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Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs

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ABSTRACT: Predators congregated in large numbers during the 1996 and 1997 spring spawning runs of eulachon *Thaleichthys pacificus* Richardson (Osmeridae) in the lower reaches of the rivers entering Berners Bay, southeastern Alaska. Predator abundance rose rapidly at the beginning of the runs and was significantly correlated with an index of eulachon abundance within years. Gulls (Laridae) were the most abundant predators, with a daily average peak of 40 000 during the 1996 run, at a density of 3000 km^{-2}. A daily average peak of over 250 Steller sea lions *Eumetopias jubatus* and harbor seals *Phoca vitulina* fed on eulachon early in the run in both years. Daily average counts of bald eagles *Haliaeetus leucocephalus* approached 600 on the lower reaches of the rivers, and many others foraged upstream. Eulachon are unusually high in lipid content, and many of the prodigious spawning runs in Alaska and British Columbia occur in spring, when predator energy demands are high. We suggest that spring spawning runs of eulachon and other forage fishes are an ecological cornerstone for regional coastal ecosystems, supporting large numbers of wildlife species.

KEY WORDS: Eulachon · *Thaleichthyes pacificus* · Osmeridae · Southeast Alaska · Steller sea lion · Harbor seal · Laridae

INTRODUCTION

Many ecosystems are influenced by seasonal pulses of resources that can have important effects on populations and communities (Odum et al. 1995). A marine example is found in the North Pacific, where spawning runs of anadromous salmon *Oncorhynchus* spp. enrich both freshwater and riparian systems with marine-derived nutrients (Cederholm et al. 1999, Wipfli et al. 1999) and provide important seasonal food resources for wildlife (Willson & Halupka 1995, Willson et al. 1998) in late summer and fall. Salmon thus form an ecological link between marine and terrestrial/freshwater systems, but other anadromous fishes might be similarly important to coastal ecosystems. However, very little is known about the ecology of these species in terms of their interactions with predators and potential roles in ecosystem dynamics

We describe here the magnitude and timing of predator response to spring spawning runs of eulachon *Thaleichthys pacificus* Richardson (Osmeridae) in Berners Bay, southeastern Alaska. Eulachon, small but energy-rich forage fish, spawn in freshwater streams along the North Pacific coast of North America. To our knowledge, this is the first study to examine predator-prey interactions for eulachon, and our work suggests that this interaction may be ecologically important to coastal ecosystems. Our descriptive study thus provides a springboard for subsequent, more detailed, studies of the ecological role of eulachon runs in coastal ecosystems and, more generally, contributes to the growing field of data demonstrating ecological links between marine and freshwater systems.

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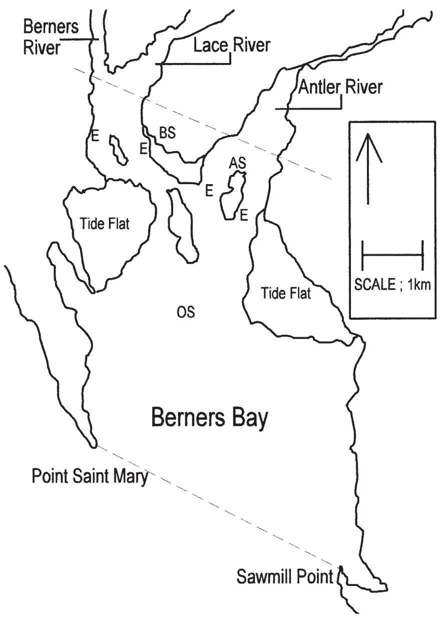

Fig. 1. Berners Bay study area with locations of eulachon *Thaleichthys pacificus* census areas (E), and predator counting stations on the Antler River (AS), Berners/Lace River (BS), and the Bay (OS). Predator census plots covered area between dashed lines

MATERIALS AND METHODS

Study site. Berners Bay is located in a ~390 km^2 roadless watershed of the Tongass National Forest, 65 km north of Juneau, Alaska (58.75° N, 135° W) (Fig. 1). Two river systems (Antler and Berners/Lace) converge on a broad delta, which includes about 10 km^2 of tidal sand flats. Both river mainstems are opaque, because of heavy loads of glacial silt, but there are some clearwater tributaries. Eulachon spawn in the lower reaches of all rivers.

