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VERTICAL DISTRIBUTION AND MASS MORTALITY OF PRAWNS, *PANDALUS PLATYCEROS*, IN SAANICH INLET, BRITISH COLUMBIA

Prawn, or spot prawn, *Pandalus platyceros* Brandt, 1851, British Columbia's largest shrimp species, is extensively fished in Canada and is of considerable economic importance (Noakes and Jamieson 1986). The species ranges from California to Alaska and, being largely associated with rocky terrain, is fished with traps in many of the region's coastal inlets (Butler 1980).

This study reports a fortuitous observation of catastrophic mortality of prawn in Saanich Inlet, noted during a series of observations on the vertical distribution of prawn on the walls of this fjord using a submersible. These observations are important because, under the circumstances involved, these mobile benthic organisms had ample opportunity to avoid the apparent rapid intrusion of lethal environmental conditions by moving upwards, and thereby remaining in a favorable environment.

Well-documented sudden mass deaths of adult marine invertebrates in subtidal environments have usually been associated with man-induced environmental perturbation, such as an oil spill, pollutant discharge, entrainment of organisms into a lethal environment (e.g., dredge or power plant cooling water intake), or the entrapment of benthic organisms by some lethal environmental event (Tulkki 1965). However, the selective high mortality of one or only a few species in a subtidal community, with no associated physical habitat perturbation and with apparent opportunity for escape, has been infrequently described in documented catastrophic mortalities (Brongersma-Sanders 1957; Swanson and Sindermann 1979; Levings 1980a, b; Tunnicliffe 1981; Burd and Brinkhurst 1984, 1985; Renaud 1986). It is known that species differ in their relative tolerances to environmental stress (e.g., Renaud 1986), but for subtidal invertebrates, the proximity to lethal conditions of the majority of a population for extended time periods has not been generally noted. This study shows that prawn may occur close to lethal environmental conditions, and that abrupt mortality results if lethal water conditions suddenly intrude. In certain locations, such mortality may be more frequent than previously recognized and may justify a unique exploitation strategy.

Materials and Methods

This study was conducted between 6 and 10

October 1986, at Bamberton (lat. 48°35′N, long. 123°31′W), located half-way down Saanich Inlet, a 24 km long fjord on the southeast coast of Vancouver Island. Because of its close proximity to regional oceanographic laboratories, this inlet has been well studied oceanographically (Carter 1934; Herlinveaux 1962; Richards 1965; Anderson and Devol 1973; Pickard 1975; Emerson et al. 1979; Thomson 1981) and biologically (Tunnicliffe 1981; Burd and Brinkhurst 1984, 1985). At its mouth, it has a submerged (75 m) sill behind which there is a deep (maximum depth = 234 m) basin, and water below the sill depth is typically isolated, oxygen-deficient, and may contain hydrogen sulphide. The basin is flushed only when water above the sill is sufficiently dense to cascade into it. Throughout the year, there typically remains one or more oxyclines in the water column structure. The study area is generally characterized by a 20–30° slope to about 70 m, and a 30–60° slope from this depth to the bottom of the inlet (209 m).

Observations were made by two people from the submersible *Pisces IV*, which has been previously described by Mackie and Mills (1983). Two 3-h dives were made each day—one typically starting at 1300 and the other at 1900, about one hour after sunset. Dives to the bottom of the inlet were conducted at random locations over a 3 km length of shoreline and began with a direct descent to the bottom of the inlet. The submersible was then moved upwards, horizontal and about 1 m from the cliff, from the bottom of the inlet to a depth of 20 m. After surfacing, the submersible was then towed to another dive location, where the process was repeated. A total of 17 ascents were completed during the 8 dives.

Ascent speed varied according to habitat complexity, slope, and crustacean abundance, but was slow enough to permit recording of the species observed except in areas where extremely dense concentrations of animals were found. Observers were stationed on opposite sides of the submersible, with no overlap in their visual field. Each observer was able to scan approximately 90° on one side of the submersible's path.

As discussed by Richards and Schnute (1986), a general problem with use of submersibles has been the quantification of species abundance. Both the presence of lights and the submersible itself might affect animal behavior and hence bias observations. Prawns tend to be cryptic and were frequently found in association with bottom debris, and occasionally in holes. After extensive observations, including moving at specific locales with lights on or off and

moving at variable speeds, it was concluded that prawns and other demersal crustaceans were not apparently affected by *Pisces*'s presence, allowing them to be effectively studied. On the approach of *Pisces*, demersal crustaceans would occasionally swim a short distance with rapid flicks of their abdomens, but in most cases, they would simply assume an aggressive stance towards the submersible and continuously face it as it passed by. They did not retreat under cover.

Visibility of benthic animals varied somewhat because of changes in bottom topography and its effect on distance of the submersible from the substrate. Water clarity was generally good (>7 m), but resolution was poor at the perimeter of the illuminated area (about 5 m maximum).

