Trophic Role of the Pacific Whiting, *Merluccius productus*

P. A. LIVINGSTON and K. M. BAILEY

Introduction

Pacific whiting, *Merluccius productus*, constitutes the most abundant groundfish resource off the west coast of the continental United States (Nelson and Larkins, 1970). Thus, it may play a central role in the dynamics of biomass transfer in the food web of the California Current system. Previous studies have identified whiting as a predator on commercial fish and shrimp (Gotshall, 1969 a, b; Alton and Nelson, 1970; Outram and Haegele, 1972; Livingston, 1983). Additionally, whiting may provide a significant food source for other fish, marine mammals, and birds. Therefore, changes in whiting abundance or production may affect the abundance or production of the whiting's predators and prey. Here, we examine the food web links which involve Pacific whiting and comment on their importance.

Pacific Whiting: The Predator

General Prey Items

Several studies over the past 20 years have examined various aspects of the food habits of Pacific whiting. A general description of prey types consumed by whiting is summarized from the results of these studies in Table 1.

Gotshall (1969a) sampled a wide size range of whiting over 1 year on the shrimp beds of northern California. These whiting consumed (by volume) mostly pandalid shrimp (44 percent), fishes (29 percent), and euphausiids (18 percent). Off Washington and Oregon, Alton and Nelson (1970) found that the whiting diet (in terms of weight) consisted of 53 percent euphausiids, 37 percent fish (mostly eulachon, *Thaleichthys pacificus*), and only 8 percent pandalid shrimp. Similarly, Outram and Haegele (1972) reported a declining frequency of occurrence of shrimp (3 percent) in whiting stomachs taken southwest of Vancouver Island, British Columbia. There, euphausiids occured in 94 percent of the stomachs sampled, and Pacific sand lance, *Ammodytes hexapterus*, in 26 percent. Livingston (1983) also noted the decreasing importance of shrimp (< 5 percent by weight) and the increasing importance of euphausiids (15-98 percent) and schooling fish, such as eulachon and Pacific herring, *Clupea harengus pallasi* (13-69 percent), in the diets of adult whiting off Oregon, Washington, and British Columbia.

Overall, the common food item consumed by adult whiting over its range of major abundance (from California to British Columbia) was euphausiids. Other items dominated the diet, depending on the area: Pandalid shrimp were the major dietary component in northern California, while schooling fish were important in the food of whiting from Oregon to British Columbia. The general tendency seems to be for whiting to consume prey items which occur in patches or schools, such as euphausiids and pelagic fish (like eulachon and herring). Additionally, the majority of whiting prey, such as pandalid shrimp and the pelagic fishes, are also euphausiid predators (Pearcy, 1970; Wailes, 1936; Barraclough, 1964). Thus, euphausiids appear to be the most important item in describing the diet of adult whiting; they attract not only whiting but also

The authors are with the Northwest and Alaska Fisheries Center, 7600 Sand Point Way N.E., Bin C15700, Seattle, WA 98115.

Table 1.—Summary of studies on the feeding habits of Pacific whiting.

Study	Sampling location	Sampling period	Whiting size range (cm)	Major prey in % wt. (W), % vol. (V), or % freq. occur. (FO)
Gotshall, 1969a	N. California	July 1964-Sept. 1965	10-81	(V) 44% pandalid shrimp, 29% fish, 18% euphausiids
Alton and Nelson, 1970	Wash., Oregon	May-Sept. 1964-65	46-66	(W) 8% pandalid shrimp, 37% fish, 53% euphausiids
Outram and Haegele, 1972	SW Vancouver Isl.	August 1970	42-71	(FO) 3% pandalid shrimp, 26% sand lance, 94% euphausiids
Livingston, 1983	Wash., Oregon	April-July 1967	49-50	(W) <1% pandalid shrimp, 13% fish, 86% euphausiids
	California	October 1980	10-20	(W) 98% euphausiids
	Oregon	April-May 1980	35-45	(W) 98% euphausiids
	Oreg., Wash., SW Vancouver Isl.	April-Sept. 1980	45-65	(W) 3% pandalid shrimp, 69% fish, 15% euphausiids
Sumida and Moser, 1980	California	March 1975	0.3-1.1	(V) 74% adult copepods, 17% copepodites, 5% copepod nauplii

other organisms which then become vulnerable to whiting predation.