Sampling methods. Preliminary observations and sampling protocols were established during short visits to the bay in 1994 and 1995. In 1996 and 1997, daily counts of eulachon and predator abundance began on April 25, before eulachon began to enter the rivers, and ended on May 18 or 19, when no more incoming fish were caught. Observations in 1994 and 1995 showed that avian predators were concentrated in the lower 4 km of the rivers in tide-flat habitats and that marine mammals concentrated at the river mouths, as found in other studies (Hart & McHugh 1944, Franzel & Nelson 1981, Bishop et al. 1989, Horwood 1990, Drew 1996). Therefore, our subsequent observations were concentrated in these areas.

Eulachon abundance was indexed with a catch per unit effort (CPUE) system of dip netting at 4 predetermined areas along the Antler and Berners/Lace Rivers among all major channels available for eulachon migration and spawning (Fig. 1). The dip nets were 31 cm deep with a 31 × 31 cm opening and 5 mm mesh, attached to a telescoping 5 m pole. In 1996, each dip-net area was sampled twice per day at slack high and low tides. We found no difference in relative abundance between high and low tides (fish/dip = 0.53, SE = 0.23, and 0.49, SE = 0.25, Student's t = 0.259, df = 19, p = 0.79), so 1997 samples were taken at high tide only. Each daily sample consisted of 10 downstream sweeps of the dip net separated by one to several meters to spread out the sampling. Total eulachon catch was divided by the number of sweeps to obtain a daily CPUE index for each river system and for the whole area. The reliability of our dip-net CPUE was compared with another sample method, a fixed trap that sampled at night in the Antler River. Relative abundances from the fixed trap were not significantly different from those obtained by dip netting (n = 21) in that channel (Wilcoxon, p = 0.203). All captured fish were checked for spawning status (gravid or spent) and released.

Table 1. Mean eulachon abundance indices (catch per unit effort, CPUE) and mean predator counts at Berners Bay. Z: Wilcoxon signed-rank Z statistic and probabilities

Location	Mean eulachon CPUE (n = 11)	Z	Mean predator counts	Z
Antler River				
1996	1.07 (0.40 SE)	1.95; p = 0.05	1256 (259 SE; n = 13)	2.9; p = 0.003
1997	0.16 (0.07 SE)		1261 (262 SE; n = 11)	
Berners River				
1996	0.00 (0.00 SE)	No test	2894 (583 SE; n = 15)	0.36; p = 0.72
1997	0.24 (0.16 SE)		2888 (1122 SE; n = 11)	
Area-wide				
1996	0.56 (0.22 SE)	1.6; p = 0.11	22 938 (3261 SE; n = 11)	2.5; p = 0.01
1997	0.22 (0.09 SE		9673 (2378 SE; n = 11)	

Predators of eulachon were counted within 13 plots that encompassed the lower rivers and upper bay (Fig. 1). The plots were triangular, with landmarks defining the outer corners and mountain sides or river banks defining the triangle base, such that predators were counted only within those marks from the observation point at the triangle apex. These plots facilitated an efficient count of the tide-flat and lower bay area with simultaneous tallies of all plots at predetermined times. Two observers occupied each of 3 counting stations for each count, and observers rotated among stations daily. At each station observers tallied the number of predators seen within plots at that station. Tallies at all stations were done simultaneously, at 15 min intervals around the high and low slack tides of daylight hours. These simultaneous tallies were summed for the area-wide tallies, and the daily area-wide mean was the average of those tallies ($n = 6\ d^{-1}$ in 1996 and $10\ d^{-1}$ in 1997). In addition, we used the highest area-wide tally per day as the maximum predator count for that day. Bird density was calculated by dividing plot means by plot area, derived from topographic maps. Marine mammal density could not be calculated satisfactorily, because they were concentrated at the river mouths, where plot areas accessible to marine mammals varied with tide levels. Daily notes of predators upriver or outside of the plots were also kept by observers. In addition, an estimate of species composition of the gull flock, which was not possible during plot counts, was obtained twice during each run with direct counts of roosted flocks. Experienced observers used spotting scopes to count the number of each species within all identifiable flocks on the estuary; several counts (minimum n = 5) were averaged for each estimate. Two estimates were made, an early count during the first 2 d of the spawning run, and a late count 1 wk later. These 2 counts were averaged to estimate the proportion of each species during the eulachon run. This proportion was then multiplied by the daily gull count to estimate daily abundance for each species.

