploitation likely changed balances in carbon budgets involving forage fishes.

Answers to the many questions we have in Alaska about forage fishes and their role in marine ecosystems are slowly emerging, but it will be some time before we have a much improved understanding. For two species of particular importance, sand lance and capelin, we have very little quantitative data on abundance at any time or in any location, let alone on the range of fluctuations in the abundance of particular populations. Sadly, for these species our quantitative units are little better than "present" and "absent." Experimental efforts, such as closures to fishing and other disturbance in areas surrounding selected sea lion rookeries, will possibly give insights into effects of the activities of fishing, including particularly the removal of fish (Fritz et al. 1996). Experimental approaches to understanding bottom-up factors originating with changes in weather and climate are not so easily achieved. For this, we must look to the long term with observational programs, and should be developing hypotheses that will be tested in time scales appropriate to those of interest, i.e., the decade or longer. Interannual variability in most parameters is high and can be caused by numerous factors, yet long-term patterns are likely driven by a less complex set. The growing commitment to long-term research efforts, exemplified by programs of the Exxon Valdez Oil Spill Trustee Council, the Pacific Marine Environmental Laboratory, the National Marine Fisheries Service, the U.S. Fish and Wildlife Service, and the North Pacific Universities Marine Mammal Research Consortium is encouraging and is the proper direction to take into the twenty-first century.

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Table 1. Forage fish species and their role in the marine ecosystem.

Common name[a]	Scientific name	Study area	Role	Page	Authors (this volume)
Clupeidae					
Pacific herring	*Clupea pallasi*	Prince William Sound	Diet	257	Kline
				11	Willette et al.
Pacific herring	*Clupea pallasi*	Prince William Sound	Prey	699	Hayes & Kuletz
				703	Kuletz et al.
				175	Maniscalco & Ostrand
Pacific herring	*Clupea pallasi*	Pacific and Atlantic oceans	Environment/population	559	Hay & McCarter
Pacific herring	*Clupea pallasi*	North Pacific	Prey/environment	191	Logerwell & Hargreaves
				655	Schweigert
Pacific herring	*Clupea pallasi*	North Pacific	Stock recruitment	365	Zheng
Pacific herring	*Clupea pallasi*	Northeast Pacific	Proximate composition	721	Payne et al.
Pacific herring	*Clupea pallasi*	Prince William Sound	Proximate composition	725	Anthony & Roby
Atlantic herring	*Clupea harengus*	Baltic Sea	Diet/prey	77	Arrhenius
				41	Köster & Möllmann
				281	Hansson et al.
Atlantic herring	*Clupea harengus*	Barents Sea	Prey	591	Bogstad & Mehl
Atlantic herring	*Clupea harengus*	Norwegian and Barents seas	Prey	683	Anker-Nilsson et al.
Atlantic herring	*Clupea harengus*	North Atlantic	Stock recruitment	365	Zheng
Atlantic herring	*Clupea harengus*	North Atlantic	Assessment	431	Hagen & Able
Baltic herring	*Clupea harengus membras*	Baltic Sea	Prey	293	Ojaveer et al.
Pacific sardine	*Sardinops sagax*	North Pacific	Stock recruitment	365	Zheng
Pacific sardine	*Sardinops sagax*	California	Fisheries/prey/modeling	731	Mackinson et al.
Pacific sardine	*Sardinops sagax*	Pacific Ocean	Environment/population	545	Klyashtorin
Japanese sardine	*Sardinops melanostictus*	Pacific Ocean	Environment/population	545	Klyashtorin
Peruvian sardine	*Sardinops sagax*	Pacific Ocean	Environment/population	545	Klyashtorin
Spanish sardine	*Sardina pilchardus*	North Atlantic	Stock recruitment	365	Zheng
Sardines	*Sardinops spp.*	Venezuela	Fisheries	731	Mackinson et al.
Sprat	*Sprattus sprattus*	Baltic Sea	Diet/prey	41	Köster & Möllmann
Sprat	*Sprattus sprattus balticus*	Baltic Sea	Diet	293	Ojaveer et al.
Clupeid	*Clupeidae*	World ocean	Fisheries	311	Fischer et al.

[a] Common names of forage fish species occurring off North America follow Robins et al. (1991, American Fisheries Society Special Publication 20), and may vary from names used by symposium authors from other countries.

Table 1. Forage fish species and their role in the marine ecosystem (cont'd.).

