JELLYFISH AS COMPETITORS AND PREDATORS OF FISHES

Restoration Project (APEX) 98163S

Annual Report

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ABSTRACT

At high densities, jellyfish can seriously effect populations of zooplankton and ichthyoplankton, and may be detrimental to fisheries through competition for food with fishes and by direct predation on the eggs and larvae of fish. In this project report, I examine the roles of jellyfish as competitors and predators of fishes. This was accomplished by participating in ongoing APEX research cruises in Prince William Sound, in which zooplankton, and medusa and ctenophore distributions and densities were determined. Additionally, medusae and ctenophores were collected for gut content analysis and gut passage time experiments in order to calculate feeding rates on zooplankton. This project has coordinated with other APEX investigators, who provided logistic support in the field, and sampling for zooplankton. I have compared jellyfish diets with forage fish diets from previous APEX research, in order to determine dietary overlap and the potential for competition. In collaboration with APEX and SEA scientists, I have compiled historical, and existing data in order to better understand the importance of jellyfish in the food web of Prince William Sound. In this year, one submitted publication has resulted from such collaboration.

Study History. In July, 1996, I was invited to participate in the SEA sampling in Prince William Sound by Dr. Gary Thomas. During the field work, I observed the abundance of jellyfish in northern Prince William Sound from aerial surveys and from trawls and acoustic surveys. Massive aggregations of *Aurelia* 1/4 to 2 km long were seen commonly from the air and by acoustics. *Cyanea* and *Aequorea* were distributed throughout Prince William Sound, but had higher densities in some areas (e.g. Irish Cove). The plane and acoustics boat would notify the seiner where to set his net on a fish school, but often more jellyfish than fish were in the net. I also compiled existing data from the Alaska Dept. Of Fish and Game collected during SEA cruises that showed in drift seines, which were not set specifically on fish schools, jellyfish biomass often exceeded fish biomass in Prince William Sound. Researchers from SEA and APEX observed the great abundance of jellyfish in Prince William Sound and recognized the need to understand their effects on the zooplankton and fish populations there.

In anticipation of EVOS funding starting in October, 1997, APEX investigators invited me to participate in the July-August cruise. The jellyfish populations were considerably different from 1996, being generally less abundant and with *Aequorea* in low numbers. Specimens of five species (*Cyanea, Aurelia, Aequorea, Clytia, Pleurobrachia*) were collected for gut content analysis.

INTRODUCTION

Not only do jellyfish and ctenophores feed on the same zooplankton foods as fish larvae and zooplanktivorous fishes, but they eat the eggs and larvae as well (Purcell, 1985; 1990, Purcell and Grover, 1990; Baier and Purcell, 1997). The dual role of soft-bodied plankton as predators

and competitors of fishes has been suggested many times (e.g. Purcell, 1985; Arai, 1988), but seldom has been evaluated directly (existing studies are Purcell and Grover, 1990; Baier and Purcell, 1997). Jellyfish predation on zooplankton could affect the larvae of numerous fish species, many of which are commercially important (e.g. herring, rockfish, cod, flatfish; Fancett, 1988; Purcell, 1989, 1990) as well as the juveniles and adults of zooplanktivorous fish species (e.g. herring, walleye pollock, sandlance, pink salmon) that are important as forage fish of marine vertebrates, specifically piscivorous fish, sea birds, and harbor seals. The following background provides details of research on gelatinous species to determine their effects on zooplankton and ichthyoplankton populations.

Dietary analyses. Copepods are the main prey items of most gelatinous predators. Several estimates of predation effects of gelatinous species on copepod populations suggest that the effects are too small to cause prey population declines (e.g. $\leq 10\%$ d^{-1}; Kremer, 1979; Larson, 1987a,b; Purcell et al., 1994b). However, some studies indicate much higher predation and possible reduction of zooplankton standing stocks (e.g. Deason, 1982; Matsakis and Conover, 1991; Purcell, 1992). Copepod capture by *Chrysaora quinquecirrha* was significantly related to prey density, medusa size, and temperature. During July and August 1987 and 1988 in two tributaries of Chesapeake Bay, medusae consumed from 13 to 94% d^{-1} of the copepod standing stocks, and may have caused the observed copepod population decline. The predation effect is directly dependent on the jellyfish population size (Purcell, 1997)

The possibility of competition for food among jellyfish and fish has been directly examined in only a few studies. Potential competition between medusae and first-feeding herring during one spring in British Columbia was found unlikely to be important due to the great abundance of copepod nauplii consumed by the larvae (Purcell and Grover, 1990). However, when the prey were copepodites, chaetognaths consumed significant percentages of the same prey as fish larvae off the southeast U.S. coast (Baier and Purcell, 1997).

The diets of some species include high proportions of fish eggs and larvae when available. Such predators include hydromedusae, in particular *Aequorea victoria*, whose diet consisted of almost exclusively Pacific herring (*Clupea pallasi*) larvae in April when the larvae hatched (Purcell and Grover, 1990) and a variety of eggs and larvae of other species of fish later in the spring in addition to gelatinous and crustacean prey (Purcell, 1989). Semaeostome scyphomedusae also may contain large numbers of ichthyoplankton prey when available in addition to gelatinous and crustacean prey (e.g. *Cyanea capillata, Chrysaora quinquecirrha* in Fancett, 1988 and Purcell et al., 1994a). Predation effects by pelagic cnidarians on fish eggs and larvae often are substantial ($\geq 30\%$ d^{-1} of the populations) in environments where predators are numerous, as for *C. quinquecirrha* and *A. victoria* (Purcell, 1989; Purcell and Grover, 1990; Purcell et al., 1994a). Other estimates, based on laboratory experiments, of predation effects by pelagic cnidarians on fish eggs were low (0.1 to 3.8% d^{-1}; Fancett and Jenkins, 1988).

At high jellyfish densities, as can occur especially in semi-enclosed bodies of water (Purcell, 1990), such as Prince William Sound (Prince William Sound), predation on copepods may limit

copepod populations and cause competition for food with zooplanktivorous fish species and fish larvae . Predation by jellyfish on fish eggs and larvae can be very severe. Medusae have potentially great effects on fish populations because of their often great abundances and feeding that increases directly with prey density without saturation.

OBJECTIVES

1.   Determine annual variation in species composition, size distributions, and abundances of jellyfish and ctenophores in Prince William Sound.

2.   Collect gut content data for key gelatinous predators (*Aurelia, Cyanea, Chrysaora, Aequorea* and other hydromedusae, *Pleurobrachia* ctenophores) in order to evaluate the diet of the several key species and to evaluate interannual variation..

3.   Determine the gut passage (digestion) times for key predator species fed key prey taxa (i.e. copepods, larvaceans).

4.   Calculate size-specific feeding rates for each key predator species based on gut contents and gut passage times, and correlate feeding rates with medusa size and prey densities in order to be able to estimate feeding impacts in other years from jellyfish size distributions and jellyfish and zooplankton densities.

5.   Calculate dietary overlap indices for medusae and forage fish species.

6.   Calculate predation impacts on key prey taxa based on feeding rates and densities of predator and prey species.

7.   Contribute these results to the APEX, SEA and overall EVOS modeling efforts.

8.   Compile historical data (Gulf of Alaska) and all available EVOS data (Prince William Sound) on jellyfish distributions and abundances.

METHODS

Distribution and abundance of zooplankton and jellyfish

In July, 1997 and 1998, zooplankton samples were collected at 8 previously determined stations at each of three areas, northeastern, central, and southwestern Prince William Sound at night in 60 m vertical hauls by APEX investigator Dr. Tom Shirley using a 20 cm diameter bongo plankton net (see Table 2, 97163A Annual Report). Zooplankton were identified and counted from subsamples by my technician. Small gelatinous species (ctenophores and hydromedusae)

were counted from whole samples. In addition, Tucker trawl samples were taken by Dr. Shirley at night, and the hydromedusae were removed for later identification by my technician. CTD data were collected (see Table 1, 97163A Annual Report), and will be made available to me for all appropriate cruises.

In order to determine the abundance of large jellyfish (*Cyanea, Aurelia, Aequorea*) samples were taken with a 20 m herring seine. In 1998, the seine was set at the same 24 stations as above (see Table 3, 97163A Annual Report). The samples were processed on board ship; the medusae were identified, counted, the swimming bell diameter measured, and biovolumes of each species measured. Abundances of the large jellyfish were estimated by calculating the volume of water filtered by the seine (57,642 m^3).

Analysis of predation rates on zooplankton

In order to determine the gut contents of jellyfish, in both 1997 and 1998, small hydromedusae (*Clytia*), ctenophores (*Pleurobrachia*), and large medusae (*Cyanea, Aurelia, Aequorea*) were dipped from the surface at the above sampling locations, and were immediately preserved in 5% Formalin. Prey in the guts were identified, counted, and measured using a dissecting microscope.

In order to measure the gut passage times for zooplankton prey, in 1998, individual medusae were collected in dip nets and maintained at ambient water temperatures in 94 liter coolers filled with filtered (32 μm) seawater with some *Artemia* nauplii. One or more medusae were preserved immediately, and then one or more medusae were preserved at 1 or 2 h intervals. The gut contents of the medusae were analyzed later in the laboratory for partly digested prey. The length of time when the different prey types are no longer recognized in the gut contents are used in calculations of feeding rates.

In order to calculate jellyfish feeding rates and effects on zooplankton populations, data on the numbers of prey in the guts are divided by gut passage times to calculate feeding rate (No. of prey eaten h^{-1} medusa^{-1}). The individual feeding rates are multiplied by medusa densities and divided by prey densities to determine the impacts of the medusae on the prey populations.

Underwater video. In order to determine the frequency of associations of juvenile pollock and aggregations of *Aurelia* medusae, and to determine swimming behavior in the aggregations, four aggregations were videotaped using a Hi-8 VCR and monitor attached to a closed-circuit underwater camera system (Fisheye, Inc). The videotapes were analyzed with an editing Hi-8 VCR. Those results are presented in the attached manuscript.

Data compilation from SEA and APEX investigators. In addition to the field work on jellyfish, data were sent from several collaborators and analyzed by my technician. Dr. Paul Anderson sent historical data on large jellyfish from shrimp trawls in the Gulf of Alaska from 1973-1995. Dr. Ken Coyle sent SEA data on hydromedusae from Prince William Sound in 1994

- 1997. Dr. Kevin Stokesbury sent SEA seine data from 1996. Evelyn Brown sent data on *Aurelia* aggregations from aerial surveys in 1995, 1996, and 1997. Dr. Molly Sturdevant sent zooplankton, hydromedusa, and forage fish dietary data from the summers of 1995 and 1996.

RESULTS The following results and analyses are preliminary.

Distribution and abundance of zooplankton and jellyfish

Zooplankton. Sample analyses (1997, 1998) were completed. The densities of zooplankton appeared to be greater in 1996 than in either 1995 or 1997 (Fig. 1). The Percent Similarity Indices (PSI. Schoener 1974), were calculated to compare the proportions of zooplankton taxa among regions and years (1995, 1996, 1997, 1998). The similarity was $\geq$ 86% for all comparisons, indicating that the different regions and years were very similar in percentage composition, which allowed further analysis comparing jellyfish and forage fish diets.