Changes in Diet With Whiting Size

Pacific whiting larvae possess relatively large mouths that enable them to feed on a wide range of prey sizes from 50-400 μm in width. Sumida and Moser (1980) found that the food of whiting larvae consisted primarily of adult copepods (74 percent by volume). Other prey items were copepod eggs, copepodids, and copepod nauplii.

The diet of juveniles has not been studied very extensively. Livingston (1983) discovered juvenile whiting in the 100-200 mm size range fed almost exclusively on euphausiids off California (98 percent by weight).

As noted previously, adults feed on euphasiids, pelagic fishes, and pandalid shrimp. Several studies have shown that the weight or frequency of these items in the diet may change with increasing adult whiting length. Gotshall (1969b) calculated the average number of pandalid shrimp per whiting stomach by 100 mm size classes of whiting off northern California. Whiting 400-490 mm in length had about 1-2 shrimp per stomach, while stomachs from whiting >500 mm in length contained 2-8 shrimp each. Off British Columbia, the frequency of occurrence of schooling fish increased from 21.8 percent in whiting 420-510 mm in length to 34.4 percent in whiting 620-710 mm in length (Outram and Haegele, 1972). Figure 1 shows the differences mainly in the percent by weight of fish in the diets of whiting. Whiting <450 mm in length ate virtually no fish. Whiting in the 450-550 mm size group ate 37 percent fish by weight off Oregon and 66 percent fish by weight off Washington and Vancouver Island. Whiting >550 mm consumed 94 percent and 90 percent fish by weight, respectively, in the two areas. Figure 2 depicts the increase in frequency of occurrence of herring in whiting stomachs of increasing size. All these studies point to a change in diet occurring when the whiting reach
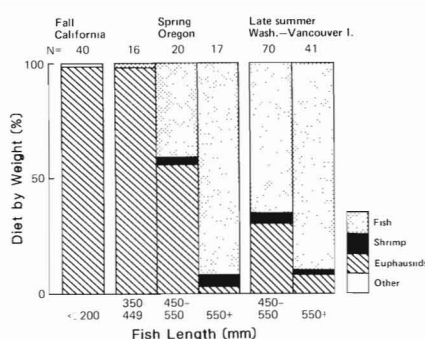

Figure 1.—Percentage by weight of major prey categories in the diet of Pacific whiting, *Merluccius productus*, for different whiting length groups sampled at various locations in 1980.

Figure 2.—Percent frequency of occurrence of Pacific herring, *Clupea harengus pallasi*, in stomachs of different whiting length groups sampled in late summer 1980 off Washington and Vancouver Island, B.C.

a length of about 400-500 mm. As their size increases, whiting seem to consume larger prey such as fish or shrimp and fewer euphausiids.

It is possible to quantify whiting's prey size preference by calculating the frequency distribution of predator weight to prey weight ratios, as described in detail by Ursin (1973), and actually computed for whiting by Livingston (1983). Basically the method involves calculating predator-prey size ratios using information on the total weight in grams (W_j) and total number (ΣN_j) of each prey type j in a collection of predator stomachs. The individual mean weight of each prey type ($\bar{w}_j$) is calculated and compared with the mean predator weight ($\bar{w}_i$). The frequency distribution of the ratios of predator weight to prey weight ($\bar{w}_i/\bar{w}_j$) is usually log-normal in shape. Therefore a plot of $\ln(\bar{w}_i/\bar{w}_j)$ vs. ΣN_j should produce a normal curve.

However, the proportion of a prey item in a predator's diet is a function not only of the predator's choice of that prey but also of the availability of the prey (Lawlor, 1980). So the observed proportions of prey items in a predator's stomach reflect predator preference only when the abundances of all prey items in nature are equal. This situation can be simulated by assuming the numbers of each prey
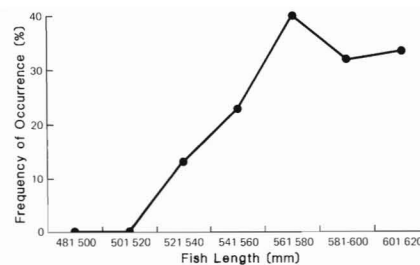
type in the environment are inversely proportional to prey weight (Ursin, 1973). Thus, to offer equal numbers of each prey size to a predator one would multiply the total number of each prey type j (ΣN_j) by the mean weight of each prey ($\bar{w}_j$). The result would then be divided by $\bar{w}_i$ to adjust for predator size.