Common name[a]	Scientific name	Study area	Role	Page	Authors (this volume)
Engraulidae					
Northern anchovy	*Engraulis mordax*	California	Fisheries/prey/modeling	731	Mackinson et al.
Northern anchovy	*Engraulis mordax*	Oregon	Prey/environment	505	Emmett et al.
Northern anchovy	*Engraulis mordax*	California	Stock recruitment	365	Zheng
Peruvian anchovy	*Engraulis ringens*	Pacific Ocean	Environment/population	545	Klyashtorin
Peruvian anchovy	*Engraulis ringens*	Peru	Fisheries	731	Mackinson et al.
Peruvian anchovy	*Engraulis ringens*	Peru	Stock recruitment	365	Zheng
South African anchovy	*Engraulis capensis*	South Africa	Stock recruitment	365	Zheng
Salmonidae					
Pink salmon	*Oncorhynchus gorbuscha*	Prince William Sound	Diet	257	Kline
				11	Willette et al.
Pink salmon	*Oncorhynchus gorbuscha*	Bering Sea	Diet	337	Nagasawa et al.
Pink salmon	*Oncorhynchus gorbuscha*	Prince William Sound	Diet/energy content	707	Paul & Willette
Sockeye salmon	*Oncorhynchus nerka*	Prince William Sound	Diet	257	Kline
Sockeye salmon	*Oncorhynchus nerka*	Bering Sea	Diet	337	Nagasawa et al.
Sockeye salmon	*Oncorhynchus nerka*	North Pacific	Diet/environment	655	Schweigert
Chum salmon	*Oncorhynchus keta*	Prince William Sound	Diet	257	Kline
				11	Willette et al.
Chum salmon	*Oncorhynchus keta*	Bering Sea	Diet	337	Nagasawa et al.
Coho salmon	*Oncorhynchus kisutch*	North Pacific	Environment	655	Schweigert
Chinook salmon	*Oncorhynchus tshawytscha*	North Pacific	Environment	655	Schweigert
Salmon	*Oncorhynchus* spp.	Prince William Sound	Prey	725	Anthony & Roby
Salmon	*Oncorhynchus* spp.	North Pacific	Environment/population	545	Klyashtorin
Salmonid	Salmonidae	World ocean	Fisheries	311	Fischer et al.
Dolly Varden	*Salvelinus malma*	Bering Sea	Diet	337	Nagasawa et al.
Osmeridae					
Capelin	*Mallotus villosus*	Prince William Sound	Diet	257	Kline
Capelin	*Mallotus villosus*	Prince William Sound	Prey	699	Hayes & Kuletz
				703	Kuletz et al.
				175	Maniscalco & Ostrand
Capelin	*Mallotus villosus*	Kachemak Bay	Population	441	Bechtol
Capelin	*Mallotus villosus*	Western Gulf of Alaska	Population	531	Anderson et al.
				197	Hansen

Table 1. Forage fish species and their role in the marine ecosystem (cont'd.).

Common name[a]	Scientific name	Study area	Role	Page	Authors (this volume)
Capelin	*Mallotus villosus*	Cook Inlet	Prey	231	Roseneau & Byrd
Capelin	*Mallotus villosus*	Northwest Atlantic	Environment/fisheries	457	Carscadden & Nakashima
				383	Nakashima & Borstad
Capelin	*Mallotus villosus*	Icelandic waters	Prey	105	Pálsson
Capelin	*Mallotus villosus*	Barents Sea	Prey/fisheries	469	Gjøsæter
				591	Bogstad & Mehl
				469	Gjøsæter
				617	Tjelmeland
Capelin	*Mallotus villosus*	Norwegian and Barents seas	Prey	683	Anker-Nilssen et al.
Capelin	*Mallotus villosus*	North Atlantic	Fisheries	311	Fischer et al.
Capelin	*Mallotus villosus*	North Atlantic	Fisheries	645	Stephenson
Capelin	*Mallotus villosus*	Northeast Pacific	Proximate composition	721	Payne et al.
Capelin	*Mallotus villosus*	Prince William Sound	Proximate composition	725	Anthony and Roby
Surf smelt	*Hypomesus pretiosus*	Northeast Pacific	Proximate composition	721	Payne et al.
Surf smelt	*Hypomesus pretiosus*	Puget Sound	Spawning habitat	395	Penttila
Eulachon	*Thaleichthys pacificus*	British Columbia	Environment/population	509	Hay et al.
Eulachon	*Thaleichthys pacificus*	Northeast Pacific	Proximate composition	721	Payne et al.
Rainbow smelt	*Osmerus mordax*	Northeast Pacific	Proximate composition	721	Payne et al.
Smelt	*Osmerus eperlanus eperlanus*	Baltic Sea	Diet	293	Ojaveer et al.
Smelts, not capelin	Osmeridae	Cook Inlet	Populations	441	Bechtol
Bathylagidae					
Northern smoothtongue	*Leuroglossus schmidti*	Bering Sea	Distribution	337	Nagasawa et al.
Northern smoothtongue	*Leuroglossus schmidti*	Pacific slope, north Kuril Is.	Prey	209, 323	Orlov
Bathylagidae	Bathylagidae	Northeast Pacific	Proximate composition	721	Payne et al.
Myctophidae					
Northern lampfish	*Stenobrachius leucopsarus*	Prince William Sound	Diet	257	Kline
Northern lampfish	*Stenobrachius leucopsarus*	Bering Sea	Prey	337	Nagasawa et al.
Northern lampfish	*Stenobrachius leucopsarus*	Pacific slope, north Kuril Is.	Prey	209, 323	Orlov
Garnet Lampfish	*Stenobrachius nannochir*	Pacific slope, north Kuril Is.	Prey	209, 323	Orlov
Bigeye lanternfish	*Protomyctophum thompsoni*	Pacific slope, north Kuril Is.	Prey	209, 323	Orlov
Lanternfishes	Myctophidae	World oceans	Diet/prey	271	Tsarin
Lanternfishes	Myctophidae	Northeast Pacific	Proximate composition	721	Payne et al.