	PSI (%)
1995 versus 1996	93.9
1995 versus 1997	86.6
1995 versus 1998	86.0
1996 versus 1997	92.3
1996 versus 1998	88.9
1997 versus 1998	92.3

Jellyfish densities. Hydromedusa abundances were compared among 1995, 1996, and 1997, and found to be greater in 1996 (Fig. 2). Densities of *Aurelia* medusae also were greater in 1996 than in 1995 or 1997 (see Appendix 1). Jellyfish biovolumes measured from purse seine hauls in 1998 were similar among regions (North 0.34 ml m³, Central 0.56 ml m³, South 0.45 ml m³), and the three large species had similar biovolumes overall (*Cyanea* 0.14 ml m³, *Aurelia* 0.21 ml m³, *Aequorea* 0.38 ml m³). Those seine hauls did not include any aggregations, and the biovolume of *Aurelia* would be greater if those were included.

Analysis of predation by jellyfish on zooplankton

Gut content analysis (Fig. 3) showed that *Aurelia* and *Pleurobrachia* ate mainly crustaceans (copepods < 1.5 mm, and cladocerans). By contrast, *Cyanea* and *Aequorea* ate mainly larvaceans plus some crustaceans. Very few fish eggs or larvae have been found in the gut contents, therefore it appears that in July, when small ichthyoplankton were not numerous, the jellyfish are not consuming large numbers. Data for jellies collected in 1997 are complete. *Aequorea* and *Aurelia*, but not *Cyanea*, have been analyzed for 1998. Similar patterns were seen for forage fish, with juvenile walleye pollock, sandlance and herring consuming mostly small copepods, and pink salmon eating mostly larvaceans (Fig. 3). Prey selection indices (Pearre 1982) showed statistically significant (p < 0.05) positive selection for cladocerans by *Aurelia*,

Pleurobrachia, and *Cyanea,* for small copepods by *Aurelia,* and for larvaceans by *Cyanea* and *Aequorea* (Fig. 4A). Significant negative selection against copepods was shown for *Pleurobrachia, Cyanea,* and *Aequorea,* and against larvaceans by *Aurelia.* Among forage fish species, juvenile walleye pollock showed significant positive selection for large copepods and negative selection against small copepods (Fig. 4B). Pink salmon showed significant negative selection against copepods, and positive selection for larvaceans. Sandlance and herring showed weak and mixed selection for the various prey categories.

Comparisons of diet similarity among jellyfish intermediate PSI values for most species, with *Aurelia* and *Pleurobrachia,* the main crustacean eaters having the most similar diets. Among forage fish, juvenile walleye pollock, sandlance and herring had high PSI values, and pink salmon had low PSI values when compared with other species.

1997 Jellyfish	PSI (%)
Aurelia versus *Pleurobrachia*	84.2
Aurelia vs *Aequorea*	65.1
Aequorea versus *Pleurobrachia*	50.1
Cyanea versus *Aequorea*	48.7
Cyanea versus *Aurelia*	38.9
Cyanea versus *Pleurobrachia*	28.4

1995 Forage Fish	
pollock versus sandlance	77.7
pollock versus herring	71.0
Sandlance versus herring	51.1

1996 Forage Fish	
sandlance versus herring	81.5
herring versus pink salmon	34.2
sandlance vs pink salmon	16.9

Percent diet similarities comparing jellyfish and forage fish showed the highest PSI values among mainly crustacean-eating species (highlighted top left) and among mainly larvacean-eating species (highlighted bottom right).

	Percent Diet Similarity (%)			
	Pollock	Sandlance	Herring	Salmon
Aurelia	67.2	61.6	67.4	18.7
Pleurobrachia	41.1	47.8	45.2	5.3
Cyanea	34.8	29.6	42.5	78.1
Aequorea	55.2	43.4	56.0	59.0

Digestion experiments of 6 - 8 hr duration were conducted for *Cyanea* (11 exper.), *Aurelia* (4 exper.), and *Aequorea* (2 exper.). Gut contents of specimens from only one experiment for each species have been analyzed so far. These preliminary results agree with the sparse published data (Martinussen and Båmstedt 1999) that *Cyanea* digests copepods in about 1.5 h, but *Aurelia* digests them in about 4 h. No previous data exist for digestion of larvaceans.

Because gut content (1998) and digestion rate sample analyses are incomplete, and because no abundance data exist for large jellyfish in 1997, I have not attempted to calculate feeding rates (Objective 4) and predation impacts (Objective 6) at this time. Those objectives will be met in 1999-2000.

Data compilation from SEA and APEX investigators. Hydromedusa data were received from Drs. Coyle and Sturdevant and compiled. Further analysis of hydromedusae is pending receipt of data from Robert Foy after the completion of his dissertation. Results from my analysis of hydromedusa, zooplankton, forage fish dietary data sent by Dr. Molly Sturdevant appear in previous sections of this report. Historical data on jellyfish by-catches from trawls in the Gulf of Alaska, sent by Dr. Anderson, showed a large biomass peak in 1980, when a faunal shift from shrimp and forage fish to ground fish was occurring (Fig. 5). Further analysis of these data are pending comparisons with climatological data. Analyses of data on aggregations of *Aurelia* appear in the following manuscript, which has been submitted to *Marine Ecology Progress Series*. Data on jellyfish diets and abundance were given to Thomas Okey for inclusion in the Ecopath model for Prince William Sound.

CONCLUSIONS

Among the years examined to date (1995, 1996, 1997), 1996 had markedly higher zooplankton, hydromedusa, and *Aurelia* abundances than the other years. This may have been due to apparently lower stratification in 1996 than in the other years.

The various jellyfish species ate a variety of zooplankton, and their diets overlapped substantially with those of forage fish species. Two main groups emerged -- species that ate mainly crustaceans (copepods and cladocerans); *Aurelia, Pleurobrachia,* juvenile walleye pollock, herring and sandlance, and species that ate mainly larvaceans; *Cyanea, Aequorea,* and pink salmon. These groups also were reflected by prey selection indices.

These data provide the basis for comparing the biomasses and predation pressure on zooplankton among jellyfish and forage fish in Prince William Sound.

ACKNOWLEDGMENTS

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FIGURE CAPTIONS

Fig. 1. Zooplankton (numbers per m^3) in North (N), Central (C), and South (S) regions of Prince William Sound. Cope = copepods. Data of Sturdevant (1995, 1996) and Purcell/Shirley (1997). Samples collected with 243 or 250 μm mesh plankton net.

Fig. 2. Densities of small jellyfish (hydromedusae) in Prince William Sound were greater in 1996 (mean 11.2 medusae m^{-3}) than in 1995 (2.2 m^{-3}) or in 1997 (2.5 m^{-3}). Data of Sturdevant (1995, 1996) and Purcell/Shirley (1997).

Fig. 3. Gut contents of jellyfish and forage fish from Prince William Sound. Cope = copepods. Data of Purcell (jellyfish) and Sturdevant (fish).

Fig. 4. Prey selection by (A) jellyfish and (B) fish from Prince William Sound. The percentages of samples showing statistically significant (p < 0.05) differences from percentages of zooplankton available in the environment. Data of Purcell (jellyfish) and Sturdevant (fish).
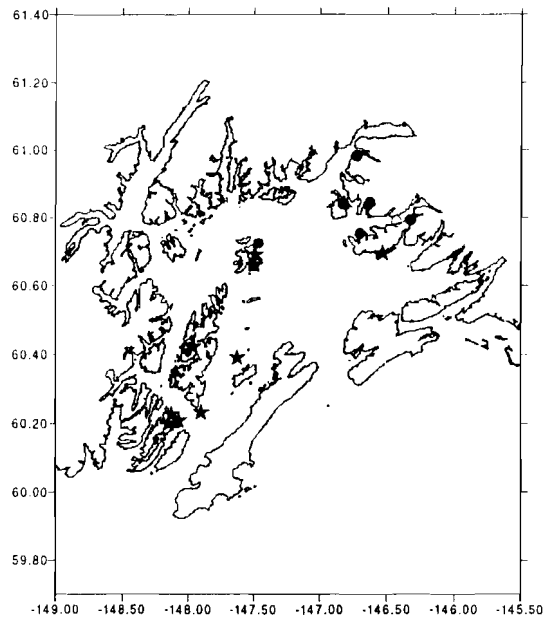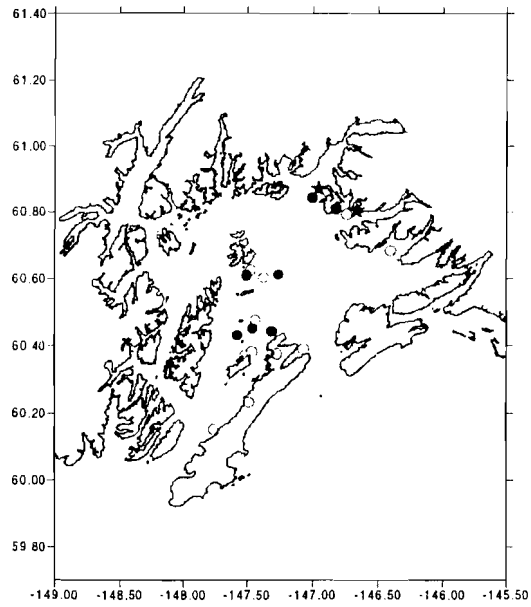
Fig. 5. Extremely large biomass of jellyfish occurred in the Gulf of Alaska in 1980. This was during the dramatic faunal shift from shrimps to ground fish (Anderson et al. 1997).