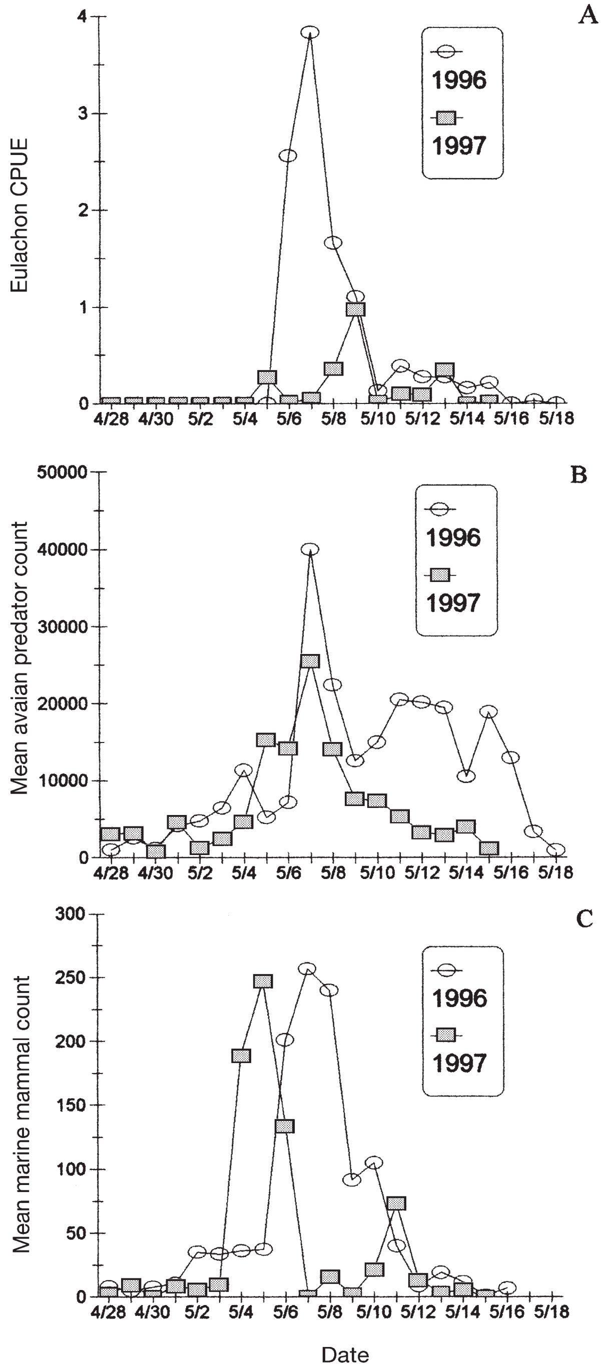

Fig. 2. (A) Eulachon catch per unit effort, cpue, (B) avian predator count and (C) marine mammal count at Berners Bay. Dates presented as mo/d

RESULTS

Spawning run

Eulachon in Berners Bay began their spawning runs between May 3 and May 6 in 1995 (preliminary observations), 1996, and 1997, ending 10 to 12 d later (Fig. 2A), although spent fish or a few late spawners remained in the rivers until the end of May. The area-wide mean index of relative abundance for 1996 was more than twice that of 1997, but was not significantly different (Table 1). In 1996 the proportion of caught fish that were spent reached 100% on May 12, 5 d after the run began, and all fish caught after that date were also spent. In 1997 all caught fish were spent on May 7, only 2 d after the run began, but some pulses of gravid fish were detected until May 13.

Predator counts

Predators responded quickly to the beginning of the eulachon run (Fig. 2B,C). The temporal distribution of predator abundance differed between years (Kolmogorov-Smirnov [K-S], p = 0.006), although the temporal distribution of fish abundance did not differ between years (K-S, p = 0.31). Daily mean predator abundance was positively associated with the relative abundance of eulachon in both years (Spearman's rank correlation: 1996 $r_s = 0.79$, $n = 20$, $p < 0.01$; 1997 $r_s = 0.52$, $n = 18$, $p < 0.03$). Corresponding to yearly trends in mean fish abundance indices (Table 1), 1996 predator counts were significantly higher than 1997, on the Antler River and area-wide. Although abundance estimates for bald eagles were not significantly correlated with relative abundance of eulachon in 1996 ($r_s = 0.31$, $n = 20$, $p > 0.10$), they were so in 1997 ($r_s = 0.62$, $n = 18$, $p < 0.01$).