Table 1. Forage fish species and their role in the marine ecosystem (cont'd.).

Common name[a]	Scientific name	Study area	Role	Page	Authors (this volume)
Gonostomatidae					
Lightfish	*Gonostoma gracile*	Pacific slope, north Kuril Is.	Prey	323	Orlov
Gadidae					
Walleye pollock	*Theragra chalcogramma*	Prince William Sound	Diet	257	Kline
				11	Willette et al.
Walleye pollock	*Theragra chalcogramma*	Prince William Sound	Proximate composition	725	Anthony & Roby
Walleye pollock	*Theragra chalcogramma*	Gulf of Alaska	Diet/prey/fisheries	71	Ciannelli & Bodeur
				351	Byrd et al.
				435	Wilson
Walleye pollock	*Theragra chalcogramma*	Kachemak Bay	Population	441	Bechtol
Walleye pollock	*Theragra chalcogramma*	Bering Sea	Environment	573	Brodeur et al.
Walleye pollock	*Theragra chalcogramma*	North Pacific Ocean	Environment/population	545	Klyashtorin
Walleye pollock	*Theragra chalcogramma*	Gulf of Alaska	Diet/population	87, 633	Paul et al.
Walleye pollock	*Theragra chalcogramma*	Pacific slope, north Kuril Is.	Prey	209	Orlov
Walleye pollock	*Theragra chalcogramma*	North Pacific	Fisheries	311	Fischer et al.
Walleye pollock	*Theragra chalcogramma*	Western Gulf of Alaska	Population	531	Anderson et al.
Walleye pollock	*Theragra chalcogramma*	Northeast Pacific	Proximate composition	721	Payne et al.
Pacific cod	*Gadus macrocephalus*	Western Gulf of Alaska	Population	531	Anderson et al.
Pacific cod	*Gadus macrocephalus*	Aleutian Is.	Diet	277	Yang
Pacific cod	*Gadus macrocephalus*	North Pacific Ocean	Environment/population	545	Klyashtorin
Pacific cod	*Gadus macrocephalus*	North Pacific	Diet/environment	655	Schweigert
Pacific cod	*Gadus macrocephalus*	Kachemak Bay	Population	441	Bechtol
Pacific cod	*Gadus macrocephalus*	Prince William Sound	Proximate composition	725	Anthony & Roby
Pacific tomcod	*Microgadus proximus*	Prince William Sound	Proximate composition	725	Anthony & Roby
Arctic cod	*Boreogadus saida*	Barents Sea	Prey/fisheries	485	Gjøsæter & Ushakov
				591	Bogstad & Mehl
Atlantic cod	*Gadus morhua*	Baltic Sea	Prey	41	Köster & Möllmann
Atlantic cod	*Gadus morhua*	Barents Sea	Diet/fisheries	591	Bogstad & Mehl
				617	Tjelmeland
Atlantic cod	*Gadus morhua*	North Atlantic	Fisheries	311	Fischer et al.
Atlantic cod	*Gadus morhua*	Icelandic waters	Diet	105	Pálsson
Atlantic cod	*Gadus morhua*	North Atlantic	Fisheries	645	Stephenson
Pacific hake	*Merluccius productus*	North Pacific	Environment	655	Schweigert
European hake	*Merluccius merluccius*	Portuguese waters	Diet	127	Silva et al.

Table 1. Forage fish species and their role in the marine ecosystem (cont'd.).