1995 PWS Hydromedusae Abundance   **1996 PWS Hydromedusae Abundance**   **1997 PWS Hydromedusae Abundance**
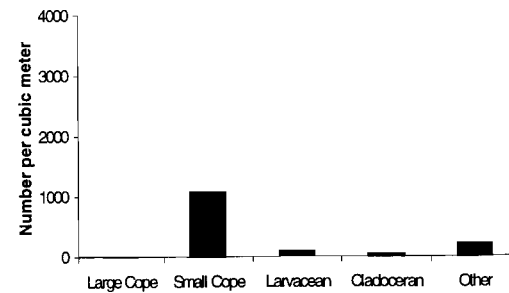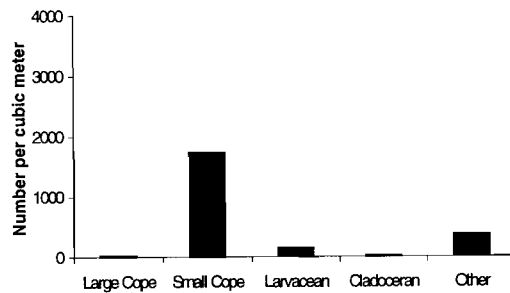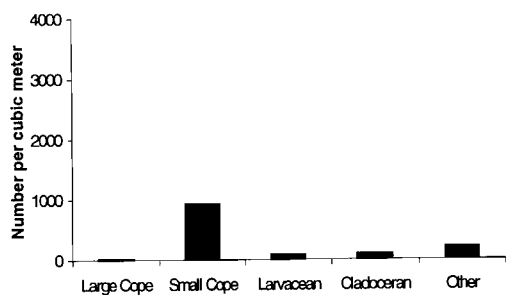

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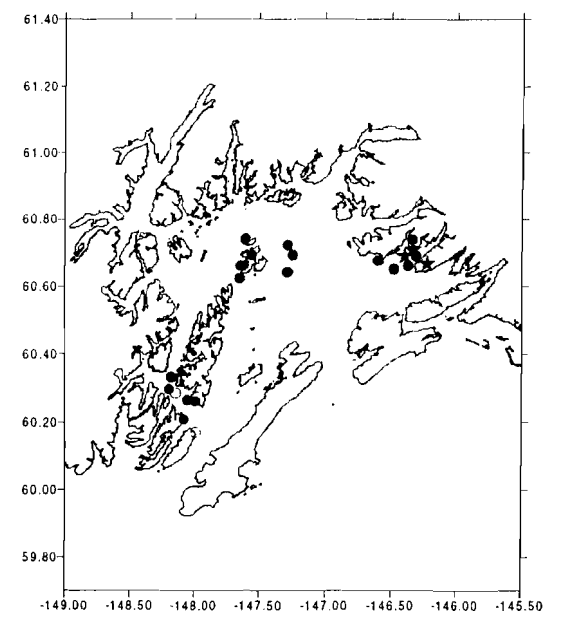
★   **> 5/m^3**   ●   **>1/m^3**   ○   **<1/m^3**

1995 Zooplankton

1996 Zooplankton

1997 Zooplankton
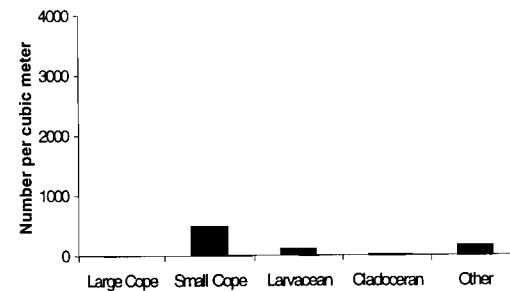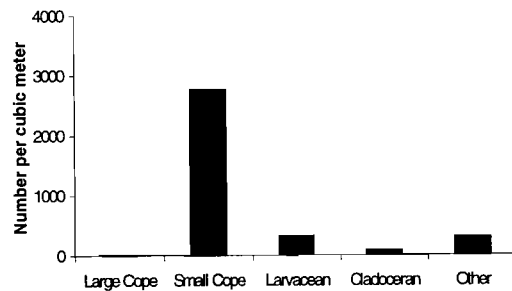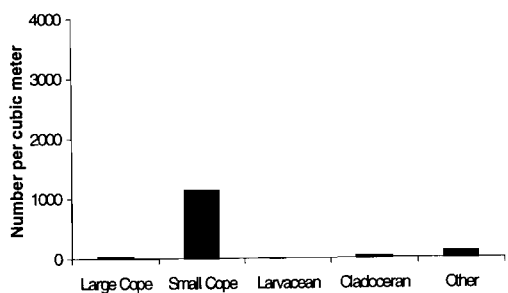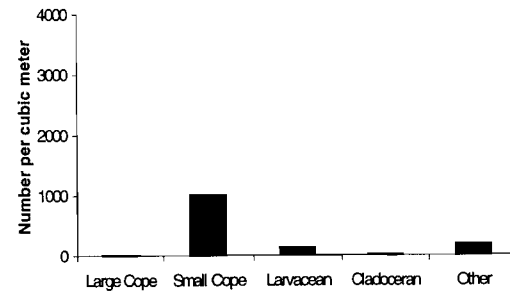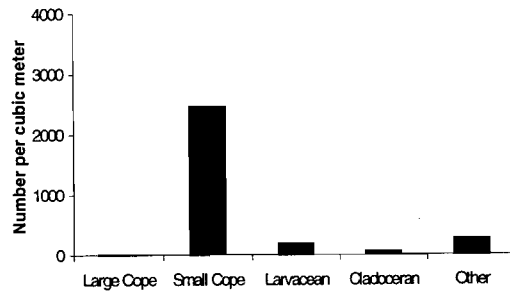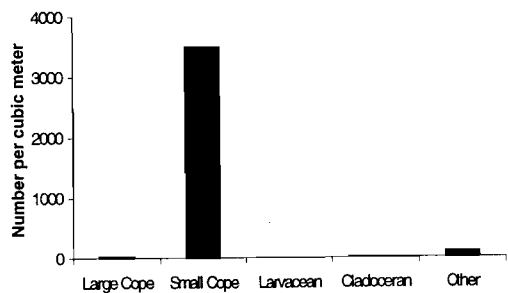
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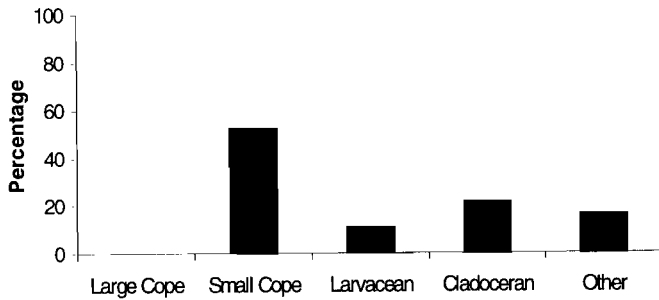
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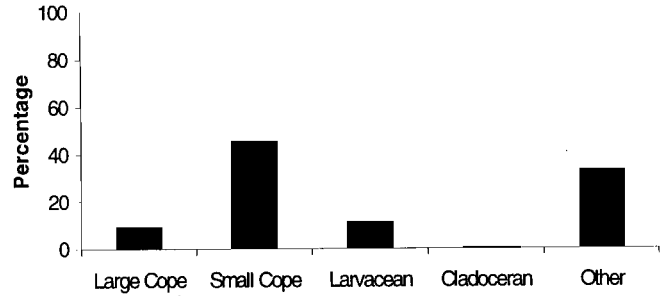
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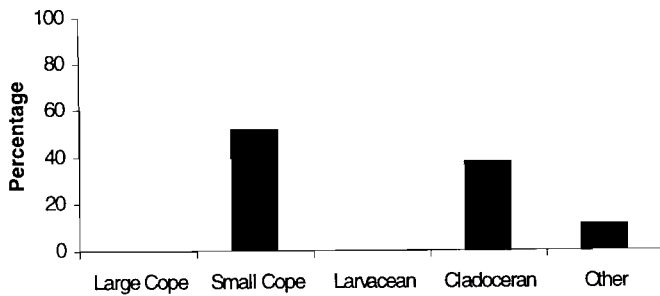
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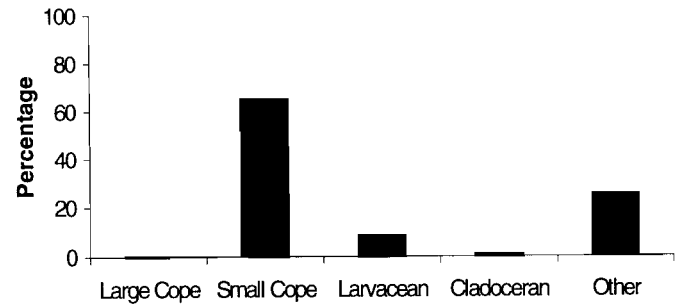
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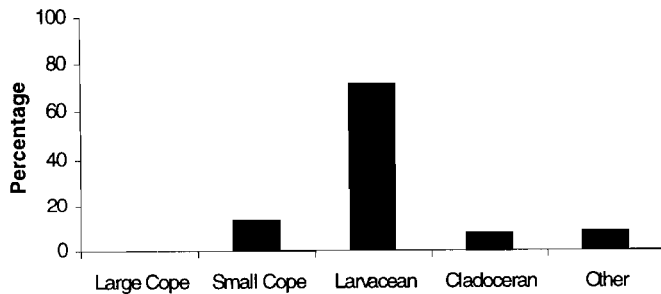
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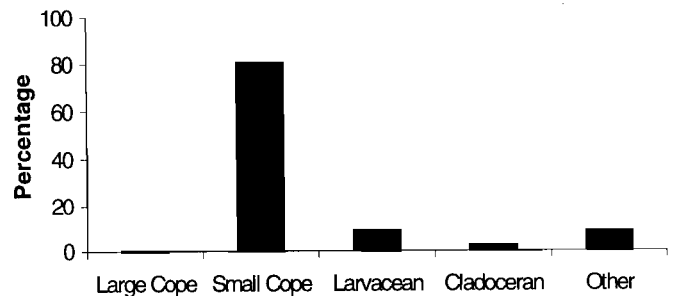
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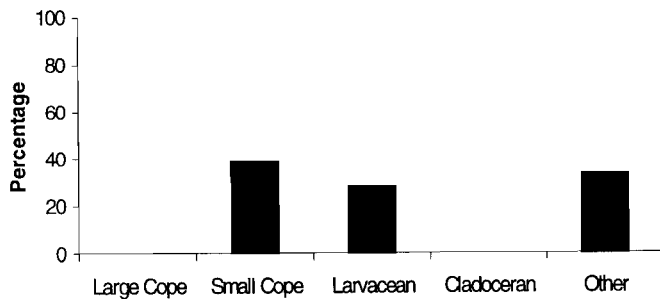
1996 PWS Salmon Gut Contents -North

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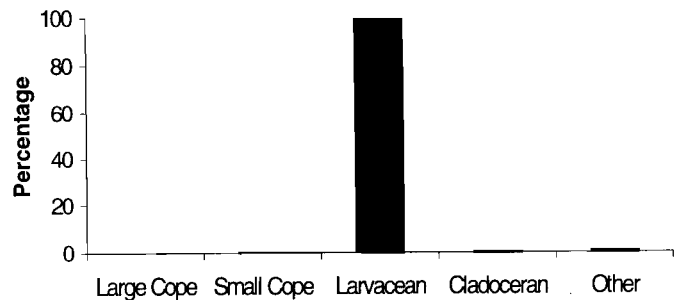
1997 PWS Jellyfish Selection Aurelia (3)

Significant Selection (%)

100, 50, 0, -50, -100

Large Cope, Small Cope, Larvacean, Cladoceran, Other
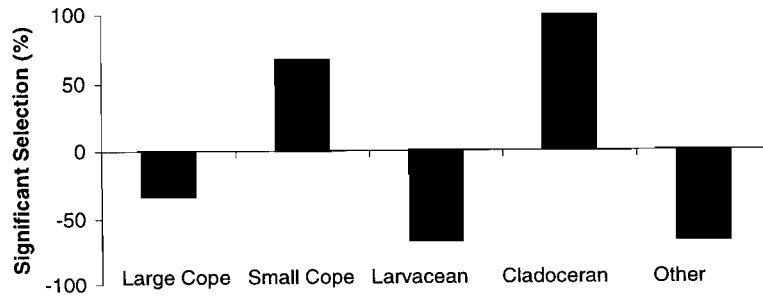
1997 PWS Jellyfish Selection Pleurobrachia (12)

