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In situ observations of the association between juvenile fishes and scyphomedusae in the Bering Sea

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ABSTRACT: In September 1995, dense aggregations of large scyphomedusae (mainly *Chrysaora melanaster*) were observed in 27 midwater deployments of a remotely operated vehicle (ROV) near the Pribilof Islands in the Bering Sea. Age-0 walleye pollock *Theragra chalcogramma* appeared to be frequently associated with these gelatinous zooplankton. During daytime, up to 30 pollock were observed swimming within the tentacles of these medusae, but when approached by the ROV, the pollock generally left the vicinity of the jellyfish. At night, few such associations were observed and juvenile pollock moved closer to the surface, apparently feeding in loose aggregations, while the medusae remained close to the thermocline (35-40 m). Prowfish *Zaprora silenus* were also observed near large medusae, but tended to be found closer to the bell rather than within the tentacles. The lack of any gelatinous material in the stomachs of the pollock suggests that juvenile pollock associate to gain shelter from predation or possibly as a thigmotactic response to biotic structure. The implications of this commensal behavior with gelatinous zooplankton are discussed relative to pollock recruitment in the Eastern Bering Sea.

KEY WORDS: Juvenile pollock · *Theragra chalcogramma* · Scyphomedusae · Commensalism · Underwater video

INTRODUCTION

Numerous studies have examined the association between the early life stages of marine fishes and the physical environment in which they live. Although physical conditions may often play an important role in the developmental rate, distribution, and dispersion of ichthyoplankton, it is apparent that, by the late larval and juvenile stages, biological factors (e.g. food availability and predator abundance and encounter rate) become increasingly important in influencing distribution and abundance. Although often overlooked, biotic structure in the pelagic environment may play an important role in the distribution and survival of juvenile fishes. Examples of biotic structures include large aggregates (e.g. marine snow), floating seaweeds and algae, and gelatinous zooplankton (Kingsford 1993).

Gelatinous zooplankton are recognized as important and occasionally obligate hosts for many invertebrates (Thiel 1976, Laval 1980). Associations with a wide diversity of fish taxa are also well known (Mansueti 1963, Thiel 1978, Arai 1988, 1997, Kingsford 1993). Associations of juvenile North Atlantic gadoid fishes with gelatinous zooplankton are well-documented due to the high abundance and considerable economic importance of gadoids in boreal waters (Dahl 1961, Mansueti 1963, Bailey 1975, Koeller et al. 1986, Hay et al. 1990).

Walleye pollock *Theragra chalcogramma* is the most abundant commercially exploited gadoid species in the North Pacific Ocean and Bering Sea and plays a critical role in these ecosystems (Springer 1992). Juvenile pollock are particularly important because they provide an important link through which energy flows between the lower trophic levels and apical predators (Springer 1992, Brodeur & Wilson 1996a, Brodeur et al. 1996). The relationship between gelatinous zooplankton and juvenile pollock is poorly understood and most

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available information is anecdotal. Schools of late larval (17 to 24 mm) pollock were found to be associated with the scyphomedusa *Cyanea capillata* in near-surface waters of Prince William Sound in the northern Gulf of Alaska by van Hyning & Cooney (1974). These authors noted that the pollock were not found within the tentacles and speculated that the association may have been mainly due to an attraction to floating objects. Based on observations by scuba divers, Hamner (1983) reported that small age-0 pollock swam within the tentacles of medusae (*Chrysaora* sp.) in the Bering Sea, but no quantitative information was presented.

In this paper, I provide evidence, based on *in situ* underwater video observations, that age-0 walleye pollock are commonly associated with large scyphomedusae in the Bering Sea, document other fishes commensal with these medusae, examine diel occurrence and vertical distribution of these associations, and discuss the implications of this commensal behavior for the recruitment dynamics of juvenile pollock.

METHODS

Sampling methodology. During 11 to 25 September 1995, a Super Phantom 2 ROV (remotely operated vehicle; Deep Ocean Engineering, San Leandro, CA, USA) was deployed from the NOAA RV 'Miller Freeman' at locations around the Pribilof Islands in the Eastern Bering Sea (Fig. 1). A downweight (108 kg) was attached to the 320 m umbilical cord to provide stability and to prevent the ROV from trailing while the vessel drifted. The ROV was attached to an additional 25 m of umbilical beyond the downweight which allowed free movement in all directions. The ROV contained an Osprey OE1323 Silicon Intensifier Target low-light video camera and a Hitachi HV-C20 CCD color camera. Two 250 W tungsten-halogen lights provided illumination. An on-deck console with camera, light, and thruster controls and real-time depth readout and video monitor provided the operator with the ability to maneuver the ROV along transects or track individual objects.