Common name[a]	Scientific name	Study area	Role	Page	Authors (this volume)
Blue whiting	*Micromesistius poutassou*	Portugal, South Biscay Gulf	Prey/fisheries	127	Silva et al.
European whiting	*Merlangius merlangus*	Icelandic waters	Diet	105	Pálsson
Haddock	*Melanogrammus aeglefinus*	North Sea	Diet	591	Bogstad & Mehl
Haddock	*Melanogrammus aeglefinus*	Icelandic waters	Diet	105	Pálsson
Haddock	*Melanogrammus aeglefinus*	North Atlantic	Fisheries	645	Stephenson
Pollock	*Pollachius virens*	Icelandic waters	Diet	105	Pálsson
Zoarcidae					
Eelpouts	Zoarcidae	Cook Inlet	Populations	441	Bechtol
Gasterosteidae					
Three-spined stickleback	*Gasterosteus aculeatus*	Baltic Sea	Diet	293	Ojaveer et al.
Nine-spined stickleback	*Pungitius pungitius*	Baltic Sea	Diet	293	Ojaveer et al.
Trichodontidae					
Pacific sandfish	*Trichodon trichodon*	Gulf of Alaska	Diet/populations	87	Paul et al.
Pacific sandfish	*Trichodon trichodon*	Northeast Pacific	Proximate composition	721	Payne et al.
Bathymasteridae					
Ronquils and searchers	Bathymasteridae	Cook Inlet	Populations	441	Bechtol
Stichaeidae					
Slender eelblenny	Lumpenus fabricii	Prince William Sound	Proximate composition	725	Anthony & Roby
Slender eelblenny	Lumpenus fabricii	Prince William Sound	Prey	699	Hayes & Kuletz
Arctic shanny	Stichaeus punctatus	Prince William Sound	Proximate composition	725	Anthony & Roby
Pholidae					
Crescent gunnel	*Pholis laeta*	Prince William Sound	Proximate composition	725	Anthony & Roby
				699	Hayes & Kuletz
Zaproridae					
Prowfish	*Zaprora silenus*	Prince William Sound	Proximate composition	725	Anthony & Roby
Prowfish	*Zaprora silenus*	Northeast Pacific	Proximate composition	721	Payne et al.
Ammodytidae					
Pacific sand lance	*Ammodytes hexapterus*	Prince William Sound	Diet/prey	257	Kline
				699	Hayes & Kuletz
				703	Kuletz et al.
				175	Maniscalco & Ostrand

Table 1. Forage fish species and their role in the marine ecosystem (cont'd.).

Common name[a]	Scientific name	Study area	Role	Page	Authors (this volume)
Pacific sand lance	*Ammodytes hexapterus*	Cook Inlet	Prey	231	Roseneau & Byrd
Pacific sand lance	*Ammodytes hexapterus*	Cook Inlet, Kodiak	Life history	409	Blackburn & Anderson
Pacific sand lance	*Ammodytes hexapterus*	Western Bering Sea	Stock ID, fisheries/prey	427	Grigorev & Sedova
Pacific sand lance	*Ammodytes hexapterus*	Puget Sound	Spawning habitat	395	Penttila
Pacific sand lance	*Ammodytes hexapterus*	In situ	Digestion	95	Ciannelli
Pacific sand lance	*Ammodytes hexapterus*	Northeast Pacific	Proximate composition	721	Payne et al.
Pacific sand lance	*Ammodytes hexapterus*	Prince William Sound	Proximate composition	725	Anthony & Roby
Sand lance	*Ammodytes marinus*	North Sea	Prey/fisheries	147	Furness & Tasker
Sand lance	*Ammodytes* spp.	Norwegian and Barents seas	Prey	683	Anker-Nilsson et al.
Sand lance	*Ammodytes* spp.	Northeast Atlantic	Fisheries	645	Stephenson
Scombridae					
Horse mackerel	*Trachurus trachurus*	Portuguese waters	Diet	127	Silva et al.
Atlantic mackerel	*Scomber scombrus*	Portuguese waters	Diet	127	Silva et al.
Atlantic mackerel	*Scomber scombrus*	North Atlantic	Stock recruitment	365	Zheng
Chub mackerel	*Scomber japonicus*	Japan	Stock recruitment	365	Zheng
Jack mackerel	*Trachurus symmetricus*	Pacific Ocean	Environment/population	545	Klyashtorin
Tunas	*Thunnus* spp.	Pacific Ocean	Environment/population	545	Klyashtorin
Scorpaenidae					
Rockfishes	*Sebastes* spp.	Barents Sea	Prey	591	Bogstad & Mehl
Hexagrammidae					
Atka mackerel	*Pleurogrammus monopterygius*	Aleutian Is.	Diet/prey/fisheries	277	Yang
Atka mackerel	*Pleurogrammus monopterygius*	Pacific slope, north Kuril Is.	Diet/prey	209, 323	Orlov
Atka mackerel	*Pleurogrammus monopterygius*	Northeast Pacific	Proximate composition	721	Payne et al.
Cottidae					
Sculpins	Cottidae	Prince William Sound	Prey	725 699	Anthony & Roby Hayes & Kuletz
Sculpins	Cottidae	Pacific slope, north Kuril Is.	Prey	209	Orlov
Agonidae					
Poachers	Agonidae	Cook Inlet	Populations	441	Bechtol
Liparidae					
Snailfishes	Liparidae	Pacific slope, north Kurile Is.	Prey	209	Orlov

Table 2. Predators of forage fishes.