Estimates of predator abundances showed that large numbers of foragers gathered during the eulachon runs, although there was some annual variation. Avian predator abundance peaked at 43 000 and marine mammals at 419 during 1995 preliminary counts. In 1996 the highest daily mean counts were 40 000 total avian predators, including 585 bald eagles, and 250 marine mammals. Maximum area-wide tallies in 1996 were 46 000 avian predators, including 650 bald eagles, and 450 marine mammals (see also Gende et al. 2001). The highest daily mean counts for 1997 were 25 000 total avian predators, including 326 bald eagles, and 250 marine mammals. Maximum area-wide tallies in 1997 were 36 500 avian predators, including 536 bald eagles, and 422 marine mammals.

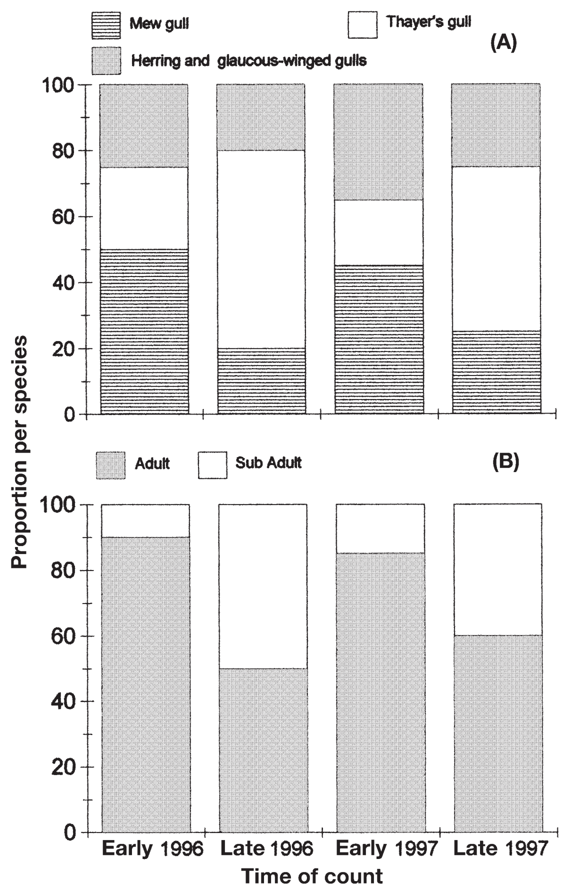

Fig. 3. Gull species composition (A) and age distributions (B) during eulachon spawning runs in Berners Bay

Thirty-four species of bird consumers were observed to forage on eulachon, including 12 gulls and terns (Laridae), 10 ducks (Anatidae), 4 shorebirds (Scolopacidae), a kingfisher (Alcedinidae), 3 raptors (Falconidae), and 4 passerines (2 Corvidae, Motacillidae, Emberizidae). Gulls were the primary avian predators. Mew gulls *Larus canus* dominated the flocks early in the run, and larger gulls later (herring gull *L. argentatus*; glaucous-winged gull *L. glaucescens*; Thayer's gull *L. thayeri*) (Fig. 3A). Mew gulls often foraged farther upstream than the larger gulls. Bonaparte's gulls *L. philadelphia* were rare in 1997 and were seen only occasionally in 1996. Thayer's gulls dominated the flocks toward the end of May, numbering at least 6000. Additionally, the relative abundance of juvenile gulls increased as the run progressed (Fig. 3B). The principal mammalian predators were Steller sea lions *Eumetopias jubatus* and harbor seals *Phoca vitulina*; humpback whales *Megaptera novaeangliae* were occasionally encountered. The abundance of marine mammal predators was high early in the run, as the fish entered the river. Seals did not appear in high abundance until sea lion numbers dropped markedly. In contrast, bald eagles (see Fig. 4) and corvids (>100 individuals) were particularly abundant and active later in the run, when many dead eulachon accumulated on the shores. Two species of salmonid fish (*Oncorhynchus kisutch* and *Salvelinus malma*) also fed on eulachon eggs or larvae in 1996 (M. Wipfli pers. comm.). In addition, large numbers of grebes *Podiceps* spp. (>100), scoters *Melanitta* spp. (15 000), mergansers *Mergus* spp. (700), and marbled murrelets *Brachyrhamphus marmoratus* (290) were seen in 1995. Other animals occasionally observed in the spawning area probably also feed on eulachon, including bears *Ursus* spp., wolves *Canis lupus*, mink *Mustela vison*, river otters *Lontra canadensis* and loons *Gavia* spp.