A total of 27 (14 day and 13 night) deployments were done at 24 locations (depth range 35 to 214 m) along specified transects or in areas which showed strong acoustic signals such as at oceanographic fronts. The main purpose of the study was to observe age-0 walleye pollock in midwater (Brodeur et al. 1997). A Simrad EK-500 echo integrator interfaced to 38 and 120 kHz split-beam transducers was used to locate acoustic sign likely to be age-0 fish based on target strength information (Brodeur & Wilson 1996b). Water column structure (Conductivity/Temperature/Depth) was measured at most stations with a Seabird Model SBE-9 CTD system (Brodeur et al. 1997). Net sampling was conducted at all stations with a 100 m^2 anchovy trawl containing a 3 mm mesh liner (Brodeur et al. 1995), which was towed through the depth range examined with the ROV to determine taxonomic and size composition of the animals observed. This gear effectively samples the full range of juvenile fish sizes likely to be present at this time of year (Brodeur unpubl. data).

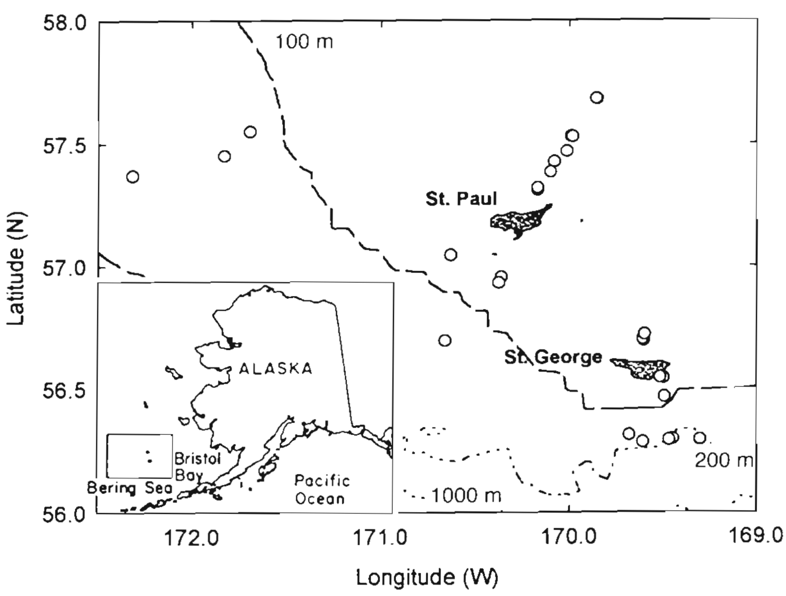

Fig. 1. Locations (O) of 27 ROV (remotely operated vehicle) deployments around the Priblilof Islands, Bering Sea, during September 1995

The trawl catches were sorted to species on deck and length measurements were made on juvenile pollock and other fishes to the nearest millimeter. Umbrella diameters were measured to the nearest 5 mm on a subsample of large scyphozoan and hydrozoan medusae. In addition, total weights were taken for each taxon caught in the trawls. Catches were converted to densities per 1000 m^3 based on estimates of volume filtered for each trawl (Wilson et al. 1996).

Data analysis. The videos were recorded on NTSC standard Hi-8 format tapes and were time coded (date, hour, minute, second) to facilitate multiple viewing and comparison with real-time field notes on depth and environmental conditions. The tapes were reviewed by a trained observer who tabulated data on species composition of medusae and fish seen in the videos. This observer was unaware of the diel period or location of

Fig. 2. *Theragra chalcogramma* and *Chrysaora melanaster.* Juvenile pollock swimming among the tentacles of *C. melanaster* in the Bering Sea during a daytime (19:50 h Alaska Daylight Time, ADT) ROV deployment (38 m depth)

the deployment in order to minimize observational bias. Only medusae that were entirely and clearly visible in the frame were included in the analysis, but the individuals which were only partially observed (umbrella or tentacles only) were also logged.

Due to uncertainties in the volume of water observed by the ROV at different times of day and in waters of varying clarity, density estimates were not derived for the medusae or pollock from these observations. However, during some deployments, the entire water column was sampled equally without stopping at any one depth and these segments of the videotapes were analyzed for vertical distribution of pollock and medusae. Data were summarized as to the number of occurrences of medusae observed both with and without juvenile fishes, the number of fish per individual medusae, and the number of occurrences of fish without any medusae observed nearby. The location of the fish with respect to the body of the medusae was also noted for all associations.

RESULTS

ROV observations

Scyphomedusae (*Chrysaora melanaster* and *Cyanea capillata*) were the most visible macrofauna observed in the water column and were seen during 26 of the 27 deployments. A total of 3196 *C. melanaster* were observed in video footage, of which 580 were clearly and completely visible for analysis of fish associations. Although it was not possible to get quantitative estimates of their abundance or size from the videos, at least 1 large *C. melanaster* was within view at all times in the densest aggregation layers (20–40 m). In most cases, the medusae pulsated in an upright fashion with the long tentacles (estimated to be >10 m in some cases) streaming down (Fig. 2). *C. capillata*, with many densely packed but shorter (<2 m) tentacles, swam in a similar fashion but were far less common (n = 18) than *C. melanaster*. Other scyphomedusae (*Aurelia* sp.), hydromedusae (mainly *Aequorea* sp.), and ctenophores (*Beroe* sp.) were also infrequently observed in the video footage.