Predator scientific name[a]	Predator common name	Prey scientific name	Prey common name	Page	Authors (this volume)
Atheresthes evermanni	Kamchatka flounder	*Leuroglossus schmidti*	Northern smoothtongue	209	Orlov
Atheresthes evermanni	Kamchatka flounder	*Myctophidae*	Lanternfishes	209	Orlov
Atheresthes evermanni	Kamchatka flounder	*Theragra chalcogramma*	Walleye pollock	209	Orlov
Atheresthes evermanni	Kamchatka flounder	*Pleurogrammus monopterygius*	Atka mackerel	209	Orlov
Atheresthes evermanni	Kamchatka flounder	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Brachyramphus marmoratus	Marbled murrelet	*Ammodytes hexapterus*	Sand lance	703	Kuletz et al.
Brachyramphus marmoratus	Marbled murrelet	*Mallotus villosus*	Capelin	703	Kuletz et al.
Brachyramphus marmoratus	Marbled murrelet	*Clupea pallasi*	Pacific herring	703	Kuletz et al.
Brachyramphus marmoratus	Marbled murrelet	*Gadidae*	Cods	703	Kuletz et al.
Cepphus columba	Pigeon guillemot	*Pholidae*	Gunnels	725	Anthony & Roby
Cepphus columba	Pigeon guillemot	*Pholidae*	Gunnels	699	Hayes & Kuletz
Cepphus columba	Pigeon guillemot	*Pholidae*	Gunnels	703	Kuletz et al.
Cepphus columba	Pigeon guillemot	*Stichaeidae*	Pricklebacks	725	Anthony & Roby
Cepphus columba	Pigeon guillemot	*Stichaeidae*	Pricklebacks	699	Hayes & Kuletz
Cepphus columba	Pigeon guillemot	*Stichaeidae*	Pricklebacks	703	Kuletz et al.
Cepphus columba	Pigeon guillemot	*Gadidae*	Cods	699	Hayes & Kuletz
Cepphus columba	Pigeon guillemot	*Ammodytes hexapterus*	Sand lance	699	Hayes & Kuletz
Clupea harengus	Atlantic herring	*Gadus morhua*	Atlantic cod	591	Bogstad & Mehl
Clupea harengus	Atlantic herring	*Mallotus villosus*	Capelin	469	Gjøsæter
Clupea harengus	Atlantic herring	*Sprattus sprattus*	Sprat	591	Bogstad & Mehl
Coryphaenidae	Dolphins	*Myctophidae*	Lanternfishes	271	Tsarin
Delphinapterus leucas	Beluga whale	*Boreogadus saida*	Arctic cod	485	Gjøsæter & Ushakov
Delphinus delphis	Common dolphin	*Micromesistius poutassou*	Blue whiting	127	Silva et al.
Eumetopias jubatus	Steller sea lion	*Clupea pallasi*	Pacific herring	351	Byrd et al.
Eumetopias jubatus	Steller sea lion	*Mallotus villosus*	Capelin	197	Hansen
Eumetopias jubatus	Steller sea lion	*Oncorhynchus spp.*	Salmon	351	Byrd et al.
Eumetopias jubatus	Steller sea lion	*Pleurogrammus monopterygius*	Atka mackerel	351	Byrd et al.
Eumetopias jubatus	Steller sea lion	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Eumetopias jubatus	Steller sea lion	*Theragra chalcogramma*	Walleye pollock	351	Byrd et al.
Evermannellidae	Sabertooth fishes	*Myctophidae*	Lanternfishes	271	Tsarin
Fratercula arctica	Atlantic puffin	*Ammodytes marinus*	Sand lance	147	Furness & Tasker
Fratercula arctica	Atlantic puffin	*Ammodytes spp.*	Sand lance	683	Anker-Nilssen et al.
Fratercula arctica	Atlantic puffin	*Clupea harengus*	Atlantic herring	683	Anker-Nilssen et al.
Fratercula arctica	Atlantic puffin	*Gadidae*	Rockling	147	Furness & Tasker
Fratercula arctica	Atlantic puffin	*Gadidae*	Cods	147	Furness & Tasker

[a] Common names of forage fish species occurring off North America follow Robins et al. (1991, American Fisheries Society Special publication 20), and may vary from names used by symposium authors from other countries.

Table 2. Predators of forage fishes (cont'd.).