Figures 3-5 show the results of these calculations for different size groups of whiting. The solid lines depict the frequency distributions of predator-prey size ratios uncorrected for prey availability. The dashed lines show the shapes of curves resulting from simulating the effects of offering equal numbers of each prey size to whiting predators.

Whiting <200 mm whose diet was mostly euphausiids, have a narrow prey-size selection curve reflecting the limited size range of items in their diet (Fig. 3). The selection curve (solid line) for this size group of whiting follows the preference curve (dashed line) indicating these whiting are actually consuming their preferred prey.

Intermediate-sized whiting, 350-549 mm in length, have a selection curve (Fig. 4) which reflects the numerical dominance of euphausiids in their actual diet. The preference curve shifts and is bimodal, with the largest mode at a predator-prey size ratio of about 100:1, and the second mode reflecting
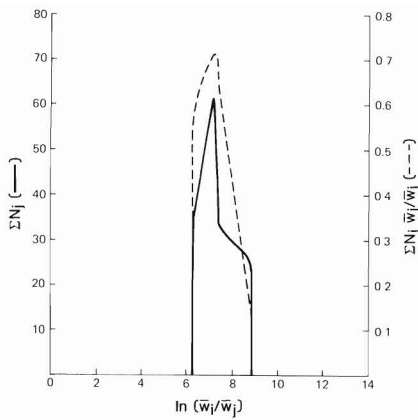
Figure 3.—Frequency distribution of predator-prey size scores for Pacific whiting less than 200 mm as the predator, with an average weight ($\bar{w}_i$) of 13.2 g, under natural (line) and simulated (dashes) conditions.
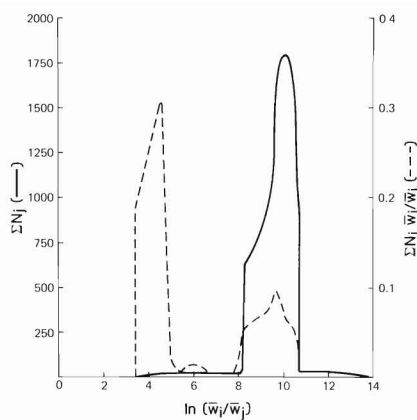

Figure 4.—Frequency distribution of predator-prey size scores for Pacific whiting 350-549 mm in length as the predator, with an average weight ($\bar{w}_i$) of 876.2 g, under natural (line) and simulated (dashes) conditions.
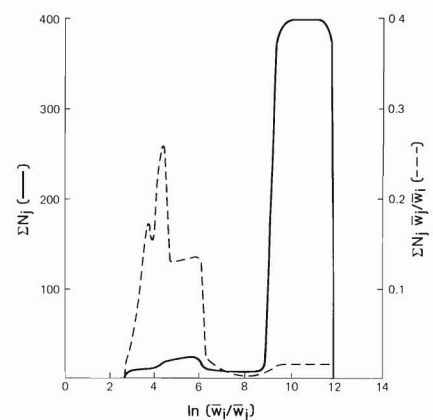

Figure 5.—Frequency distribution of predator-prey size scores for Pacific whiting larger than 550 mm as the predator, with an average weight ($\bar{w}_i$) of 1,441.3 g, under natural (line) and simulated (dashes) conditions.

a continued preference for euphausiids. A non-normal selection curve shape can arise when prey items occur in such dense patches that the predator may consume more than one prey item at a time (Ursin, 1973).

Large whiting (>550 mm) also have a selection curve (Fig. 5) which shows the numerical dominance of euphausiids in their diet. The preference curve looks more closely unimodal with the main peak corresponding to a predator-prey size ratio of 130:1 (about the ratio of a large whiting predator to a herring-sized prey). These whiting appear to prefer large-sized prey, but will actually consume mostly euphausiids — possibly because the dense nature of euphausiid patches allows whiting to exploit patches as a food source efficiently.