Significant Selection (%)

100, 50, 0, -50, -100

Large Cope, Small Cope, Larvacean, Cladoceran, Other
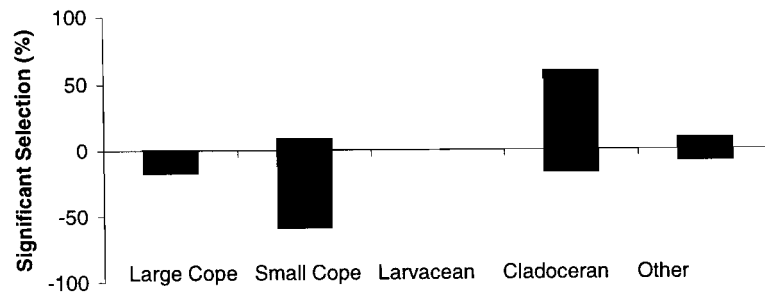
1997 PWS Jellyfish Selection Cyanea (16)

Significant Selection (%)

100, 50, 0, -50, -100

Large Cope, Small Cope, Larvacean, Cladoceran, Other
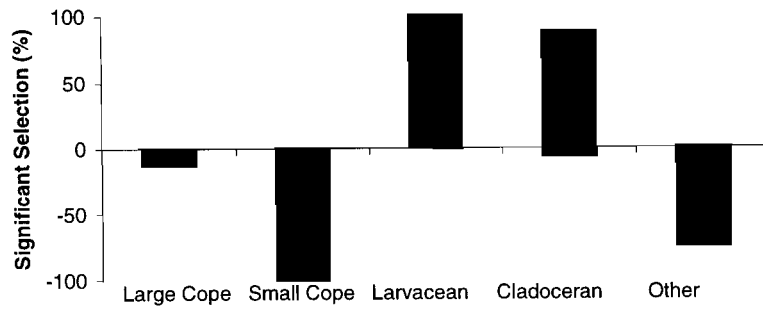
1997 PWS Jellyfish Selection Aequorea (1)

Significant Selection (%)

100, 50, 0, -50, -100

Large Cope, Small Cope, Larvacean, Cladoceran, Other

398
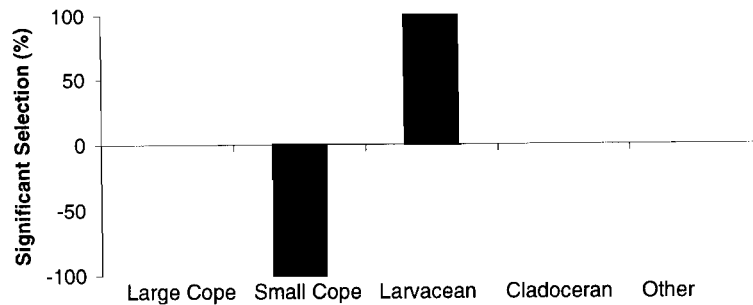
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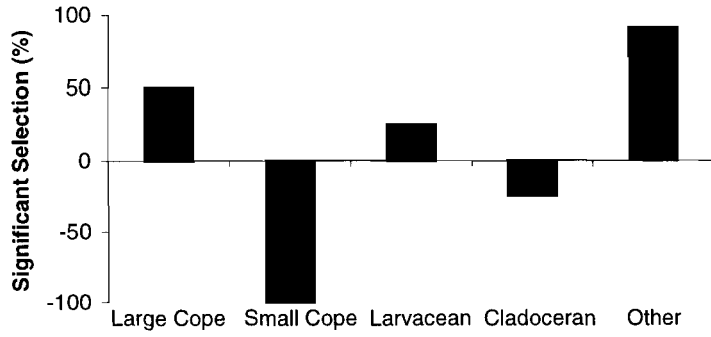
1995,1996 PWS Fish Selection Sandlance (15)
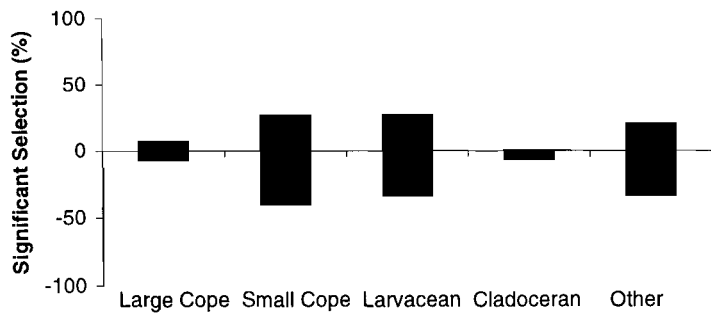
1995,1996 PWS Fish Selection Herring (14)
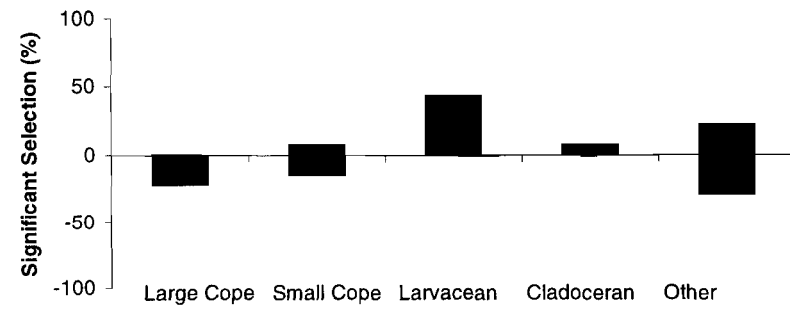
1995,1996 PWS Fish Selection Salmon (7)

399
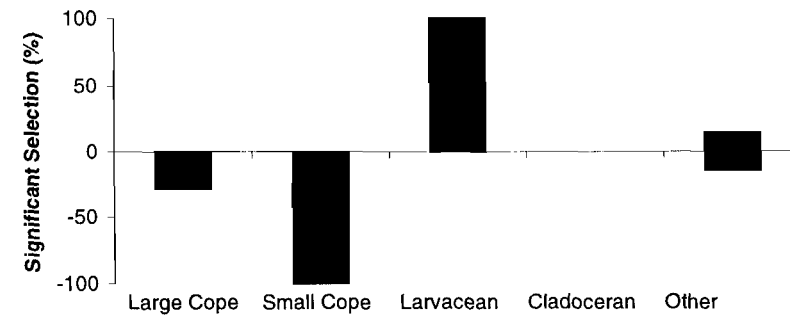
Historical Jellyfish Data (August-October)

13   Year
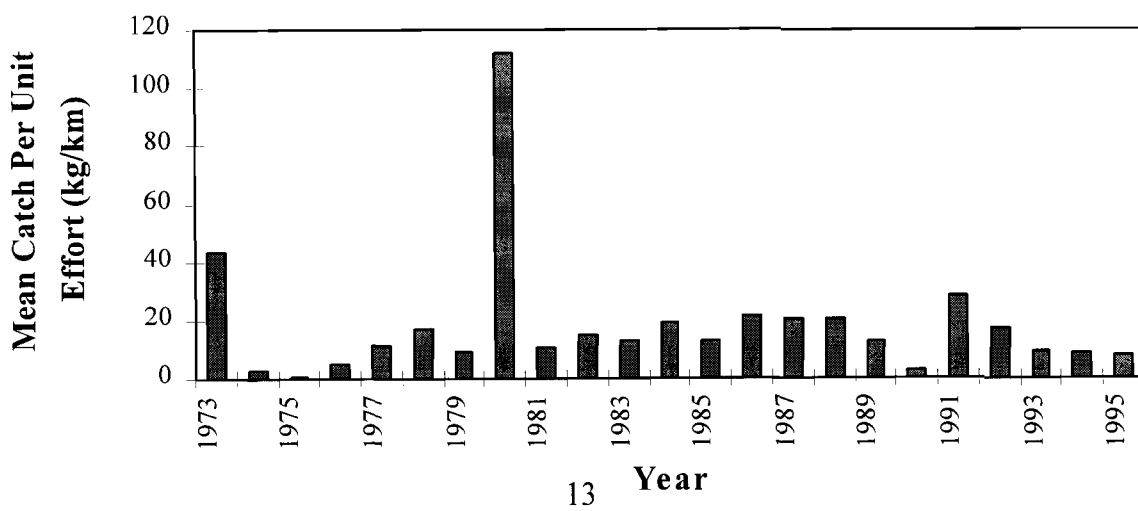
Aggregations of the jellyfish *Aurelia aurita*: Abundance, distribution, association with age-0 walleye pollock, and behaviors promoting aggregation in Prince William Sound, Alaska, USA

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Abstract

Aurelia aurita medusae occurred in aggregations with hundreds to millions of jellyfish. The aggregations wre widely distributed in inlets of Prince William Sound (PWS), Alaska. Aerial surveys of PWS in June to August in 1995, 1996, and 1997 showed marked interannual variation in the numbers of aggregations observed, from a minimum of 38 in 1997 to a maximum of 557 in 1996. Acoustic surveys showed that the aggregations extended from 0- 5 to 15 m depth. Age-0 walleye pollock (*Theragra chalcogramma*) were associated with *A. aurita*, both within and below the aggregations. All seine catches that contained pollock also contained jellyfish. Underwater video analysis showed that all medusae swam in the same direction, either up or down, in dense parts of the aggregations, suggesting that they were orienting in response to water column flow or shear, possibly generated from tidal exchange in the deep, narrow bays.

Introduction

   Aurelia aurita, commonly called the "moon jelly", is a cosmopolitan scyphomedusan occurring between 70° N to 40° S (reviewed in Möller 1980). It is undoubtedly the most studied jellyfish in the world, and several recent ecological studies exist from many countries (e.g. Grøndahl 1988, Båmstedt 1990, Behrends and Schneider 1994, Lucas and Williams 1994, Olesen et al. 1994, Sullivan et al. 1994, Nielsen et al. 1997, Toyokawa et al. 1997). Great numbers of *A. aurita* medusae often occur in semi-enclosed bays and inlets, where they have been shown to reduce zooplankton and ichthyoplankton densities and change zooplankton species compositions (Möller 1980, Behrends and Schneider 1994, Olesen et al. 1994, Schneider and Behrends 1998).

   Aurelia aurita medusae have been reported in discrete, high-density aggregations in many locations (Yasuda 1969, Möller 1980, Hernroth and Grøndahl 1985, Papathanassiou et al. 1987, Hamner et al. 1994, Toyokawa et al. 1997). The factors that lead to formation of aggregations are unknown, but jellyfish probably react behaviorally to physical conditions in the water column. *A. aurita* sometimes are found at the surface in convergences between Langmuir circulation cells (Hamner and Schneider 1986, Purcell unpublished data). In Saanich Inlet, British Columbia, Canada, medusae swam towards the southeast in sunlight, regardless of the sun's position, and aggregated along the eastern shore of the inlet (Hamner et al. 1994). Most jellyfish in the aggregations occurred in the surface 2 m, and reached densities of nearly 75 medusae m^{-3}. Acoustical records at 50 and 200 kHz were used to describe the circular to eliptical aggregations in Tokyo Bay, Japan, which began 6 to 8 m below the surface and reached depths of 16 to 20 m (Toyokawa et al. 1998).