Predator scientific name[a]	Predator common name	Prey scientific name	Prey common name	Page	Authors (this volume)
Fratercula arctica	Atlantic puffin	*Mallotus villosus*	Capelin	683	Anker-Nilssen et al.
Fratercula arctica	Atlantic puffin	*Clupea harengus*	Atlantic herring	683	Anker-Nilssen et al.
Fratercula arctica	Atlantic puffin	*Sprattus sprattus*	Sprat	147	Furness & Tasker
Fratercula cirrhata	Tufted puffin	*Ammodytes hexapterus*	Pacific sand lance	351	Byrd et al.
Fratercula cirrhata	Tufted puffin	*Ammodytes hexapterus*	Pacific sand lance	175	Maniscalco & Ostrand
Fratercula cirrhata	Tufted puffin	*Ammodytes hexapterus*	Pacific sand lance	231	Roseneau & Byrd
Fratercula cirrhata	Tufted puffin	*Clupea pallasi*	Pacific herring	175	Maniscalco & Ostrand
Fratercula cirrhata	Tufted puffin	*Clupea pallasi*	Pacific herring	703	Kuletz et al.
Fratercula cirrhata	Tufted puffin	*Gadus macrocephalus*	Pacific cod	351	Byrd et al.
Fratercula cirrhata	Tufted puffin	*Hexagrammidae*	Greenlings	351	Byrd et al.
Fratercula cirrhata	Tufted puffin	*Mallotus villosus*	Capelin	175	Maniscalco & Ostrand
Fratercula cirrhata	Tufted puffin	*Mallotus villosus*	Capelin	231	Roseneau & Byrd
Fratercula cirrhata	Tufted puffin	*Oncorhynchus spp.*	Salmon	725	Anthony & Roby
Fratercula cirrhata	Tufted puffin	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Fratercula cirrhata	Tufted puffin	*Theragra chalcogramma*	Walleye pollock	725	Anthony & Roby
Fratercula cirrhata	Tufted puffin	*Theragra chalcogramma*	Walleye pollock	351	Byrd et al.
Fratercula cirrhata	Tufted puffin	*Zaprora silenus*	Prowfish	725	Anthony & Roby
Fratercula corniculata	Horned puffin	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Fulmarus glacialis	Northern fulmar	*Ammodytes marinus*	Sand lance	147	Furness & Tasker
Gadidae	Cods	*Myctophidae*	Lanternfishes	271	Tsarin
Gadus macrocephalus	Pacific cod	*Clupea pallasi*	Pacific herring	655	Schweigert
Gadus macrocephalus	Pacific cod	*Mallotus villosus*	Capelin	531	Anderson et al.
Gadus macrocephalus	Pacific cod	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Gadus morhua	Atlantic cod	*Boreogadus saida*	Arctic cod	591	Bogstad & Mehl
Gadus morhua	Atlantic cod	*Clupea harengus*	Atlantic herring	591	Bogstad & Mehl
Gadus morhua	Atlantic cod	*Gadus morhua*	Atlantic cod	591	Bogstad & Mehl
Gadus morhua	Atlantic cod	*Mallotus villosus*	Capelin	591	Bogstad & Mehl
Gadus morhua	Atlantic cod	*Mallotus villosus*	Capelin	469	Gjøsæter
Gadus morhua	Atlantic cod	*Mallotus villosus*	Capelin	105	Pálsson
Gadus morhua	Atlantic cod	*Mallotus villosus*	Capelin	617	Tjelmeland
Gadus morhua	Atlantic cod	*Melanogrammus aeglefinus*	Haddock	591	Bogstad & Mehl
Gadus morhua	Atlantic cod	*Sebastes spp.*	Rockfish	591	Bogstad & Mehl
Gempylidae	Snake mackerels	*Myctophidae*	Lanternfish	271	Tsarin
Hippoglossoides platessoides	American plaice	*Mallotus villosus*	Capelin	105	Pálsson
Hippoglossus stenolepis	Pacific halibut	*Ammodytes hexapterus*	Pacific sand lance	231	Roseneau & Byrd

Table 2. Predators of forage fishes (cont'd.).