Daily Ration

To determine the impact a predator stock has on a prey population, it is important to calculate the total annual consumption of a particular prey by the whole predator stock. This type of calculation requires several types of information: An estimate of the size of the predator stock; a determination of the relative contribution of the prey item in the predator's diet through stomach content analysis; and an estimate of the total amount of food consumed by the predator, which requires the calculation of daily ration.

Livingston (1983) calculated daily ration for whiting from field data, which requires stomach samples taken at different times throughout the day. The gastric evacuation rate estimate for whiting (required for the calculations) uses the Elliott and Persson (1978) model which assumes an exponential, temperature-dependent evacuation rate, R. If stomach samples are collected at intervals of t hours, the mean stomach content weight as a percentage of fish weight, S_i, in each interval i is calculated for a total of m intervals over the 24-hour period. The daily ration, ΣC_t (in terms of percent body weight), is derived from:

$$\Sigma C_t = 24\bar{S}R,$$

where $\bar{S} = \Sigma S_i/m$. Durbin and Durbin's (1980) estimate of the relationship between gastic evacuation rate (R) and water temperature (T) for marine fish eating small food organisms was used for the calculation where:

$$R = 0.0416e^{0.105T}.$$

Livingston's (1983) estimate of the daily ration for whiting, using Equations (1) and (2), was equal to 2.5 percent body weight per day during the feeding season for a Pacific whiting with an average length of 500 mm, assuming the average water temperature at sample collection time and depth to be 8.2°C.

This estimate compares with those for a similar fish in the northwest Atlantic, silver whiting, *Merluccius bilinearis*, whose daily ration values range from 0.6 to 2.7 percent body weight per day (Durbin et al., 1983; Cohen and Grosslein, 1981; Pennington, 1981), although the Pacific whiting's estimate falls in the high end of this range. Francis (1983) used a bioenergetics approach to calculate daily ration for Pacific whiting and arrived at somewhat lower values — between 0.71 and 1.09 percent body weight per day for whiting during their feeding season. Since adult whiting do not feed continuously throughout the year, Francis (1983) estimated the annualized average value for whiting consumption at 0.4-0.5 percent body weight per day using a bioenergetic approach.

Although this value seems low in comparison with other published values, it seems reasonable considering the seasonality of feeding in Pacific whiting. If Livingston's estimate of 2.5 percent body weight per day was annualized to account for nonfeeding periods, it would probably be about 1.2 percent body weight per day.

Francis (1983) calculated the differences in total annual consumption by the Pacific whiting population between unexploited and exploited conditions which would correspond to the time periods 1952-65 (unexploited) and 1966-77 (exploited). The average annual difference in the whiting population's total food consumption was estimated to be 412,000 t/year over its range from California to Vancouver, B.C. The pandalid shrimp fishery off the coast operates mainly in the Eureka-Columbia International North Pacific Fisheries Commission (INPFC) areas, and the difference that whiting exploitation could make in pandalid shrimp consumption by the whiting population can be calculated for these areas. According to Francis (1983), the total difference in average annual food consumption by whiting between the exploited and unexploited condition in these areas is about 258,000 t. Whiting food habit data in the same areas indicate that the diet of whiting >450 mm in length (about age 5+) consists of between 0.3 percent and 4.5 percent by weight of pandalid shrimp. About 54 percent of the whiting population is age 5+ in those areas, as estimated from age composition data in bottom and midwater trawl samples (Dark et al., 1980). Thus, the pandalid shrimp consumption by whiting in the Eureka-Columbia INPFC areas would decrease by between 417 t and 6,255 t when whiting are exploited. The average catch of pandalid shrimp increased from 1,800 t when whiting were unexploited (1952-65) to 12,000 t when whiting were exploited (1966-77). This increase, however, does not seem attributable to decreased predation by whiting; the average catch per unit effort of pandalid

shrimp has not changed appreciably in the two periods (from 274 kg/h to 269 kg/h), and one would expect CPUE to increase if more shrimp were to become available to the fishery. An analysis of the history of the pandalid shrimp fishery reveals that total catch increased largely because the total effort in terms of vessels landing shrimp in Oregon increased from 45 boats in 1967 to 117 boats in 1976 (Pacific Fishery Management Council, 1980). Thus, there does not seem to be strong evidence pointing towards a large predator-prey interaction between whiting and pandalid shrimp.