Scavenging and caching

In contrast to gull species that fed heavily on upriver migrating eulachon, corvids, eagles, waterfowl, and shorebirds were mainly observed to feed on dead or dying fish. Corvids cached eulachon by burying the fish in sand bars or hiding them in grassy meadows or trees. The 1996 run attracted many non-breeding ravens (up to 30 roosted nightly in trees within one of the plots after feeding on dead eulachon from tidal flats) and nesting ravens traveled to nearby territories. Eagles congregated on the river bars and fed on stranded fish in tidal pools that were separated from the main river channels as the tides receded. This foraging behavior was more often seen than active capture of eulachon, but some eagles were observed diving for migrating fish in the mainstem with considerable success. Waterfowl and shorebirds fed on eulachon as well, usually by tearing off pieces of muscle and strips of skin. Shorebird and waterfowl species were also seen gleaning small prey items from river margins, possibly including eulachon eggs that were stranded there.

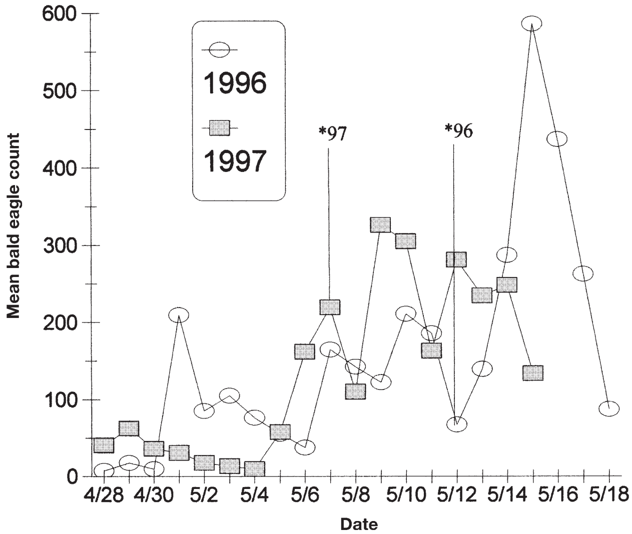

Fig. 4. Bald eagle abundance counts and earliest dates on which 100% of eulachon CPUE was spent. *Earliest dates upon which all sampled fish were spent for 1996 (*96) and 1997 (*97). Dates presented as mo/d

DISCUSSION

Correlations of fish and predator abundance

At Berners Bay, eulachon were preyed upon by numerous predators throughout the spring spawning run and for some time afterward, as spawned-out fish drifted seaward. In general, predator abundance mirrored trends in relative prey abundance within and between years, except for annual differences on the Berners/Lace River. This river system has extensive tide flats that are favored by roosting gulls and our consistently high counts reflected roosting birds that foraged also on the Antler River. At least some of the annual differences in predator abundance may reflect the fact that herring spawned on rocky shores in the bay in 1996, just before the eulachon run, but not in 1997, and this resource attracted numerous gulls and eagles.

The correlations between the relative abundance of eulachon and numbers of bald eagles were not consistent, in part because eagles concentrated on spent and stranded fish. Eulachon are commonly semelparous (Hart & McHugh 1944, Smith & Saalfeld 1955), and spent or partially spent fish are weak and easily captured by eagles, as are fish stranded in tidal pools or along beaches. In both years, eagle numbers rose above 250 at Berners Bay only after the first day upon which all sampled fish were spent (Fig. 4). Spent fish were available earlier and irregularly in 1997, and eagle numbers closely followed the CPUE that year, but in 1996 both eagles and spent fish became abundant in a single peak that did not reflect the CPUE trend.