Predator scientific name[a]	Predator common name	Prey scientific name	Prey common name	Page	Authors (this volume)
Hippoglossus stenolepis	Pacific halibut	*Mallotus villosus*	Capelin	231	Roseneau & Byrd
Hippoglossus stenolepis	Pacific halibut	*Clupea pallasi*	Pacific herring	655	Schweigert
Hippoglossus stenolepis	Pacific halibut	*Oncorhynchus spp.*	Salmon	209	Orlov
Hippoglossus stenolepis	Pacific halibut	*Mallotus villosus*	Capelin	209	Orlov
Hippoglossus stenolepis	Pacific halibut	*Theragra chalcogramma*	Walleye pollock	209	Orlov
Hippoglossus stenolepis	Pacific halibut	*Gadus macrocephalus*	Pacific cod	209	Orlov
Hippoglossus stenolepis	Pacific halibut	*Pleurogrammus monopterygius*	Atka mackerel	209	Orlov
Hippoglossus stenolepis	Pacific halibut	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Histiophoridae	Spearfishes	*Myctophidae*	Lanternfish	271	Tsarin
Larus glaucescens	Glaucous-winged gull	*Ammodytes hexapterus*	Pacific sand lance	175	Maniscalco & Ostrand
Larus glaucescens	Glaucous-winged gull	*Clupea pallasi*	Pacific herring	175	Maniscalco & Ostrand
Larus glaucescens	Glaucous-winged gull	*Mallotus villosus*	Capelin	175	Maniscalco & Ostrand
Larus marinus	Great black-backed gull	*Ammodytes marinus*	Sand lance	147	Furness & Tasker
Latimeria chalumnae	Gombessa	*Myctophidae*	Lanternfish	271	Tsarin
Pleuronectes bilineatus	Rock sole	*Clupea pallasi*	Pacific herring	655	Schweigert
Lophius spp.	Monkfish	*Micromesistius poutassou*	Blue whiting	127	Silva et al.
Melanogrammus aeglefinus	Haddock	*Mallotus villosus*	Capelin	105	Pálsson
Melanostomiidae	Scaleless black dragonfishes	*Myctophidae*	Lanternfish	271	Tsarin
Merlangius merlangus	European whiting	*Mallotus villosus*	Capelin	105	Pálsson
Merluccius merluccius	European hake	*Micromesistius poutassou*	Blue whiting	127	Silva et al.
Merluccius productus	Pacific hake	*Clupea pallasi*	Pacific herring	655	Schweigert
Morus bassanus	Northern gannet	*Ammodytes marinus*	Sand lance	147	Furness & Tasker
Morus bassanus	Northern gannet	*Clupea harengus*	Atlantic herring	147	Furness & Tasker
Morus bassanus	Northern gannet	*Scombridae*	Mackerel	147	Furness & Tasker
Oncorhynchus gorbuscha	Pink salmon	*Stenobrachius leucopsarus*	Northern lampfish	337	Nagasawa et al.
Oncorhynchus keta	Chum salmon	*Stenobrachius leucopsarus*	Northern lampfish	337	Nagasawa et al.
Oncorhynchus kisutch	Coho salmon	*Clupea pallasi*	Pacific herring	655	Schweigert
Oncorhynchus kisutch	Coho salmon	*Engraulis mordax*	northern anchovy	505	Emmett et al.
Oncorhynchus nerka	Sockeye salmon	*Clupea pallasi*	Pacific herring	655	Schweigert
Oncorhynchus nerka	Sockeye salmon	*Stenobrachius leucopsarus*	Northern lampfish	337	Nagasawa et al.
Oncorhynchus tshawytscha	Chinook salmon	*Clupea pallasi*	Pacific herring	655	Schweigert
Paralepididae	Barracudinas	*Myctophidae*	Lanternfishes	271	Tsarin
Perca flavescens	Yellow perch	*Alosa pseudoharengus*	Alewife	243	Hansson et al.
Perca flavescens	Yellow perch	*Perca flavescens*	Yellow perch	243	Hansson et al.

Table 2. Predators of forage fishes (cont'd.).

Predator scientific name[a]	Predator common name	Prey scientific name	Prey common name	Page	Authors (this volume)
Phalacrocorax aristotelis	Cormorant	*Ammodytes marinus*	Sand lance	147	Furness & Tasker
Phoca groenlandica	Harp seal	*Boreogadus saida*	Arctic cod	485	Gjøsæter & Ushakov
Phoca hispida	Ringed seal	*Boreogadus saida*	Arctic cod	485	Gjøsæter & Ushakov
Phoca vitulina	Harbor seal	*Mallotus villosus*	Capelin	197	Hansen
Phoca vitulina	Harbor seal	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Phocoenoides dalli	Dall's porpoise	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Pleurogrammus monopterygius	Atka mackerel	*Myctophidae*	Lanternfishes	323	Orlov
Pleurogrammus monopterygius	Atka mackerel	*Microstomatidae*	Deepsea smelts	323	Orlov
Pleurogrammus monopterygius	Atka mackerel	*Gonostoma gracile*	Lightfish	323	Orlov
Pollachius virens	Pollock	*Mallotus villosus*	Capelin	105	Pálsson
Puffinus griseus	Sooty shearwater	*Clupea pallasi*	Pacific herring	191	Logerwell & Hargreaves
Raja radiata	Thorny skate	*Mallotus villosus*	Capelin	105	Palsson
Reinhardtius hippoglossoides	Greenland halibut	*Microstomatidae*	Deepsea smelts	209	Orlov
Reinhardtius hippoglossoides	Greenland halibut	*Myctophidae*	Lanternfishes	209	Orlov
Reinhardtius hippoglossoides	Greenland halibut	*Theragra chalcogramma*	Walleye pollock	209	Orlov
Reinhardtius hippoglossoides	Greenland halibut	*Mallotus villosus*	Capelin	105	Pálsson
Rissa tridactyla	Black-legged kittiwake	*Ammodytes hexapterus*	Pacific sand lance	725	Anthony & Roby
Rissa tridactyla	Black-legged kittiwake	*Ammodytes hexapterus*	Pacific sand lance	175	Maniscalco & Ostrand
Rissa tridactyla	Black-legged kittiwake	*Ammodytes hexapterus*	Pacific sand lance	231	Roseneau & Byrd
Rissa tridactyla	Black-legged kittiwake	*Ammodytes hexapterus*	Pacific sand lance	703	Kuletz et al.
Rissa tridactyla	Black-legged kittiwake	*Ammodytes marinus*	Sand lance	147	Furness & Tasker
Rissa tridactyla	Black-legged kittiwake	*Ammodytes spp.*	Sand lance	683	Anker-Nilssen et al.
Rissa tridactyla	Black-legged kittiwake	*Clupea harengus*	Atlantic herring	683	Anker-Nilssen et al.
Rissa tridactyla	Black-legged kittiwake	*Clupea pallasi*	Pacific herring	725	Anthony & Roby
Rissa tridactyla	Black-legged kittiwake	*Clupea pallasi*	Pacific herring	175	Maniscalco & Ostrand
Rissa tridactyla	Black-legged kittiwake	*Clupea pallasi*	Pacific herring	703	Kuletz et al.
Rissa tridactyla	Black-legged kittiwake	*Mallotus villosus*	Capelin	683	Anker-Nilssen et al.
Rissa tridactyla	Black-legged kittiwake	*Mallotus villosus*	Capelin	725	Anthony & Roby
Rissa tridactyla	Black-legged kittiwake	*Mallotus villosus*	Capelin	175	Maniscalco & Ostrand
Rissa tridactyla	Black-legged kittiwake	*Mallotus villosus*	Capelin	231	Roseneau & Byrd
Rissa tridactyla	Black-legged kittiwake	*Sprattus sprattus*	Sprat	147	Furness & Tasker
Rissa tridactyla	Black-legged kittiwake	*Gadidae*	Cods	703	Kuletz et al.
Salmonidae	Salmon	*Myctophidae*	Lanternfishes	271	Tsarin
Salvelinus malma	Dolly Varden	*Stenobrachius leucopsarus*	Northern lampfish	337	Nagasawa et al.
Scomber scombrus	Atlantic mackerel	*Micromesistius poutassou*	Blue whiting	127	Silva et al.