Age-0 walleye pollock were often seen swimming among the tentacles of *Chrysaora melanaster*, especially during daytime deployments (Fig. 2). A total of 203 separate co-occurrences of pollock with *C. melanaster* and 5 with *C. capillata* were observed during the 27 dives. The pollock were generally found well down the length of the tentacles away from the umbrella of the jellyfish. Up to 30 pollock were observed in association with one medusa, with an overall mean of 3.0 pollock per medusa. When approached by the ROV, the pollock would move away from the medusae. The majority of *C. melanaster* and associated pollock were observed over a narrow (30–40 m) depth range during the day (Fig. 3).

At night, a different behavior was observed in that pollock apparently left the medusae, ascended closer to the surface (5 to 30 m, Fig. 3), and were found in large, dense aggregations (Fig. 4). The random orientation of the fish and their continuous jaw movements as observed with the ROV suggested that these fish were probably feeding at this time. These juveniles did not appear to be affected by the motion of the ROV or by the camera lights. Scyphomedusae were also frequently observed during these night dives, but they were found at greater depths (25 to 45 m, Fig. 3) than the pollock and generally did not have juvenile pollock associated with them.

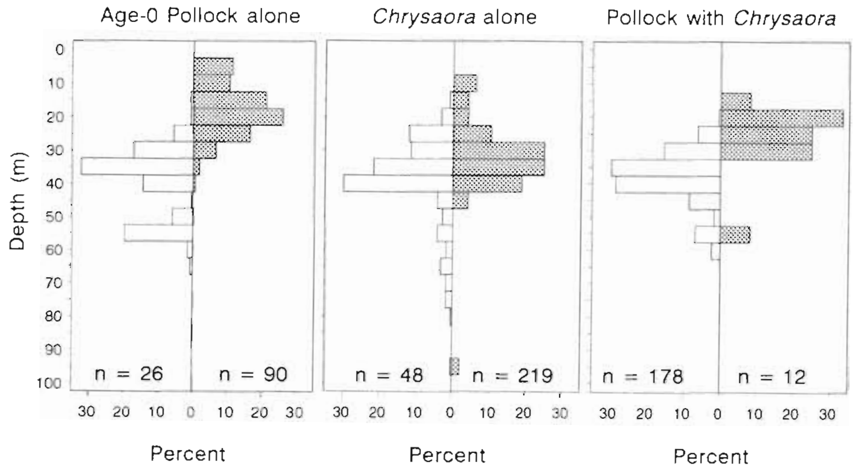

Fig. 3. *Theragra chalcogramma* and *Chrysaora melanaster*. Day (open bars) and night (filled bars) vertical distribution of age-0 pollock and *C. melanaster* both alone and in association with one another based on ROV observations. Data are the percent frequency by 5 m depth intervals of the occurrences of age-0 pollock and *C. melanaster* observed alone and the occurrence of the associations. Observations are summed from 13 daytime and 7 nighttime deployments for which sufficient depth information existed. Number of occurrences are listed at the bottom of each panel

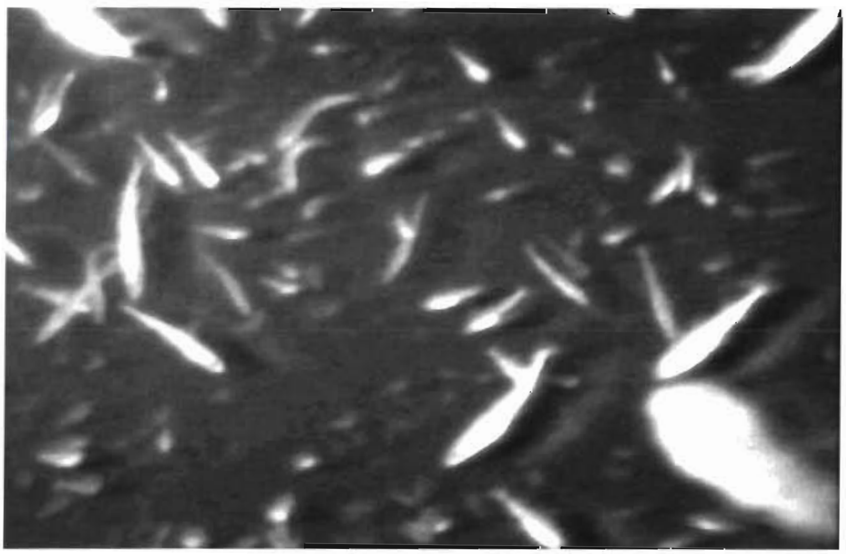

Fig. 4. *Theragra chalcogramma*. Dense aggregation of juvenile pollock observed during nighttime (03:42 h ADT) at about 15 m depth

The association between juvenile pollock and *Chrysaora melanaster* showed a marked diel pattern (Fig. 5). Both the mean number of pollock per medusa and the percentage of total quantifiable medusae which were associated with at least 1 juvenile pollock were substantially higher during daylight hours. Both these indices were at or near zero during the night (Fig. 5). Age-0 pollock and *C. melanaster* were found to associate at a significantly higher rate during the day and tended not to be found together at night (*G*-test of Association = 176.5 and 292.4 for pollock and *C. melanaster*, respectively; both $p < 0.0001$). The mean and median depths of age-0 pollock and *C. melanaster* alone and those of their co-occurrence also varied significantly between day and night (Table 1, Fig. 3).