Pacific Whiting: The Prey

Predation on Eggs and Larvae

Predation on fish eggs and larvae may be a major source of Pacific whiting mortality (Hunter, 1981). Eggs of the coastal stock are small (about 1 mm diameter) and are located mainly at the bottom of the mixed layer, at about 50 m depth. They have an extremely hard cuticle, which might make them invulnerable to some smaller grasping invertebrate predators and to some gelatinous zooplankton lacking penetrating nematocysts. In addition, whiting eggs are immobile and thus would not be vulnerable to ambush-type predators, due to the low probability of an encounter, or to nonvisual predators requiring tactile stimulation. Whiting eggs are vulnerable to raptorial or large filter feeding predators, and laboratory studies have demonstrated that amphipods, medusae, and other gelatinous zooplankton are efficient predators on whiting eggs. Euphausiids have been shown to eat anchovy eggs (Theilacker and Lasker, 1974) and are probably also able to eat whiting eggs. Filter feeding fishes may be predators on whiting eggs, as they have been shown to eat eggs of other species (Daan, 1976; Garrod and Harding, 1981; Hunter and Kimbrell, 1980).

Whiting larvae, like other gadids in general, are small (3 mm in length at

hatching) and are feeble swimmers; consequently, they are vulnerable to many invertebrate predators (Bailey and Yen, 1983; Bailey, 1984). Larvae in the yolk-sac stage are the most vulnerable to predators, being extremely small and with undeveloped escape responses. Invertebrate predators on whiting larvae include predatory copepods, amphipods, euphausiids, and gelatinous zooplankton; but by the time larvae are about 5 mm in length they are probably invulnerable to many invertebrate predators. Larvae may also be vulnerable to predatory fishes, although as with eggs, little is known of this interaction.

Field examinations of the impact of predators on the survival of whiting eggs and larvae of the coastal stock are nonexistent. Bailey and Yen (1983) suggested that invertebrate predators may have a significant impact on survival of whiting larvae in Puget Sound. Many invertebrate predators in larval nursery areas had black guts, probably from ingesting pigmented whiting larvae. Furthermore, a decline in survival from egg to feeding stages of whiting was correlated with increased numbers of invertebrate predators.

Predation on Juveniles and Adults

Juvenile and adult whiting have been found in the stomachs of many predators, including dogfish, *Squalus* spp.; rays, *Raja* spp.; sablefish, *Anoplopoma fimbria*; lingcod, *Ophiodon elongatus*; arrowtooth flounder, *Atheresthes stomias*; rockfishes, *Sebastes* spp.; tunas, Scombridae; marine mammals, and birds. Predation on whiting by fishes may be limited to young of the year and 1-year-old whiting, while mammals may eat older animals. Due to the size stratification of whiting with latitude (Dark et al., 1980), few fish predators eat whiting in the northern part of their range, where whiting are generally >30 cm. Whiting are a common prey of fishes in the juvenile nursery area, off the California coast.

In the whiting's juvenile nursery

area, rockfish, genus *Sebastes*, are abundant predators. In a 1980-81 survey, whiting were found in about 350 of 5,000 stomachs, including bocaccio, *Sebastes paucispinis*; chilipepper, *S. goodei*; widow rockfish, *S. entomelas*; yellowtail rockfish, *S. flavidus*; and copper rockfish, *S. caurinus*[1]. Almost all whiting prey were young of the year (90-150 mm) fish. Off the Oregon-Washington coast, however, the stomachs of five rockfishes (yellowtail rockfish; splitnose rockfish, *S. diploproa*; canary rockfish, *S. pinniger*; darkblotched rockfish, *S. crameri*; and Pacific ocean perch, *S. alutus*, were examined and contained no whiting (Brodeur, 1982).

Scombrids are another potentially important group of whiting predators. Mackerels are reported to eat fish larvae and juveniles. Whiting occur fairly infrequently in the stomachs of tuna; they were found in 1, 2, and 6 percent, respectively, of the stomachs of albacore, *Thunnus alalunga*; bonito, *Sarda chiliensis*; and bluefin tuna, *T. thynnus* (Pinkas et al., 1971).