Table 2. Predators of forage fishes (cont'd.).

Predator scientific name[a]	Predator common name	Prey scientific name	Prey common name	Page	Authors (this volume)
Scyliorhinus canicula	Small-spotted catshark	*Micromesistius poutassou*	Blue whiting	127	Silva et al.
Serranidae	Sea basses	*Myctophidae*	Lanternfishes	271	Tsarin
Sprattus sprattus	Sprat	*Gadus morhua*	Atlantic cod	41	Köster & Möllmann
Sprattus sprattus	Sprat	*Clupea harengus*	Atlantic herring	41	Köster & Möllmann
Stenoteuthis spp.	Squid	*Myctophidae*	Lanternfishes	271	Tsarin
Stizostedion lucioperca	Pikeperch	*Clupea harengus*	Atlantic herring	281	Hansson et al.
				293	Ojaveer et al.
Stomiidae	Scaly dragonfishes	*Myctophidae*	Lanternfishes	271	Tsarin
Trachurus trachurus	Horse mackerel	*Micromesistius poutassou*	Blue whiting	127	Silva et al.
Trichodon trichodon	Pacific sandfish	*Ammodytes hexapterus*	Pacific sand lance	87	Paul et al.
Thunnus alalunga	Albacore	*Myctophidae*	Lanternfishes	271	Tsarin
Thunnus obesus	Bigeye tuna	*Myctophidae*	Lanternfishes	271	Tsarin
Uria aalge	Common murre	*Ammodytes hexapterus*	Pacific sand lance	231	Roseneau & Byrd
Uria aalge	Common murre	*Ammodytes hexapterus*	Pacific sand lance	703	Kuletz et al.
Uria aalge	Common murre	*Ammodytes marinus*	Capelin	147	Furness & Tasker
Uria aalge	Common murre	*Ammodytes spp.*	Capelin	683	Anker-Nilssen et al.
Uria aalge	Common murre	*Clupea harengus*	Atlantic herring	683	Anker-Nilssen et al.
Uria aalge	Common murre	*Clupea pallasi*	Pacific herring	191	Logerwell & Hargreaves
Uria aalge	Common murre	*Gadidae*	Cods	147	Furness & Tasker
Uria aalge	Common murre	*Mallotus villosus*	Capelin	683	Anker-Nilssen et al.
Uria aalge	Common murre	*Mallotus villosus*	Capelin	231	Roseneau & Byrd
Uria aalge	Common murre	*Sprattus sprattus*	Sprat	147	Furness & Tasker
Uria aalge	Common murre	*Gadidae*	Cods	703	Kuletz et al.
Uria lomvia	Thick-billed murre	*Pleurogrammus monopterygius*	Atka mackerel	277	Yang
Zeus faber	John dory	*Micromesistius poutassou*	Blue whiting	127	Silva et al.