   Aggregations of some other scyphomedusan species have been described: *Stomolophus meleagris* (in Shanks and Graham 1987), *Pelagia noctiluca* (in Malej 1989), *Phyllorhiza punctata* (in Garcia 1990), *Linuche unguiculata* (in Larson 1992), *Cotylorhiza tuberculata* (in Kikinger 1992), and *Chrysaora fuscescens* (in Graham 1994). It should be noted that other large medusae (*Cyanea capillata, Aequorea forskalea*) did not aggregate in PWS.

   The relationships of jellyfish and fish have been of particular interest because of the potential effects on commercially important fisheries. These interactions include predation on ichthyoplankton by jellyfish (reviewed in Purcell 1985, 1997, Arai 1988), potential competition between jellyfish and zooplanktivorous fish and fish larvae for prey (reviewed in Arai 1988, Purcell 1997), predation by fishes on medusae (reviewed by Arai 1988, Ates 1988, Harbison 1993), and commensal associations between fish and medusae (reviewed in Mansuetti 1963). The effects of medusae on fish may be negative (predation, competition) or positive (food, protection).

   Juveniles of several fish species are known to associate with individual scyphomedusae (reviewed by Mansuetti 1963). Age-0 walleye pollock (*Theragra chalcogramma*) in Alaskan waters swim among the tentacles of *Cyanea capillata* and *Chrysaora melanaster* (van Hyning

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and Cooney 1974, Brodeur 1998). Brodeur (1998) used an ROV and observed up to 5 walleye pollock with *C. capillata* and up to 30 with *C. melanaster* at depths of 30 to 40 m during the day. Juveniles of several fish species have been seen under the swimming bell of *Aurelia aurita* medusae: cods (*Gadus* spp.), haddock (*Melanogrammus aeglefinus*), scads (*Trachurus* spp.), bluntnose jacks (*Hemicarnax amblyrhynchus*), and bumpers (*Chloroscombrus chrysurus*)(reviewed by Mansueti 1963).

Walleye pollock are an important commercial species in Alaskan waters and are primary forage fish for sea birds, marine mammals and fish including mature pollock which are cannibalistic (Clausen 1983, Hatch & Sanger 1992, Livingston 1993). Walleye pollock congregate and spawn in deep water in late March and April and the larvae occupy the upper 50 m of the water column in late May (Hinckley et al. 1991, Kendall et al. 1996). Walleye pollock metamorphose into juveniles in August and September (Hinckley et al. 1991, Kendall et al. 1996). In Prince William Sound, Alaska, juvenile walleye pollock are second only to juvenile Pacific herring (*Clupea pallasi*) in abundance nearshore (Stokesbury unpublished data).

Prince William Sound (PWS) has been the location of intensive ecological research following the *Exxon Valdez* oil spill in 1989. It is a complex fjord-type estuary (Schmidt 1977) located on the northern margin of the Gulf of Alaska at 60° N 146° W covering about 8800 m^2 and having 3200 km of shoreline (Grant and Higgens 1910) (Fig. 1). Many of the marine birds and mammals whose populations were injured by the oil spill feed on forage fish (herring *Clupea pallasi*, sandlance *Ammodytes hexapterus*, capelin *Mallotus villosus*, and walleye pollock). The research presented here is part of two multi-investigator projects -- SEA (Sound Ecosystem Assessment) and APEX (Alaska Predator Ecosystem eXperiment) that assess forage fish distribution and abundance using aerial surveys and acoustics, with seining and underwater video for target verification. Aggregations of *Aurelia aurita* were clearly visible during the aerial and acoustic surveys. Schools of age-0 walleye pollock sometimes were observed within and beneath those aggregations. Here, we report the distribution and abundance of *A. aurita* aggregations, their association with age-0 pollock, and the behavior of the jellyfish in the aggregations, in order to better understand their formation and maintenance.

Materials and Methods

Distribution and abundance of *Aurelia aurita* aggregations

Monthly broadscale aerial surveys were conducted from March through August in 1995, May through August in 1996 and June and July in 1997 (see Brown and Norcross, 1997)(Fig. 1). A total of 14,232 km^2 ground surface area was covered during broadscale surveys and the surface area flown per month was variable ranging from 244 km^2 in August of 1996 to a high of 2009 km^2 in July of 1996 (Fig. 2). The survey design was a modified line transect associated with the nearshore, although we sampled offshore areas when crossing bays and bodies of water to reach other shorelines. An altitude-dependent visual swath was established based on ability to observe fish schools and jellyfish aggregations between 20 and 40 degrees measured from the wing.

However, survey altitude was generally established at 274-366 m). Both flight path (transect) and targets were recorded during the survey. A hand held GPS connected to a lap top computer with a flight log program recorded latitude, longitude, and time of day in a 2-second interval and logging was interrupted in order to record targets. Therefore the target location was associated with the coordinates prior to the brief interruption of logging.

Jellyfish, especially *Aurelia aurita*, were easily enumerated by aerial survey because they formed large, white irregularly shaped aggregations that were clearly visible from the aircraft (Fig. 3). The shapes of the aggregations, aggregation counts and surface area estimates (by size category) were recorded during each survey. Size categories were established using a sighting tube to calibrate the ranges. The sighting tube was constructed of PVC pipe with a grid drawn on mylar on the end. The tube was calibrated for ground distance covered by reference line (X) for any survey altitude, when length of the grid reference line (L), focal length of the tube (F), and survey altitude (A) are known, by using the equation $X = A (^L /_F)$ (Lebida and Whitmore 1985; Brady 1987). The average size categories of the aggregations are given in Table 1.

For comparisons of seasonal and interannual abundance, the total numbers and surface areas of aggregations were summed over each month and then divided by the total surface area flown during that month to obtain densities. Densities were expressed as numbers of aggregations or surface area (m^2) over the survey region (km^2).

Association of *Aurelia aurita* aggregations with age-0 walleye pollock

The PWS coastline was acoustically surveyed in July 1996. Four vessels were used during each 10 day survey (12 hours per day); an acoustic vessel, a seiner, an oceanographic vessel, and a catch processing vessel. Surveys were conducted in daylight between 0800 and 2000 h.

The acoustic vessel followed a zig-zag pattern along the shore to a distances of ≈ 1 km at a speed of 14 to 17 km h^{-1}. A Wesmar model 600E search light sonar was used to locate schools along the transect. When a school of fish was encountered, the acoustic vessel slowed to 9 to 11 km h^{-1} and completed a series of parallel transects perpendicular to shore using a 120 kHz BioSonics 101 echosounder with a preamplifier dual-beam transducer mounted ≈ 1 m under the water surface (Stokesbury et al. submitted). The standard equation TS = 20 logx - 66.0 bB was used to convert reflected acoustic energy into biomass (Foote & Traynor 1988, MacLennan & Simmonds 1991).

Echo integration measurements were made in roughly 20 m (16 pings/cell at 0.5 ping s^{-1} and 2.5 to 3.0 m s^{-1} speed) horizontal by 1 m depth data cells during the July 1996 survey. Latitude and longitude was recorded simultaneously with each data cell from the GPS and provide an accurate measure of horizontal distance. Nonbiological noise was removed from these data. Species proportions and size modes per species were determined from the fish

collections (described below). The species proportions, based on the number individuals per fish species in the random subsample, were converted to biomass using length/weight regressions. The echo integration measurements (kg m^{-3}) were converted into numbers of individual fish per species by use of the species proportions obtained in each seine catch. Based on frequency distributions of the data, we assumed that cells containing <0.5 fish m^{-3} were not aggregations of fish but probably zooplankton, therefore they were removed from the data set (MacLennan & Simmonds 1991, Gunderson 1993). Fish located near the bottom were difficult to distinguish acoustically; if the signal appeared corrupted, the bottom 5 m were removed. Visual examination of the echograms and fish collections agreed with these assumptions.

Once the acoustic vessel surveyed a fish school, it was sampled to determine species composition and size structure. Fish were sampled using an anchovy seine 250.0 m long by 34.0 m deep with 25.0 mm stretch mesh. Each collection was speciated and 1000 fish were randomly subsampled and measured for fork length (mm). Jellyfish also were identified in the seine catches, and relative abundances of the different species estimated.

Vertical water profiles measuring temperature and salinity at 1 m intervals, using a SeaBird instrument (SEACAT SBE19), were collected within each bay that was acoustically sampled.

Behavior of jellyfish in the aggregations

In order to determine *Aurelia aurita* swimming behavior in the aggregations, the aggregations were videotaped using a Hi-8 VCR and monitor attached to a closed-circuit underwater camera system (Fisheye, Inc. Everett, WA). Ten aggregations were filmed in July 1996, 1997, and 1998 for a total of 80 minutes of video footage. All of the video footage was examined, and two aggregations were analysed in detail with an editing Hi-8 VCR (Sony EV-S2000NTSC) and a Panasonic high resolution monitor.

Five types of information were evaluated for medusae in the aggregations. (1)Angular swimming direction measurements were taken by marking the orientation of the oral-aboral axis relative to vertical on the video monitor and using a circular protractor to measure the swimming direction. 0° was towards the water surface, and 90° was towards the right. Video analysis was limited to two-dimensions, therefore some inaccurracy is inherent in all of our measurements. (2) Turning behavior was examined by following the paths of jellyfish for as long as each remained in view without contacting another jellyfish in low densitiy areas, and after contact with other jellyfish in high density areas of an aggregation. No quantitative analysis of the swimming paths were attempted because of the lack of three dimensional resolution and short duration that individual medusae could be tracked. (3) Frequency of the swimming beat, which was used as an index of activity, was determined by counting the number of swimming bell contractions for as long as the medusae could be followed (< 30 s). (4) The vertical distance moved relative to the body depth was used instead of actual displacement, which could not be

determined. This index should not be affected much by medusa sizes, which were very similar for medusae within an aggregation. Relative distances (vertical distance ÷ body depth) were measured from the video monitor for one full swimming beat cycle (< 3 s), and standardized to 1 s. (5) Relative densities of medusae were determined by counting the superposition of medusae on 42 points marked on the video monitor at 30 arbitrary times (10 s intervals) during the videotapes. Actual densities of medusae could not be measured.

Results

Distribution and abundance of *Aurelia aurita* aggregations

Aggregations of *Aurelia aurita* medusae were clearly visible during aerial surveys (Fig. 3). A total of 995 aggregations were observed during the 10 monthly surveys in Prince William Sound from 1995 to 1997. The majority (81.2%) of the aggregations were categorized as small (approximately 40 m² in surface area). The medium size category (approximately 100 m² in surface area) made up most of the remaining total (14.7%) (Fig. 4).

The abundance of aggregations followed a seasonal pattern (Fig. 5). Aggregations were not observed during aerial surveys of PWS in March, April and May. Aggregations were first visible in June of 1996. Both numbers of aggregations and total surface areas per km² of survey area peaked in August of 1995 and July of 1996, however, this trend was not observed in 1997. Between the months of July and August in 1995 and 1996, the abundance curve based on densities of surface areas departed from the abundance trends based on densities of numbers of aggregations. This was probably due to growth of individuals, which would increase the overall sizes of the aggregations. No aerial surveys were conducted in September, and no aggregations were observed during surveys in October.