Pacific whiting have been found in the guts of several birds, most notably in the guts of the sooty shearwater, *Puffinus griseus* (Chew, 1984). In 37 gut samples from southern California in 1976-77, whiting otoliths were found in 51 percent of the samples. However, in 1979, no whiting were found in 154 birds sampled from Monterey Bay. Although the size frequency of whiting in guts was not available, other fish prey were in the 50-80 mm range, corresponding to young-of-the-year if whiting prey are a similar size. Sooty shearwaters may be important predators because during their seasonal migration northward they are the main bird biomass along the coast[2]. Whiting have also been found as a component (2-14 percent frequency of occurrence) in the food the western gull, *Larus occiden-*

[1]T. Echeverria, Tiburon Laboratory, Southwest Fish. Cent. NMFS, NOAA, Tiburon, Calif. Pers. commun.

[2]G. Hunt, Univ. Calif. Irvine, Irvine, Calif. Pers. commun.

talis, fed to its chicks from 1972 to 1977 (Hunt and Butler, 1980). The highest occurrence of whiting in the diet was in 1977, corresponding to the presence of the strong 1977 year class as young-of-the-year fish.

Marine mammal predators on whiting include the northern elephant seal, *Mirounga angustirostris*; northern fur seal, *Callorhinus ursinus*; California sea lion, *Zalophus californianus*; Pacific white-sided dolphin, *Lagenorhynchus obliquidens*; Dall porpoise, *Phocoenoides dalli*; killer whale, *Orcinus orca*; and sperm whale, *Physeter catodon*.

Whiting may be particularly important in the diet of California sea lions, occurring in 49 percent of scats examined from San Miguel Island, off southern California (Antonelis et al., In press). Almost all whiting otoliths were from 1-2 year old fish. By contrast, farther north off the Farallon Islands, whiting otoliths from scats and spewings were predominantly from 2-3 year old fish (Ainley et al., 1982). Seventy-eight percent of identifiable hard parts such as fish otoliths or shellfish beaks were whiting otoliths.

In its southern range, the northern fur seal may consume many whiting. In fur seals sampled from 1958 to 1968 off California, an average annual value of 25 percent of stomachs contained whiting. Farther north off the Washington coast, only 4 percent contained whiting, and off British Columbia, 1 percent contained whiting (Fiscus, 1979).

Several attempts have been made to estimate consumption of whiting by marine mammals. These estimates range from 8,600 t/year of whiting consumed by northern fur seals (Antonelis and Perez, In press) to 12,000, 185,000, and 3,400 t/year of whiting consumed by northern fur seal, California sea lions, and northern sea lions respectively (Bailey and Ainley, 1982). Table 2 shows estimates of pinniped consumption of whiting from data used in Laevastu's Probub ecosystem model (Laevastu and Larkins, 1981). These estimates are much higher than those of Antonelis and

Perez, and range from a total of 134,300 t/year of whiting consumed by pinnipeds off Washington and Oregon to 152,300 t/year of whiting consumed off California. Consumption estimates are sensitive to values used for mammal population abundance and distribution, daily ration, and percent whiting in the diet. Since those studies were completed, Hawes (1983) found that in studies with captive animals, analysis of feeding habits based on mammal scats and spewings may be seriously biased. In controlled mammal feeding experiments, a high percentage of otoliths were not recovered, especially from mammals fed fish with small otoliths. Due to dissolution during digestion, fish otoliths were found to shrink; furthermore, squid beaks and large otoliths were frequently regurgitated rather than passed through the intestines. Because sacrificing mammals for their stomach contents is not desirable, Hawes suggests incorporating correction factors into consumption estimates to correct for these biases.

Summary of the Trophic Role of Pacific Whiting

Figure 6 depicts the changing array of whiting predators and prey throughout the whiting's life history stages. As whiting progress from larvae to adults, their prey choices switch from small items such as copepod eggs and copepods, to progressively larger items like euphausiids, shrimp, sand lance, eulachon, and herring. Similarly, whiting predators increase in size with the whiting's increasing size; from predatory zooplankton which consume whiting eggs and larvae, through fish which eat mostly whiting larvae and juveniles, to larger

Table 2.—Probub model estimated pinniped consumption of Pacific whiting in t/year, Washington-Oregon and California.