Juvenile prowfish *Zaprora silenus* were observed in association mainly with large *Cyanea capillata* (n = 31) but also were found with some larger *Chrysaora melanaster* (n = 5). They were most often seen swimming around the top and sides of the bell, but, when approached by the ROV, they retreated behind the tentacles or within the bell of the jellyfish. Up to 9 juvenile *Z. silenus* were observed around a single *C. capillata*. None of these fish were seen swimming in open areas any distance away from medusae. One other fish species, which has tentatively been identified as crested sculpin *Blepsias bilobus*, was observed on 1 occasion swimming around the bell of a medusa.

Acoustic patterns and trawl catches

The acoustic patterns observed varied substantially by location and time. A typical daytime (18:20 h Alaska Daylight Time, ADT) pattern seen offshore of the front north of St. Paul Island was a heavy concentration of

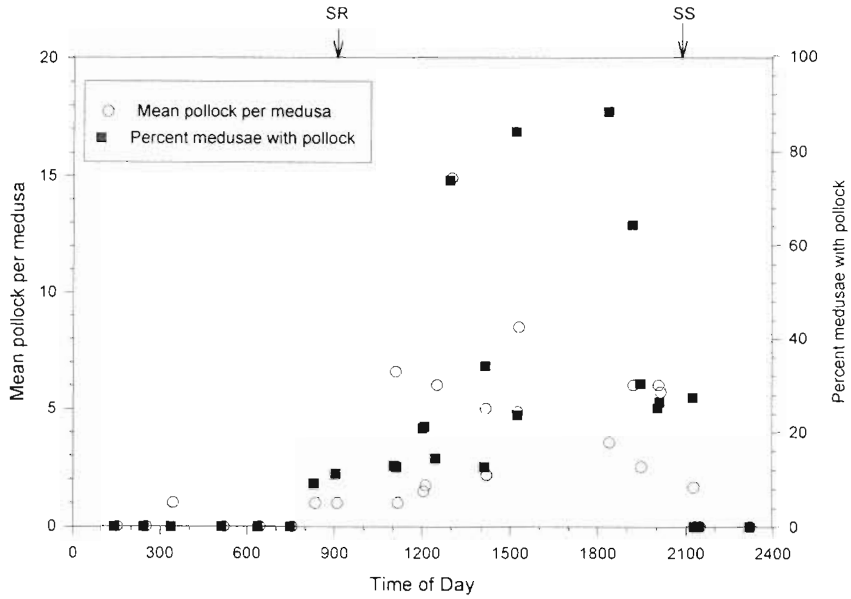

Fig. 5. *Theragra chalcogramma* and *Chrysaora melanaster*. Association of juvenile pollock with *C. melanaster* showing mean number of pollock per medusa when they co-occurred and percentage of total quantifiable medusae that were associated with walleye pollock by time of day. Time of sunrise (SR) and sunset (SS) shown at top of graph

scatterers at or above the thermocline/pycnocline with almost no acoustic targets observed above 20 m (Fig. 6). A more diffuse scattering is visible below the thermocline to within a few meters of the bottom. During nighttime (22:30 h ADT), the acoustic pattern changes substantially at the same location (Fig. 6). The bottom layer has disappeared and scatterers are found in a diffuse layer closer to the surface with only a few isolated aggregations occurring down to 40 m (Fig. 6). Based on the target strength ranges detected at these depths (−47 to −55 dB) and an empirically-derived target strength/fish length relationship (Brodeur & Wilson 1996b), these scatterers were most likely age-0 pollock.

The catch composition of the anchovy trawls was dominated by age-0 pollock among the fishes and by *Chrysaora melanaster* among the invertebrates (Table 2). Both these species occurred in all 34 trawls made and constituted the vast majority of the numerical composition of their respective categories. The next most frequently occurring species in each category (*Zaprora silenus* and *Cyanea capillata*) both had relatively low densities compared to the dominants (Table 2). The catches of age-0 pollock showed a significant positive relationship (geometric mean regression: F = 7.57, p = 0.014, n = 18) to the total catch of cnidarians in each trawl for daytime hauls, but no relationship (F = 0.33, p = 0.57, n = 16) was found for night hauls (Fig. 7). Since these anchovy trawls were targeting acoustic sign suspected to be age-0 pollock, this lack of a relationship suggests that the pollock and medusae are found in different layers at night.