Dramatic interannual variation in the numbers and densities of *Aurelia aurita* aggregations was observed. Moderate densities of aggregations occured in 1995, with two-fold greater densities in 1996 than 1995, and generally low densites for both summer months surveyed in 1997 (Fig. 5). Significantly more aggregations and greater surface areas were found in 15 inlets of PWS (Table 2) in 1996 than in 1995 (ANOVAs, $p < 0.05$) or in 1997 (ANOVAs, $p < 0.01$).

Most aggregations were observed in bays off the main sound (Fig. 6), possibly due to the concentration of survey effort there (Fig. 1). Aggregations were observed consistently in 15 bays during one or more survey in every year. The aggregations were most widely distributed in 2 - 21 July 1996 (15 of 15 bays plus other sites not occupied in other years), as compared with 9 of 15 bays plus other sites in 5 - 22 August 1995 and 5 of 15 bays in 12 - 21 June 1997 (Table 2). Bays in southwestern PWS (Whale, Drier, Jackpot) and in northeastern PWS (Port Fidalgo, Port Gravina, Simpson Bay) had the highest numbers and surface areas of aggregations in 1995 and 1996. Ewan Bay and Port Fidalgo were the only locations that had aggregations every year. Also striking was the lack of aggregations in the large inlets of northern PWS that were surveyed

by air (Unakwik Inlet, and Port Valdez and Valdez Arm)(Fig. 6).

Association of *Aurelia aurita* aggregations with age-0 walleye pollock

Schools of young-of-the-year walleye pollock were observed in videotapes and acoustically under and within aggregations of *Aurelia aurita* medusae. The juvenile fish were observed associated with 2 (in Paddy Bay and Port Gravina in July 1996) of the 10 videotaped aggregations. In Simpson and Drier Bays, where acoustic transects were completed through jellyfish aggregations, *A. aurita* appeared to extend from the water's surface to the beginning of the thermocline (Fig. 7). Mean densities of young-of-the-year walleye pollock schools observed in Simpson and Drier Bays were 13.9 m^{-3} and 35.0 m^{-3}, respectively (Table 3).

Seine catches along the transects in Simpson and Drier Bays confirmed that the acoustic targets were predominately age-0 walleye pollock. The largest catches of juvenile walleye pollock from 52 seine sets in July, 1996 in PWS were from Simpson Bay (394 fish) and Drier Bay (7,000 fish). Age-0 walleye pollock averaged 11.2 ± 28.6 m^{-3} in the other seine catches. Sizes of the fish (mean fork length < 61 mm) showed them to be young of the year.

Aurelia aurita was the only large medusa collected in the seine catch in Simpson Bay. Some *Aequorea forskalea* and *Cyanea capillata* medusae also occurred in the seine catch from Drier Bay. The jellyfish catches in Drier and Simpson Bays were much greater than in all but one of the other 50 seine sets in other locations.

In all seine sets in which they were collected (27%), age-0 walleye pollock were collected with jellyfish; they did not occur alone or with herring only (Table 4). By constrast, herring often occurred alone (27%) in the seine catches. Jellyfish, juvenile walleye pollock, and herring occurred together in 4 of 52 seine samples. Although juvenile walleye pollock were only collected with jellyfish, herring were as likely to be collected alone as with jellyfish. The difference between the two fish species occurring with and without jellyfish was significant (Chi-square = 7.9, p = 0.005). Jellyfish occurred alone in 25% of the seine samples.

Behavior of jellyfish in the aggregations

Aurelia aurita medusae were observed on videotapes of 10 aggregations. Two aggregations were studied in detail where camera motion was minimized. A video transect through Aggregation 1 was taken at 4.3 m depth on 18 July 1998 at 17:00 hr along the southwestern part of Chenega Island (60° 19.55' N, 148° 9.20' W), where bottom depth was 21.5 m. Aggregation 2, which extended from the surface to 12.3 m, was videotaped at 4.6 m at 08:00 hr on 29 July 1998 in Jackpot Bay (60° 20.22' N 148° 16.17' W). The following results for Aggregations 1 and 2 were representative of those for other aggregations.

We tested three hypotheses to explain the occurrence of *Aurelia aurita* aggregations. The first was that increased turning by medusae in response to some unknown stimulus, or after contact with one another, would lead to increased densities, such as shown for the scyphomedusa *Linuche unguiculata* (Larson 1992), and for other plankton (e.g. Buskey et al. 1996). All medusae were swimming, and most were oriented vertically (Table 5, Figs. 8, 9). Of the several thousands of medusae on the videotapes, only 29 medusae were observed turning without contact with other medusae (24 turned from horizontal to downward swimming, and 5 from horizontal to upward swimming). If turning were the mechanism for aggregation, we would expect to see a higher proportion of non-vertical medusae in the densest parts of the aggregations. In Aggregation 1, the opposite was observed; medsae in low density locations showed greater deviations from vertical (Fig. 9).

In Aggregation 2, a dense central column of upward-swimming medusae spread horizontally near the surface (96% relative density), where several layers of medusae in this sub-surface canopy swam upwards while repeatedly contacting one another. On the lower and outer edges of the horizontal canopy of the aggregation (91% relative density), some medusae were observed turning from upward to downward orientation, moving into areas of lower (25%) relative density and generally downward swimming orientations. The up-to-downward turning observed in Aggregation 2 took medusae away from the densest part of the aggregation. In both aggregations, the relative densities of the medusae were significantly different between the dense areas of medusae swimming in one direction (either upward or downward) and the areas of medusae in mixed orientations (Tables 5, 6). Eight other aggregations had a similar structure, with a dense central core oriented either vertically or in a horizontal or tilted layer, with medusae generally swimming upwards on both sides of the dense layer. We reject the first hypothesis; increased turning did not lead to increased densities of medusae.

Our second hypothesis was that swimming was reduced where medusae occurred in high densities as compared with low densities. This could result in them concentrating, as seen for *Daphnia* (Larsson and Kleiven 1996). This hypothesis was tested by using two indicators of swimming -- swimming beat frequency and vertical distance moved. Medusae in most aggregations, where individual medusae could be followed for only 2 to 3 seconds (1 full beat), did not show differences in swimming beat frequencies depending on density or orientation (Tables 5, 6). Medusae in Aggregation 1 showed very similar rates for upward- and downward-swimming medusae at high and low relative densities (ANOVA, $p = 0.36$). The beat frequencies of upward- (mean 0.43 beats s^{-1}, $n = 20$) and downward- (mean 0.41 beats s^{-1}, $n = 15$) swimming medusae were compared from the low density areas of three additional aggregations and found not to be significantly different (ANOVA, $p = 0.48$). Medusae in the high density areas of those aggregations could not be tracked long enough to determine the beat frequencies. Generally, medusae in high densities had equivalent swimming beat frequencies to those in low densities

By contrast, swimming beat frequencies differed in different areas of Aggregation 2, where individual medusae could be followed for up to 25 s (Tables 5, 6). In areas of high relative densities in Aggregation 2, uniformly upward-swimming medusae had higher beat

frequencies (0.57 beats s^{-1}) than downward-swimming medusae (0.36 beats s^{-1}), which had just reversed swimming direction at the bottom of the dense canopy of the aggregation (ANOVA, p = 4 x 10^{-8}). The reduced swimming beat frequency of the downward-turning medusae could slow their movement away from the densest part of the aggregation. In areas of low density where medusae were oriented in mixed directions, the beat frequencies of upward- and downward-swimming medusae were not significantly different (ANOVA, p = 0.16). Upward-swimming medusae also had similar beat frequencies in both high and low density areas (ANOVA, p = 0.58).

We examined Aggregation 2 to test whether the vertical distance moved relative to body depth differed between dense and less dense areas of the aggregation. There was a significant difference in relative distance s^{-1} among the different areas of the aggregation (ANOVA, F = 8.02, p = 2.44 x 10^{-4}). Medusae swimming up in low density areas moved further ((1.04 s^{-1}) than medusae swimming up in high densities or down in both low and high densities (0.30 - 0.41 s^{-1}; Table 5)(ANOVAs, F = 10.07 - 11.12, p < 0.01 for all pairs compared). Comparisons among all other pairs (downward-swimming medusae in high densities, in low densities, and upward-swimming medusae in high densities) were not significant (F = 0.21 - 1.03); the small vertical distance traveled by those medusae would help to concentrate them. Medusae oriented upward in high densities were impeded in vertical motion by collisions with other medusae. We could not reject the second hypothesis; reduced swimming, resulting from contacts among medusae, could have lead to increased densities of medusae.

Our third hypothesis was that medusae swam directionally in response to flow fields in the water column, and that differences in speed between medusa swimming and water flow resulted in aggregation. Medusae have been observed orienting and aggregating in convergent zones of Langmuir circulations and fronts (Hamner and Schneider 1986, Shanks and Graham 1987, Graham 1994). Convincing evidence supporting this hypothesis was found in Aggregation 1 (Fig. 9, Table 5). A 3-min horizontal transect through this aggregation showed three areas; one side where medusae were swimming downwards in high (46%) relative density, a central area where medusae were in mixed orientations and low (7%) relative density, and the opposite side where medusae were swimming upwards in high (22%) relative density. The relative densities were significantly different among the three areas (Table 6). Unfortunately, no data on water flow were available, and we must deduce that the highly directed swimming by medusae was most likely in response to flow or shear in the water column.

In summary, we observed three factors that could act to concentrate *Aurelia aurita* medusae. One was that their swimming was highly directional in some areas, apparently oriented against flow or shear fields in the water column. Second, upwards-swimming medusae that were already densely aggregated were unable to move as far as medusae in low density areas. And third, although some upwards-swimming medusae underneath dense aggregations reversed swimming direction taking them out of the densest areas, their swimming beat frequency and relative vertical distance moved were lower than for other medusae.

Discussion

Distribution and abundance of *Aurelia aurita* aggregations

Marked interannual differences were seen in the numbers of *Aurelia aurita* aggregations in Prince William Sound (PWS), with 1996 having by far the greatest number. 1996 also showed high densities of hydromedusae in PWS (Coyle, Cooney, and Sturdevant unpublished data). That year was characterized by deep mixing (Vaughan submitted), and high zooplankton densities (Sturdevant et al. 1997). 1997 was an unusually warm year (Haldorson and Shirley 1998), reflecting atmospheric effects of the extremely strong El Niño that developed in the southern hemisphere. 1997 also showed low densities of hydromedusae and zooplankton (Purcell and Shirley unpublished data).

Aurelia aurita aggregations were observed in nearly every small bay and inlet of PWS, however, they were noticeably absent in large inlets in the north (Unakwik Inlet, Valdez Arm and Port Valdez). These large inlets are very steep and deep, and perhaps the steep topography does not promote vertical water fluxes (Simpson and Hunter 1974) or aggregation formation. We believe that the combination of tidally-driven water circulation patterns in bays and the behavior of *A. aurita*, which appears to utilize flow or shear in the water column, promotes aggregation of the medusae in the small bays and inlets.