Anecdotal information suggests that predators aggregate at other eulachon runs in British Columbia and Alaska. At the Stikine River, up to 1600 bald

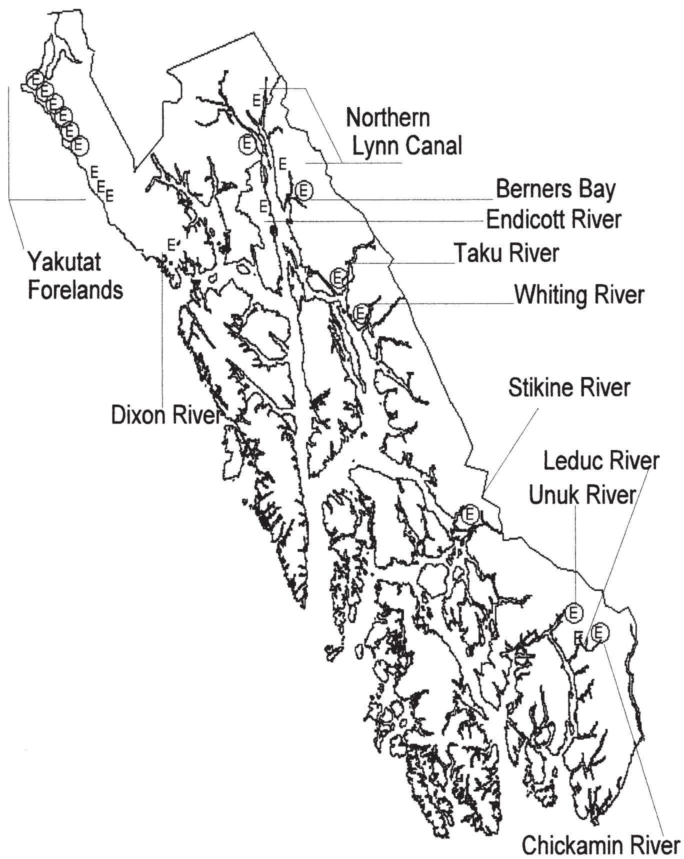

Fig. 5. Southeastern Alaska with locations of eulachon spawning runs (E) and areas where predator aggregations are known (circled)

eagles and 80 000 gulls have been seen at eulachon runs (Hughes 1982, Drew 1996), and gull numbers reached 15 000 on the Chilkat River (Bishop et al. 1989). Naturalists have noted large concentrations of marine mammals, avian predators, and some terrestrial mammals in other areas with eulachon runs (Fig. 5; Yakutat forelands: V. Harke pers. comm.; Kitimat River: Pederson et al. 1995; Copper River: D. Logan pers. comm.; Taku River: M. Jacobson pers. comm.; Unuk River: R. Nourse pers. comm.; Chilkat and Chilkoot Rivers: B. Zack pers. comm.; Horwood 1990), and some predatory fishes are known to forage heavily on eulachon (e.g. Chatwin & Forrester 1953). Harbor seals at the Copper River Delta also forage heavily on eulachon in spring and early summer (>95% of the diet: Imler & Sarber 1947, Pitcher 1977), suggesting that eulachon runs are also important spring food sources for harbor seals in that area.

Eulachon, throughout their range, typically spawn in late winter and spring (Hart & McHugh 1944, Franzel & Nelson 1981, Hay et al. 1997). However, there is some regional variation in spawning time that may reflect water temperatures in the spawning rivers: spawning runs usually occur earlier at more southern latitudes. Therefore interactions with predators and the significance of eulachon to predator biology also may differ among regions.

Ecological reasons for predator response

Our results clearly demonstrate a large predator response to spawning eulachon. We suggest that eulachon attract numerous predators for 2 reasons.

First, the energetic benefit/cost ratio for foraging on eulachon is likely to be high. In terms of benefit, eulachon are extremely high in lipids, with an energetic density much greater than most other fishes available (10.5 kJ g^{-1} wet wt: Payne et al. 1997; van Pelt et al. 1997). Prey sources with high energy density can increase digestive efficiency in seals (Lawson et al. 1997) and sea birds (Brekke & Gabrielson 1994). Eulachon oil is also comparatively high in vitamin A and iron (Drury 1985, Betts 1994). On the other hand, the cost (in time or energy) of capturing eulachon is probably relatively low. Eulachon are relatively weak swimmers, and they generally concentrate and move upriver in low-velocity shallow waters at river margins (Galesloot 1991, B. H. Marston et al. pers. obs.), where they are highly vulnerable (Willson & Marston 2002) to many predators, both aquatic and terrestrial; furthermore, many spawners die after spawning, which makes them available to scavengers as well. Ease of capture is indicated by our observations of gulls capturing 6 to 8 fish in less than 1 h. Gulls rested on sand bars for much of the day, often with eulachon tails extending from their mouths, indicating that they were filled to capacity. Because digestion of fish is often rapid in birds (Jackson & Ryan 1986, Brugger 1993, Hilton et al. 2000), gulls probably could feed to satiation more than once a day.