Overall, the mean catch per haul of age-0 pollock was slightly higher during the day trawls (23.9 fish $1000m^{-3}$) than at night (19.8 fish $1000m^{-3}$), but this difference was not significant. The size distributions of age-0 pollock collected in the anchovy trawls were similar during both day and night (Fig. 8) and the mean lengths were virtually identical (54.76 mm and

Table 1. *Theragra chalcogramma* and *Chrysaora melanaster*. Diel differences in the mean and median depths of age-0 walleye pollock alone, *C. melanaster* alone, and the association of both species. Also given are the results of a *t*-test and nonparametric Mann-Whitney *U*-test for differences in mean and median depths, respectively, by time of day. Sample sizes are given in Fig. 3. $^{**}p \le 0.01$, $^{***}p \le 0.001$

	Time	Mean depth (m)	*t*-value	Median depth (m)	*U*-value
Age-0 pollock	Day	39.3	12.3***	36	718.5***
	Night	19.8		19	
C. melanaster	Day	39.7	3.9**	38	329.1**
	Night	32.1		33	
Association	Day	37.6	7.7***	37	1079.5***
	Night	26.3		25	

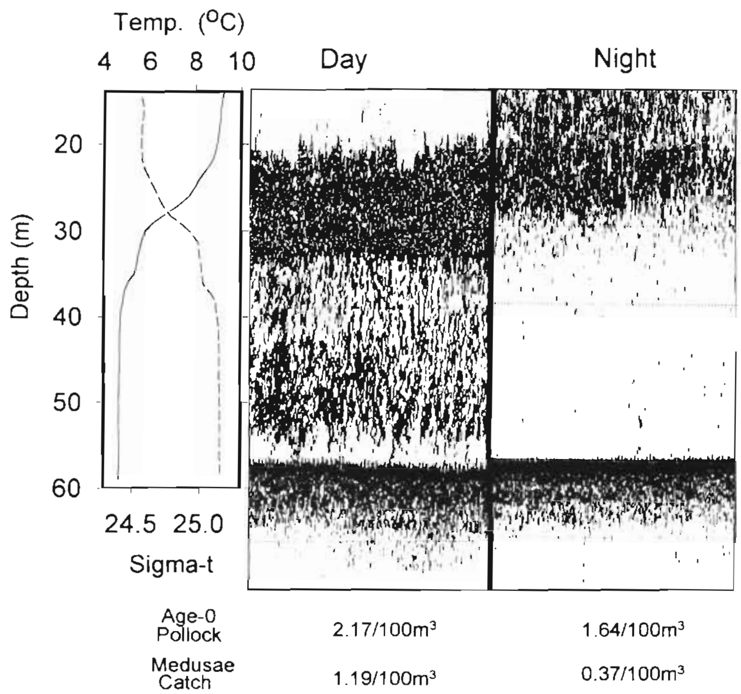

Fig. 6. Day (18:20 h ADT) and night (22:30 h ADT) differences in vertical distribution and aggregation patterns of sound scatterers at the same location (57.22° N, 170.1° W) at the frontal region north of St. Paul Island. Also shown are the temperature and density (sigma-t) profiles and the catch of age-0 walleye pollock and gelatinous zooplankton in each period corresponding to this location

54.77 mm, respectively), implying the same population was sampled at both times. The total gelatinous zooplankton mean density in the trawls was significantly ($p = 0.003$) lower during the night (4.9 ind. $1000m^{-3}$) than during the day (16.7 ind. $1000m^{-3}$). The tows were made through the high density sign observed by the 38 kHz echosounder, which corresponds mainly to pollock concentrations; this suggests that the jellyfish were not found in the same layer as the age-0 juveniles at night. The catches of the dominant scyphomedusan species (*Chrysaora melanaster*) consisted of a broad range of umbrella diameters, but the majority were less than 20 cm (Fig. 9). Among the less abundant gelatinous species, *Cynaea capillata* also occurred over a wide range of sizes, but *Aequorea forskalea* and *Aurelia aurita* were mostly restricted to <20 cm umbrella diameters.

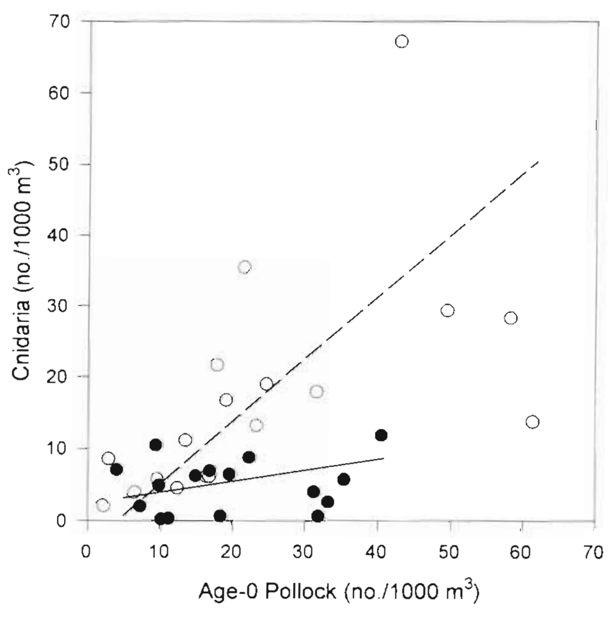

Fig. 7. Relation between the abundance of juvenile pollock and large gelatinous zooplankton caught in anchovy trawls at 32 stations around the Pribilof Islands. (○) Daytime hauls; (●) nighttime hauls. Dashed and solid lines are the geometric mean regression fits to each data set