Toyokawa et al. (1997) reported that *Aurelia aurita* aggregations drifted with the tidal currents, however Hamner et al. (1994) states that the aggregations maintained their position along the eastern shoreline of Saanich Inlet and did not move with the tides. Our sampling did not allow us to observe whether or not the aggregations drifted with the tides.

Association of *Aurelia aurita* aggregations with age-0 walleye pollock

Associations between juvenile walleye pollock and individual *Cyanea capillata* and *Chrysaora melanaster* have been described previously (summarized in Brodeur 1998). Acoustic records and seine catches in Simpson and Drier Bays in July 1996 suggest that the pollock were associated primarily with *Aurelia aurita* aggregations and not other jellyfish species. Throughout an intense 10 day broadscale survey of the nearshore ichthyofauna, young-of-the-year walleye pollock were only collected in association with *A. aurita*. Yet, young-of-the-year walleye pollock were the second most abundant fish collected during this survey (Stokesbury unpublished data). Furthermore, two schools of age-0 walleye pollock was documented by underwater video in association with aggregations of *A. aurita*. To our knowledge, the association of fish schools with jellyfish aggregations has not been reported previously.

Commensal relationships among fish and jellyfish are believed to protect the juvenile fish from their many vertebrate predators (e.g. Brodeur 1998) and possibly provide food, either as prey stolen from the jellyfish or the jellyfish themselves. Juvenile butterfish (*Peprilus*

triacanthus) were eaten by birds when displaced from their jellyfish host, *Cyanea capillata* (Duffy 1988), and are known to eat parts of the jellyfish (Mansueti 1963). Juvenile walleye pollock are eaten by a variety of fish, sea birds, and pinnepeds (Table 7). For example, young-of-the-year walleye pollock make up 19% of the diet of tufted puffins (*Fratercula cirrhata*), and those birds consumed an estimated 11 billion individuals along the Gulf of Alaska in 1986 (Hatch and Sanger 1992). Interestingly, in PWS, age-0 walleye pollock were eaten by only one bird species, but older juveniles were eaten by several species (Table 7). Perhaps the association of age-0 walleye pollock with aggregations of *Aurelia aurita* medusae reduces capture of that age class by diving birds in PWS.

Behavior of jellyfish in the aggregations

Hamner et al. (1994) described the formation of *Aurelia aurita* aggregations in Saanich Inlet, a fjord on Vancouver Island, where the jellyfish swam horizontally towards the southeast in sunlight. They did not show horizontal swimming before sunrise, when the sky was overcast, or at night. Aggregations in PWS existed during both clear and overcast days. Jellyfish in PWS (~60.5° N) would have experienced approximately 19 h of daylight in mid-June, 18.5 h in mid-July, and 15.5 h in mid-August, which is more than in Saanich Inlet (49° N). All of our sampling was in daylight, and we do not know if the aggregations dispersed during the short night in PWS, or how long each aggregation persists.

Our observations on the swimming behavior of *Aurelia aurita* medusae in aggregations concur with data on isolated medusae from Costello et al. (1998), specifically, that most individuals swim all the time (98 ± 2%) and that most swim in vertical paths. Hamner et al. (1994) reported that once *A. aurita* medusae reached an aggregation, their directed horizontal swimming changed to vertical. We did not oberve horizontal directional swimming by medusae in PWS.

In PWS, jellyfish in one part of Aggregation 1 all swam upwards and all individuals in another part swam down, suggesting that the medusae in this aggregation were swimming in a convection cell on a scale of about 10 m in diameter. This is supported by Toyokawa et al. (1997), who described "ring-like" structure of some *Aurelia aurita* aggregations. In other locations, jellyfish, including *A. aurita*, have been seen in parallel rows at the water surface. Presumably, these medusae were concentrated in Langmuir cells, which are wind-driven, surface convection cells that are perpendicular to the wind direction (Hamner and Schneider 1986, Larson 1992). In PWS, aggregations of *A. aurita* were generally elongated (Table 1) and began either near the surface or at about 4 m below the water surface. We believe that the convection currents experienced by *A. aurita* in PWS probably were from multiple origins, including wind-driven Langmuir cells that form in the inlets (S.M. Gay, pers. comm.). Also, the kinetic energy of high-speed currents is converted to strong vertical water flows by friction over shallow bottom topography (Mackas et al. 1985). The large tides (about 8 m amplitude) in the narrow fjords of PWS may frequently create regions of strong shear in the water column. In summary, we believe

that the directional swimming observed in aggregations of *A aurita* suggests that the medusae orient to differences in flow or shear in the water column, and that this determines whether or not an aggregation forms.

A few species of jellyfish, including *Aurelia aurita, Chrysaora fuscesens,* and *Stomolophus meleagris,* have been observed swimming against the prevailing water flow, which concentrates them in downwelling convergences between Langmuir cells (Hamner and Schneider 1986), and also occurs in aquaria with circular flow (Purcell, Graham pers. obs.). The swimming currents generated ("bioconvection") by the medusae in the aggregations may promote formation and persistence of the aggregations, as for microorganisms (Kils 1993). The mechanism by which medusae orient to flow is not known. *Aurelia aurita* has oscelli for sensing light, and statocyts for sensing gravity at eight evenly-spaced locations around the swimming bell margin (Hyman 1940). Thus, the sensory capabilities exist to control their orientation.

Behavioral mechanisms probably are responsible for maintaining aggregations of *Aurelia aurita* in PWS. They swam in straight paths and therefore did not maintain the aggregations by swimming in circles, as seen for *Linuche unguiculata* (Larson 1992), or increased rates of turning (klinokinesis) as used for swarm formation in copepods (Buskey et al. 1996). Our results are in contrast to those of Hamner et al. (1994), who reported "constant collision and turning" by *A. aurita* in high density aggregations. Reduced swimming, which acted to concentrate *Daphnia* in high food concentrations (Larsson and Kleiven 1996), may act to concentrate *A. aurita* in dense aggregations where contacts between medusae occur.

We do not know if chemical cues attracted medusae to aggregate. Chemoreception that could facilitate intraspecific interactions has not been investigated for any gelatinous zooplankton, to our knowledge. Observations of the mating behavior of male cubomedusae, *Tripedalia cystophora,* did not demonstrate chemoreception, but it was not tested directly (Stewart 1996). The only example of distance chemoreception between different species of medusae of which we are aware is for hydromedusae; *Stomotoca atra* ceased swimming in the presence of *Aequorea victoria,* a potential predator (Lenhoff 1964). Other examples suggest that chemoreception is used to locate food. *Aurelia aurita* medusae aggregated near high food (*Artemia* nauplii) concentrations and water conditioned by the prey in laboratory experiments (Arai 1992). *Beroe* spp. ctenophores may use chemoreception to locate their ctenophore prey (Falkenhaug et al. 1995). These tantalizing examples suggest that gelatinous species may use distance chemoreception in a variety of ways.

Aurelia aurita medusae may gain several advantages from aggregation. First, Hamner et al. (1994) found that about 5% of male *Aurelia aurita* were releasing sperm in aggregations, and concluded that the aggregations function to increase fertilization success. Second, vertical swimming is displayed by a variety of estuarine organisms, which serves to retain them in the estuaries (e.g. Wooldridge and Erasmus 1980, Tankersly et al. 1995). Retention near shore is advantageous because *A. aurita* medusae release planulae that settle on hard substrata (Hernroth and Grondahl 1985). Third, there may be advantages for feeding. Plankton densities are greater

near shore than off shore in PWS (Cooney, Coyle, Sturdevant, Purcell, and Shirley unpublished data). Also, plankton organisms are concentrated in convergences and fronts (e.g. Graham 1984), so the medusae would aggregate where food densities are greatest. Thus, the potential advantages of aggregation are numerous.

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Table 1. Average size categories for jellyfish aggregations according to length (L) and width (W) using sighting tube during aerial surveys of Prince William Sound.

Category	L X W (Tube units)	L X W (m at 308 m altitude)	Surface Area (m² at 308 m)
dab	0.25 X 0.10	4.9 X 2.0	10
small	0.50 X 0.20	9.7 X 3.9	38
medium	1.00 X 0.25	19.5 X 4.9	96
large	2.00 X 0.50	39.0 X 9.7	378

Table 2. *Aurelia aurita*. Numbers of aggregations and their combined surface areas in Prince William Sound in bays where they most frequently occurred. Data are presented for the survey in each year having the greatest number of aggregations. The bays are listed from southwest PWS clockwise around the coastline.

Location	5-22 August 1995		2-21 July 1996		12-21 June 1997	
	No.	Area (m²)	No.	Area (m²)	No.	Area (m²)
Whale Bay	7	498	17	646	0	0
Drier Bay	8	478	145	8544	0	0
Jackpot Bay	18	916	68	3222	0	0
Ewan Bay	3	172	7	324	2	20
Paddy Bay	0	0	7	266	5	200
Naked Island	0	0	7	266	0	0
Eaglek Bay	0	0	81	3460	18	602
Wells Bay	0	0	54	2052	0	0
Jack Bay	0	0	4	152	0	0
Galena Bay	0	0	45	2206	2	48
Port Fidalgo	28	2034	17	2122	1	38
Port Gravina	16	898	22	1864	0	0
Orca Bay	3	173	4	550	0	0
Sheep Bay	1	378	3	144	0	0
Simpson Bay	10	380	12	688	0	0

Table 3. *Aurelia aurita* and *Theragra chalcogramma*. Characteristics of acoustic transects in Simpson and Drier Bay in Prince William Sound. Depths of jellyfish aggregations and densities and depths of walleye pollock were determined by acoustics. Percentages of the catch and size (fork length) of walleye pollock were determined from seine catches. Numbers represent means ± 1 standard deviation.

	Simpson Bay	Drier Bay
Date	2 Jul 1996	8 Jul 1996
Latitude and longitude	60.676° N 145.858° W	60.320° N 147.775° W
Bottom depth (m)	26.8 ± 13.6	39.5 ± 3.2
A. aurita (% of seine catch)	99%	97%
Depth (m)	0 - 10	0 - 20
T. chalcogramma (No. m⁻³)	13.9 ± 28.3	35.9 ± 76.8, 34.4 ± 59.7
% of seine catch	1%	3%
Mean depth (m)	12.8 ± 7.6	16.1 ± 11.6
Size (mm)	49.9 ± 6.3	60.8 ± 4.6

Table 4. *Aurelia aurita*, *Theragra chalcogramma*, and *Clupea pallasi*. Matrix of occurrence in 52 seine catches in Prince William Sound in 2 - 11 July, 1996. Seine sets were made on fish schools located acoustically. Catches having just jellyfish are at the intersection of the jellyfish row and column. Only 4 catches contained jellyfish, walleye pollock, and herring, and these are not included in any column.