Second, the spring spawning runs in our region occur at a time of year when many predators have high energy costs. Pinnipeds in our region give birth and mate in spring (Calkins 1984, Pitcher 1984, B. H. Marston et al. pers. obs.); males may fast for long periods (Riedman 1990), and females have the high costs of lactation. Lactation costs are the highest energy demand of reproduction in mammals (Gittleman & Thompson 1988, Costa 1991); for example, female harbor seals lose up to 80% of their stored fat during lactation (Bowen et al. 1992). For illustrative purposes, we use information from the literature to compare estimates of feeding capacity with lactation costs in a currency of numbers of eulachon (mean mass in our rivers = 33 g, SE = 0.5, n = 115; energy density 10.5 kJ, as given above), in order to indicate the potential role of eulachon in supporting lactation. Female sea lions (average body mass 290 kg) may consume as much as 27 kg of prey per day (over 9% of body mass: Hoover 1988b; Davis et al. 1996) or about 830 eulachon. Lactation costs about 21 550 kJ d^{-1} (based on information in Higgins et al. 1988, Costa 1991), or the equivalent of about 78 eulachon d^{-1}. A female sea lion filled to capacity could obtain about 11 days' worth of lactation energy in 1 d of eulachon feeding, or about 23% of total lactation costs. In contrast, if a sea lion fed on pollock *Theragra chalcogramma*, which has a low energy density (Anthony & Roby 1997, van Pelt et al. 1997), over twice as many fish might be needed to achieve the same level of energy intake. Female harbor seals (average mass 76 kg: Hoover 1988a) can consume at least 8.4 kg of prey per day (up to 11% of body mass: Ashwell-Erickson & Elsner 1981, Hoover 1988a), or a possible capacity of about 255 eulachon d^{-1}. If a female seal ate to capacity for just a few days, she could readily obtain (and store) most of the energy needed for reproduction (based on information in Ashwell-Erickson and Elsner 1981). Migratory birds such as Thayer's gull use stored body fat in migration (Berthold 1996), and reproductive performance is greater for female gulls in good condition with good food supplies (Pierotti & Bellrose 1986, Meathrel & Ryder 1987, Meathrel et al. 1987, Pierotti & Annett 1990, Bolton et al. 1992).

We have shown that predators aggregated in large numbers at a eulachon run and suggest that they may be important to predator ecology. We can draw some parallels to the more intensively studied Pacific salmon, which often return to spawn in high densities in small streams. Many predators congregate during these seasonal runs, and reproductive and population consequences of salmon foraging have been documented for some predators. For example, brown and black bears *Ursus* spp. feed heavily on salmon just before periods of long fasting (hibernation) and reproduction. Body size, average litter size, and population density are all positively correlated with salmon availability (Hilderbrand et al. 1999). We suggest that further studies of eulachon subsidies may find similar effects on predator reproductive success; for instance, Steller sea lions (at least in some areas) forage heavily on eulachon before long periods of fasting on the breeding rookeries. Continuing studies are examining the relationship between eulachon foraging and sea lion reproductive success and population distribution.

To generalize these observations, we suggest that anadromous fishes may be critical components of coastal ecosystems. Prey pulses that are seasonally available in spawning runs can be considered ecological cornerstones of coastal ecosystems.

Conservation considerations

The association of predators with eulachon runs raises conservation concerns. Eulachon spawn in a limited number of low-gradient streams on the west coast of North America. Anthropogenic effects on eulachon spawning habitats, such as altering river flow and temperature, dredging and filling of lower river reaches, and scouring when flood plains are channelized can potentially alter eulachon spawning behaviors or abundance. Anthropogenic threats to eulachon spawning habitats, and by implication to their major predators, are imminent in several locations, including Berners Bay. Development and industrial use of other areas with eulachon runs has led to displacement of eulachon runs (Smith & Saalfeld 1955, Betts 1994) and may alter their palatability to consumers (Beak Consultants Limited 1992, Hay et al. 1997). Several of the predator species recorded during the eulachon run in Berners Bay (including Steller sea lions and harbor seals) are already of special conservation concern in portions of their ranges (Payne 1995), and population declines have been linked to prey resources.

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