Table 2. Summary of the 5 most abundant fish and invertebrate species caught in the anchovy trawl arranged in order of decreasing percent frequency of occurrence (%FO)

Taxon	%FO (n = 34)	Density (no. $1000m^{-3}$) Mean	SE	% of total
Fish				
Theragra chalcogramma	100.0	22.05	2.61	99.71
Zaprora silenus	32.3	0.01	0.01	0.05
Gadus macrocephalus	26.5	0.01	0.01	0.05
Atheresthes stomias	20.9	0.04	0.01	0.16
Podothecus acipenserinus	17.6	0.01	0.01	0.04
Invertebrates				
Chrysaora melanaster	100.0	11.27	3.16	87.86
Cyanea capillata	44.1	0.38	0.10	2.98
Aequora forskalea	23.5	0.61	0.12	4.77
Aurelia aurita	23.5	0.55	0.10	4.27
Berryteuthis magister	8.8	0.02	0.03	0.11

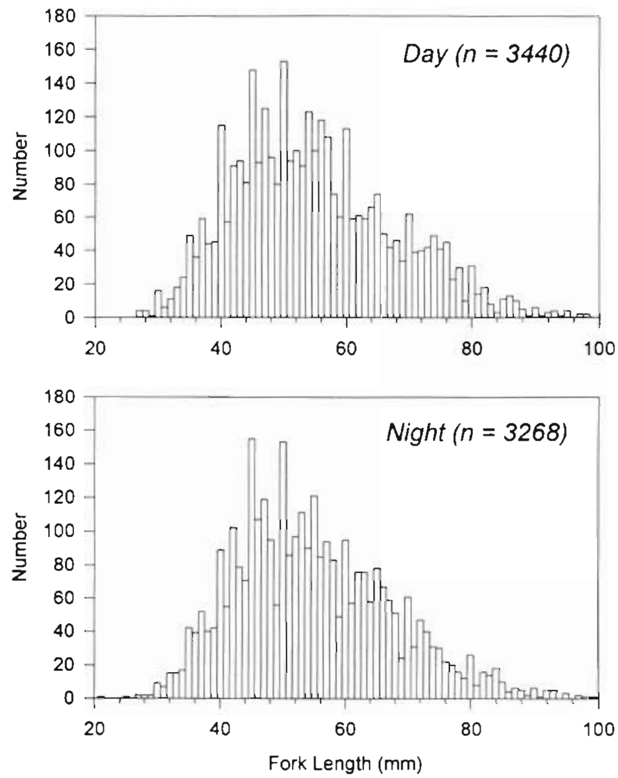

Fig. 8. *Theragra chalcogramma*. Length distributions of age-0 pollock collected in day and night hauls around the Pribilof Islands

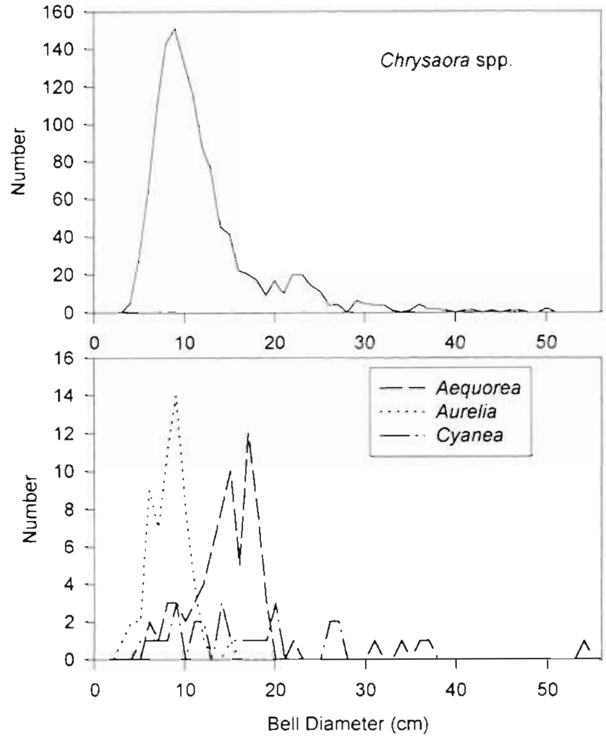

Fig. 9. Umbrella (bell) diameters of the common gelatinous zooplankton collected around the Pribilof Islands

DISCUSSION

The underwater video observations described here are some of the first made in the pelagic zone of the Eastern Bering Sea Shelf and document a potentially important aspect of walleye pollock life history not adequately described in the literature. Although previously observed from the deck of a vessel (van Hyning & Cooney 1974) and by scuba divers in surface waters (Hamner 1983), this commensal behavior generally occurred at depths between 10 and 30 m in the present study, which is beyond sustained scuba diving depths, thus necessitating the use of manned or unmanned submersibles. Moreover, despite the fact that age-0 pollock and large cnidarians dominate the catches of midwater trawl samples (Brodeur et al. 1997) and strongly tend to be associated in community studies based on classification techniques (Brodeur et al. in press) in the Bering Sea, such an association could not be inferred strictly from their coincidence in the same trawls and would therefore require *in situ* observations.