	Jellyfish	Pollock	Herring
Jellyfish	13	10	11
Pollock	--	0	0
Herring	--	--	14

Table 5. *Aurelia aurita*. Medusa swimming beat frequencies, relative vertical distance moved per second, and relative densities for areas in aggregations where medusae swimming unidirectionally up, unidirectionally down, or where medusae were in mixed orientations, as analysed from video tapes. Numbers are means $\pm$ 1 standard deviation. The numbers of measurements are in parentheses. Relative distance (distance $\div$ body depth) is a measure of the vertical displacement during one swimming beat (standarded to 1 s), because actual distances could not be determined. Relative density is a measure of the percentage of the video image covered by jellyfish, and is used to compare the abundances of jellyfish because absolute density could not be determined.

Location in aggregation

Variable	Up	Down	Mixed up	Mixed down
Swim beat (no. s⁻¹)				
Aggregation 1	0.51 ± 0.30 (7)	0.51 ± 0.09 (12)	0.51 ± 0.05 (5)	0.57 ± 0.09 (9)
Aggregation 2	0.57 ± 0.11 (18)	0.36 ± 0.06 (16)	0.59 ± 0.10 (11)	0.67 ± 0.13 (9)
Relative distance (s⁻¹)				
Aggregation 2	0.36 ± 0.32 (13)	0.41 ± 0.20 (12)	1.04 ± 0.65 (11)	0.30 ± 0.34 (10)
Relative density (%)				
Aggregation 1	22 ± 5 (10)	46 ± 11 (10)	7 ± 15 (10)	
Aggregation 2	96 ± 5 (5)	91 ± 13 (9)	25 ± 11 (5)	

Table 6. *Aurelia aurita*. F values and statistical significance from analyses (one-way ANOVAS) of the swim beat frequency (number s⁻¹ in lower left half of table) and the relative densities (% in upper right half of table) for areas where medusae swimming unidirectionally up, unidirectionally down, or where medusae were in mixed orientations. Swim beat freqencies were not significantly different overall for Aggregation 1, and for Aggregation 2, the overall significance for swim beats was F = 29.59, p = 3.58 x 10^{-10}. The relative densities were significantly different overall among areas in both aggregations, with the overall significance being F = 160.67 and p < 1 x 10^{-14} for Aggregation 1, and F = 87.67 and p = 1.27 x 10^{-10} for Aggregation 2. For the tests below, F values are presented for Aggregate 1, Aggregate 2. NS = not significant, * = p < 0.05, ** = p < 1 x 10^{-7}.

Orientation	Up	Down	Mixed
Up	-----	38.82**, 1.14 NS	65.88**, 266.43**
Down	NS, 51.30**	----	100.77**, 89.19**
Mixed -- down	NS, 4.40*	NS, 65.93**	----
Mixed -- up	NS, 0.32 NS	NS, 59.05**	NS, 2.16 NS

Table 7. Predators of juvenile walleye pollock, *Theragra chaleogramma* in Prince William Sound. NG = not given. From Okey and Pauly (1998).

Predators	Importance in diet (% by weight)	Age class of prey
Age 1-2 pollock	1.7	0
Pacific cod	7.4	0
Sablefish	10.5	0
Arrowtooth flounder	3.7	0
Halibut	57.4	0-2
Fork-tailed storm pretel	5.0	0
Common murre	25.0	1-3
Pigeon guillemot	11.8	1-3
Ancient Murrelet	13.0	1.3
Tufted puffin	13.0	1-3
Horned puffin	1.0	1-3
Harbor seal	47.0	NG

Figure Captions

Figure 1. Maps of Prince William Sound with flight paths of aerial surveys in 1995, 1996, and 1997

Figure 2. Variation in surface area covered in aerial surveys of Prince William Sound during 1995, 1996, and 1997

Figure 3. *Aurelia aurita*. Aerial photo of jellyfish aggregation in Prince William Sound in July, 1996

Figure 4. *Aurelia aurita*. Size frequency distrubution of aggregations in Prince William Sound in 1995, 1996, and 1997. d = dab, s = small, m = medium, l = large. Approximate sizes of each category are given in Table 1. The percentages of 995 aggregations in each category are given above each bar

Figure 5. *Aurelia aurita*. Seasonal and interannual variation in densities of jellyfish aggregations in Prince William Sound as estimated from aerial surveys in 1995, 1996, and 1997. Data presented as the numbers of aggregations km^{-2} and as surface areas of aggregations km^{-2}

Figure 6. *Aurelia aurita*. Distributions of aggregations of medusae in Prince William Sound during aerial surveys in June, July, and August, 1995, 1996, and 1997.

Figure 7. Depth profiles of temperature and salinity in Simpson and Drier Bays of Prince William Sound, where acoustic transects are reported (Table 2)

Figure 8. *Aurelia aurita*. Underwater videotape image from a jellyfish aggregation

Figure 9. *Aurelia aurita*. Vector diagram of mean medusa swimming direction (angle of the sticks), and abundance (length of the sticks) during a 3-min videotape transect through a jellyfish aggregation. Sticks above the horizontal axis represent swimming upwards, with straight up (0°) being vertical swimming up. Sticks below the axis represent swimming downwards, with straight down (180°) being vertical swimming down. The lengths of the sticks represent the numbers of medusae for which swimming direction was measured at each time interval. The videotape frames were "frozen" at 10 s intervals, and swimming direction determined for all medusae in that image.
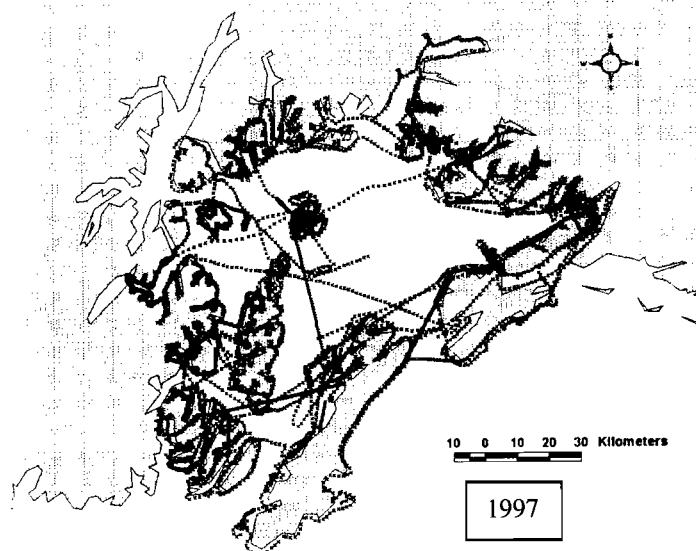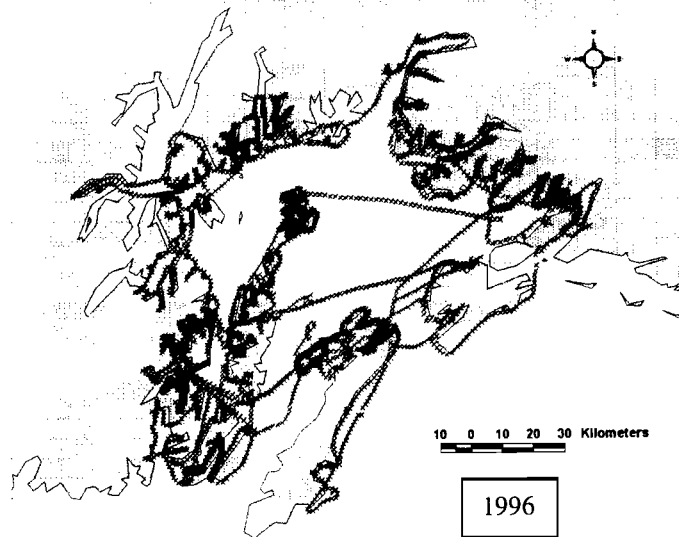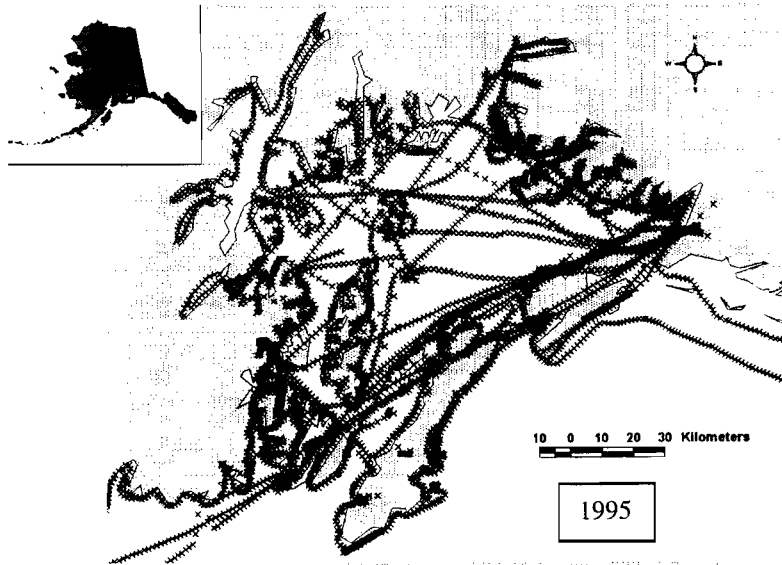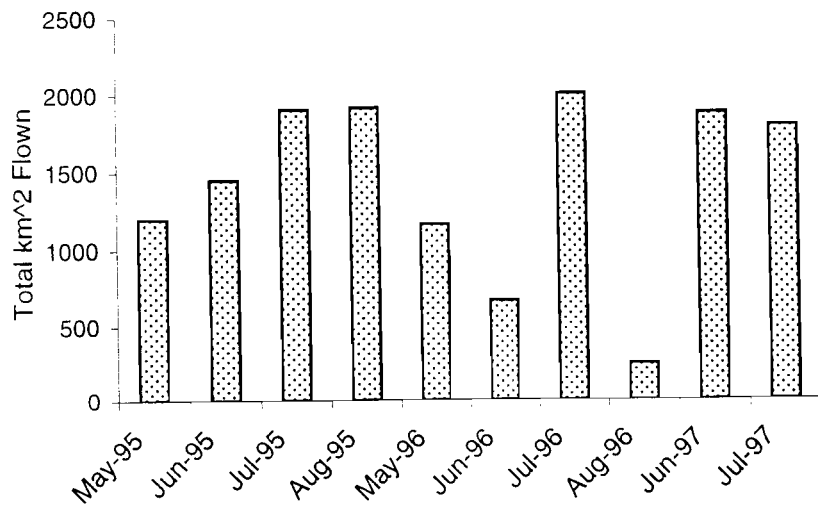
1995

1996

1997

424

Wells Bay
Jack Bay
Galena Bay
Eaglek Bay
Port Fidalgo
Sheep Bay
Simpson Bay
Naked Island
Port Gravina
Orca Bay

Paddy Bay
Ewan Bay
Oner Bay
Jackpot Bay

Whale Bay

1996
■ June
● July
△ August

10 0 10 20 Kilometers

1996
■ June
● July
△ August

10 0 10 20 Kilometers

1997
■ June
● July
△ August

10 0 10 20 Kilometers

429

Drier Bay
Temperature C

Drier Bay
Salinity o/oo

Simpson Bay
Temperature C

Simpson Bay
Salinity o/oo

430

431

Fig 7

432

Fig 9