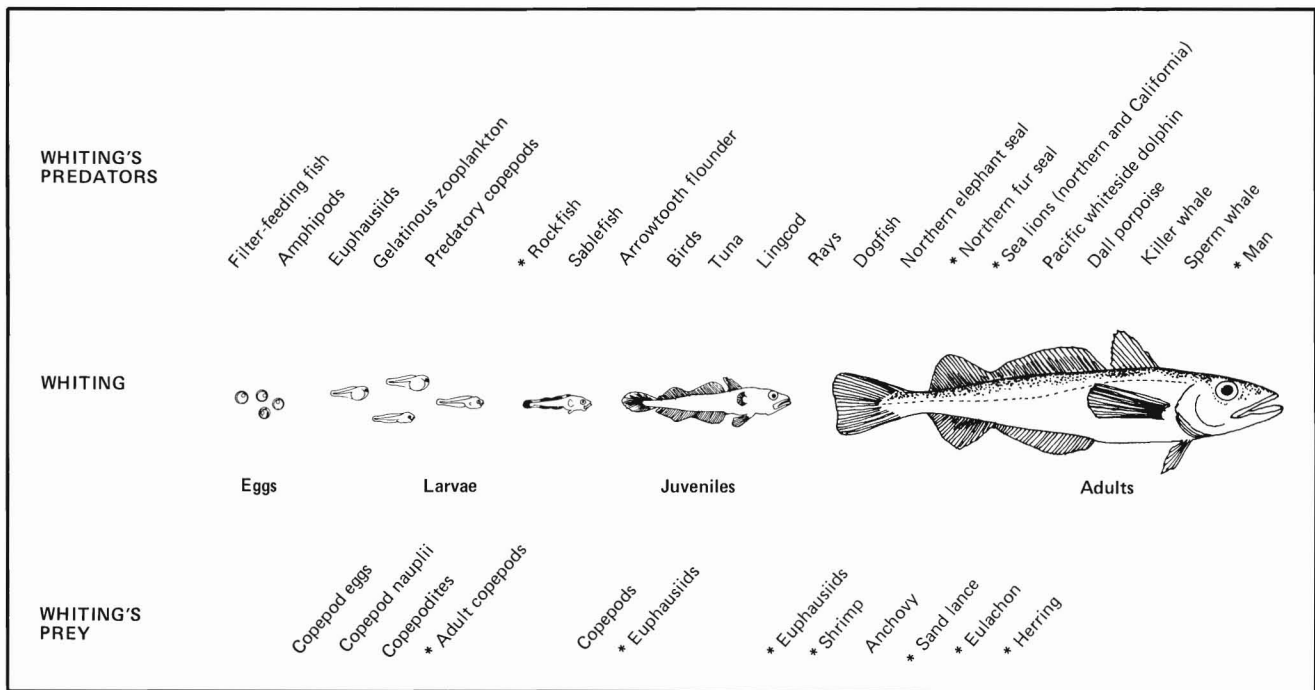| Pinniped	Washington-Oregon	California
Northern fur seals	53,700	58,900
Northern sea lions	41,300	31,300
California sea lions	9,400	19,500
Elephant seals	29,900	42,600
Total	134,300	152,300

Figure 6.—Representation of Pacific whiting's predators and prey in various life history stages of whiting. (Asterisk indicates major predators or prey.)

predators such as large fish, dogfish, and mammals which prey mostly on older juveniles and adult whiting. Also evident (Fig. 6) is the number of commercially important or protected species linked to whiting: Shrimp, anchovy, herring, rockfish, and marine mammals.

From a management point of view, it is important to identify and quantify the links between one managed species and another. Here we have identified the major links between whiting and its important predators and prey. Some quantification of the links has been performed using daily ration estimates and stomach content analysis results to estimate the rate of biomass flow between species. In particular, the link between whiting and one of its commercially important prey items, pandalid shrimp, has been calculated and compared with historical trends in the pandalid shrimp fishery. Estimating biomass

flow in the other links requires accurate daily ration estimates, seasonal and size-related definition of stomach contents, and predator population estimates. Due to inaccuracies of some of these parameters, it seems somewhat premature to place a great deal of faith in the resulting biomass flow estimates. In particular, refinement of daily ration estimates for whiting and mammals to take into account differential digestion of various prey types would be a logical step, as would better methods to evaluate stomach contents (such as an unbiased mammal stomach content analysis method). When these are obtained, a more reliable management perspective may follow.

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