Owing to the vast numbers of marine bird, mammal and fish predators known to consume juvenile pollock during their first year of life (Livingston 1993, Brodeur & Wilson 1996a), pollock can undergo adjustments and perhaps even recruitment failure during the juvenile stage despite having a seemingly adequate supply of larvae and food resources (Brodeur & Bailey 1996). In other parts of their range, such as in the Gulf of Alaska and off Japan, juvenile pollock are known to recruit to inshore nursery areas in bays and inlets, which may provide not only good feeding conditions but may also afford some protection from avian, mammalian and piscine predators which are concentrated in offshore waters. For pollock spawned over or transported to the central shelf of the eastern Bering Sea, there are relatively few enclosed areas that could serve as nursery grounds in this broad featureless region. The only land mass projecting above sea level is the Pribilof Island Archipelago, which consists of 5 relatively small islands approximately 470 km from the mainland. The waters surrounding these islands are very productive in terms of prey concentrations due to structural fronts which exist around the 50 m isobath (Kinder et al. 1983, Coyle & Cooney 1993, Brodeur et al. 1997). However, these fronts are not likely to be a haven from predation since they are the feeding grounds for a large number of land-based piscivorous birds (mainly murres *Uria* spp. and kittiwakes *Rissa* spp.) and marine mammals (mainly northern fur seal *Callorhinus ursatus*) that are known to feed on age-0 pollock (Coyle et al. 1992, Springer 1992, Decker & Hunt 1996). Since these birds and mammals are primarily visual predators, the time of greatest juvenile pollock vulnerability is likely to be during the day. Because much physical structure in the environment is lacking, it is plausible that juvenile pollock utilize biotic structures such as large medusae as refugia from predation during daytime, thereby increasing their likelihood of survival. Duffy (1988) has shown that butterfish *Peprilus triacanthus* normally commensal with *Cynaea capillata*, but which are physically dislodged from their hosts, quickly become prey to opportunistic avian predators.

Another way that juvenile pollock and other fishes might benefit from their association with medusae is if they were to consume parts of the medusae or food particles previously captured by the medusae but not yet transported to the gastric cavity (Mansueti 1963). The diets of a wide size range of age-0 walleye pollock were examined from locations where this commensal relationship with gelatinous zooplankton was observed. Most prey eaten were planktonic (copepods, euphausiids, pteropods, and chaetognaths), although the larger individuals (>70 mm) consumed some epibenthic prey (harpacticoid copepods, cumaceans) taxa (Brodeur et al. 1997). Although some pelagic prey could have been secondarily consumed from the tentacles of the medusae, there was no evidence of direct consumption of gelatinous material that would indicate that age-0 pollock consumed parts of their hosts. Even hyperiid amphipods, which are well-known parasitoids of gelatinous zooplankton (Laval 1980) and were found in abundance in the plankton tows that collected these cnidarians, were not found in the stomachs of juvenile pollock, further indicating that these fish probably feed some distance away from their hosts (see also Dahl 1961, Tolley 1987). There is no evidence presently available to suggest that the association benefits the medusae in any way (e.g. removal of ectoparasitic hyperiid amphipods by pollock); thus, the age-0 pollock are considered to be facultative commensals on these medusae. Alternatively, this relationship may result from a thigmotactic response on the part of the juveniles to any structure in the pelagic realm (Rountree 1989, Kingsford 1993), and this type of association may occur with any floating object, such as drifting kelp and flotsam (Fedoryako 1989, Kingsford 1993).

It is interesting to note that while age-0 pollock >40 mm may derive some benefit from associating with gelatinous zooplankton, there is some evidence to suggest that large medusae prey on earlier juvenile stages of pollock in the Bering Sea in the summer (Hamner 1983). In fact, one *Chrysaora melanaster* collected during this cruise was found to contain 2 partially-digested juvenile pollock (≈ 30 mm) in its gastric cavity. It is not presently known what predatory impact medusae might have on age-0 pollock, but most of the predation probably occurs on much earlier life stages than were generally present during the September cruise. Most pollock caught at this time are of a size at which they either are able to maintain a safe distance from the nematocysts in the scyphomedusan tentacles or have developed an immunity to the discharge of their host's stinging cells (Dahl 1961).

It is not surprising that prowfish were commonly associated with large medusae. One of the earliest accounts of this species in the Bering Sea documents an association with *Cyanea* (Scheffer 1940). Prowfish lack strong sustained swimming ability and their fins are adapted to making tight turns as would be required to maneuver around tentacles (cf. Horn 1975). In contrast to juvenile pollock, which left the medusae when approached by the ROV, prowfish darted for safety within the tentacles. Also, no prowfish were observed more than 1 m away from a jellyfish during any time of the day or night. Thus, it seems likely that this species is an obligate commensal with large medusae until it descends to the bottom as an adult.

The implications of the observed commensal behavior are quite apparent. If juvenile pollock are symbiotic with gelatinous zooplankton until they reach a size at which they can escape most gape-limited predators, then the amount of suitable medusae 'habitat' available to them may be a determinant of recruitment success. There are few quantitative data available on the densities of large gelatinous zooplankton present in the Bering Sea. Coyle & Cooney (1993) found that pelagic cnidarians comprised the vast majority of the biomass catch of small (1 m^2) nets in the vicinity of the Pribilof Islands in 1987 and 1988. These authors suggested that the medusae may actively aggregate or passively be concentrated in convergent fronts which encircle both main islands. Many large medusae, including both *Chrysaora melanaster* and *Cyanea capillata*, were observed in high densities along surface convergences caused by Langmuir cells in the Bering Sea (Hamner & Schneider 1986).

These large carnivorous medusae may affect earlier stages of pollock by either directly consuming them or by competing with them for potentially limited prey resources (Arai 1988). However, as hypothesized here, some positive benefit (i.e. shelter from predation) could be derived by juvenile pollock through association with medusae at a later stage. Based on by-catch of systematic trawl surveys (Brodeur et al. unpubl.), there has been a substantial increase since 1990 in the biomass of large scyphomedusae in the eastern Bering Sea similar to that seen in other ecosystems (Mills 1995). It is of interest to note that no strong year classes of walleye pollock have appeared since 1989 (V. Wespestad, Alaska Fisheries Science Center, pers. comm.), although the intervening period is too brief to draw any definite conclusions. Regardless of their effect on population levels of pollock, the meso- and fine-scale features in the distribution of medusae, such as their propensity to be found in high densities in surface convergences set up by Langmuir circulation in the Bering Sea (Hamner & Schneider 1986), may need to be taken into account in designing studies to determine the horizontal and vertical distribution patterns and assess the abundance of juvenile pollock as well as other pelagic juvenile gadoids (Koeller et al. 1986, Hay et al. 1990).

The ROV observations by depth and the limited acoustic data presented here agree with other field (Bailey 1989, Brodeur & Wilson 1996b) and laboratory (Sogard & Olla 1996a) data which suggest that at least some of the juvenile pollock migrate vertically and change their aggregation patterns on a diel basis. Although many of the age-0 pollock are co-located with gelatinous zooplankton that may have settled near the pycnocline during the day, some fish, presumably the larger individuals (Bailey 1989), migrate through the thermocline (see smaller peak around 55 m in Fig. 3). It is not known why these fish do not utilize the shelter afforded by the medusae, but perhaps they have found it more beneficial to migrate further down in the water column for trophic or energetic reasons (see Bailey 1989, Sogard & Olla 1996b). The video observations also document occurrences of pollock aggregations close to the surface during night deployments. Since the acoustic transducer was located at 14 m, it was not possible to acoustically detect the presence of near-surface aggregations of fish; however, the integrated water-column backscattering from the transducer depth to the bottom was generally greater during daytime than nighttime for the same location, which would indicate that a proportion of the total fish biomass is at depths shallower than the transducer at night (see also Brodeur & Wilson 1996b). Although no visual records of near-surface medusae similar to that done by Hamner & Schneider (1986) were made, few medusae were observed at the surface either by the ROV or from the deck of the vessel during either day or night on this cruise.

There is still much uncertainty concerning the motivation for juvenile pollock to vertically migrate on a diel basis, but there is substantial evidence that most age-0 pollock are found closer to the surface at night than during the day (Bailey 1989, Brodeur & Wilson 1996b, R. Brodeur unpubl.). Laboratory studies have shown that juvenile pollock alter their vertical distribution based upon a number of extrinsic stimuli, including the presence of a predator or thermocline (Sogard & Olla 1993). Descending to deep waters during the daytime may make these juveniles less susceptible to surface-feeding visual predators, such as marine mammals and seabirds, but migrating all the way to the bottom exposes them to potential cannibalism by older age classes of pollock (Dwyer et al. 1987, Bailey 1989) and to predation by other bottom fishes (Livingston 1993). A viable alternative for age-0 pollock is to migrate only partially down the water column during the day and take refuge within a layer of medusae accumulated near the pycnocline. This migratory and shelter-seeking behavior may be a defense employed by pollock to minimize encounters with potential predators in what is apparently a 'top-down' controlled pelagic ecosystem (Springer 1992, Verity & Smetacek 1996). More experimental and field work is clearly needed to derive a better understanding of the adaptive significance of this commensal behavior and the temporal and spatial extent of the associations.

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