Data were initially recorded into handheld tape recorders, and tapes were transcribed shortly after each dive. Prawns were individually counted and their depths of occurrence noted over a vertical transect of about 3 m. However, this procedure could not be used when live prawn abundance exceeded approximately 6 m^{-2}, because of their high density and because the prawns stirred up the substrate by their movements. This situation only occurred over a narrow depth range (between 70 and 85 m depth, depending on date of observation). Dead prawns, which often only consisted of exoskeleton fragments, were also difficult to count at a density greater than about 2 m^{-2}. In both situations, number per meter of depth was conservatively estimated by multiplying the respective minimum average density per square meter by 3 m, the transect width over which live and dead prawn abundances were being assessed.

Qualitative notes on abundance of munids, *Munida quadraspina* Benedict, 1902, the dominant benthic crustacean present, were recorded by depth interval. Observers noted other invertebrate and fish species present in each transect.

Movement of observed crustaceans was sufficiently slow, relative to the submersible's movement, to prevent their crossing the submersible's path and possible double counting by the observers. Body size of some individuals was estimated by comparing them to a 30 cm rod, marked in 10 cm intervals, that hung in front of the left viewport. Sizes were later confirmed by measurement of carapace lengths of specimens collected using the extendable arm of the submersible.

Water samples, and on some occasions crustaceans, were collected at selected depths by pumping water through jars attached to the exterior of the submersible until they had been thoroughly

flushed, and then sealing them. Samples were fixed with manganous sulphate reagent and alkaline iodide solution as soon as the submersible had surfaced and was recovered at the end of each dive, and dissolved oxygen concentrations were determined later using a modified Winkler titration procedure (Strickland and Parsons 1972). Ambient water temperature was recorded continuously during each dive. On 14 October 1986, a more comprehensive set of oceanographic measurements (temperature, salinity, and dissolved oxygen [DO_2]) was obtained by University of British Columbia (UBC) oceanographers 1 km from the study area.

Results

Substrate type was a soft, light-brown flocculent ooze at the bottom of the inlet up to a depth of about 60 m, when it became more gravelly. The floor of the inlet was relatively flat, changing to a slope of 30–60° at the walls up to a depth of about 100 m, at which point 5–10 m vertical rock cliffs often occurred. The slope then lessened at approximately 70 m depth to 20–30°, with frequent rock outcroppings observed up to the minimum depth (20 m) surveyed.

Salinity and temperature below 20 m ranged from 30.0 to 31.4‰ and from 8.0° to 11.2°C, respectively, throughout the study. During the first two days of observations, measured DO_2 levels were >1 mL · L^{-1} at depths above 20 m. Between the afternoon and evening dives of the third day (8 October), an abrupt decrease in DO_2 concentration to between 0.76 and 0.92 mL · L^{-1} was detected at depths of 75–77 m. However, at nearby depths of 71–73 m, DO_2 levels remained above 1 mL · L^{-1} (1.29–2.00 mL · L^{-1}).

Dissolved oxygen (DO_2) measurements obtained during the last two days of our study show a similar profile to those obtained four days later in the center of the inlet by the UBC team (Fig. 1). In both cases, a region of low DO_2 (<1 mL · L^{-1}) was seen in waters of intermediate depth, although the depth at which this lens of low DO_2 occurred differed by about 20 m. Minimum DO_2 level recorded during our dives was 0.76 mL · L^{-1} at 77 m on 8 October, while on 14 October in the center of the inlet, the lowest value noted was 0.44 mL · L^{-1} at 110 m. Since low DO_2 levels normally occur in the deepest waters of the inlet (Pickard 1975; Burd and Brinkhurst 1984), these results indicated that there had recently been intrusions of denser, more oxygenated water over the sill into the deeper regions of the inlet, displacing the low DO_2 layer upwards or advecting low DO_2 water into the study area.

There were clear differences in depth ranges inhabited by species commonly observed in the study area (Fig. 1). The species we observed were primarily benthic in habit, although some epibenthic species such as spotted ratfish, *Hydrolagus colliei* (Lay and Bennet, 1839); spiny dogfish, *Squalus acanthias* Linnaeus, 1758; and Pacific cod, *Gadus macrocephalus* Tilesius, 1810, were periodically observed, usually at depths below 80 m. Various rockfish (*Sebastes* sp.) were observed around rock outcroppings.

The most abundant benthic invertebrate species observed below 60 m were four species of shrimp (*Spirontocaris holmesi* Holthuis, 1947; *S. sica* Rathbun, 1902; pink shrimp, *Pandalus jordani* Rathbun, 1902; and prawn) and munids. A few Dungeness crab, *Cancer magister* (Dana, 1851) were observed at 40–80 m depth. Greatest densities of prawns generally occurred between 70 and 85 m depth, although their observed range was from 20 to 159 m (Table 1). There was no obvious difference in the depth range of major prawn concentration (70–85 m) between afternoon and night dives on the same day. However, more prawns were observed in the depth range of 20–70 m at night than during the day, but these were relatively few in comparison to those at 70–85 m depth (Table 1). During the latter part of the study, most prawns were in a narrow band between 70 and 79 m depth. An amphipod, *Orchomene obtusa* (Sars, 1890), was common on the substrate from 80–210 m water depth. Major concentrations of pelagic amphipods were observed at depths of 45–75 m and 23–90 m during the day and night, respectively. Euphausiids were most abundant at 90–135 m during the day and at 50–90 m at night.

Munids were not observed above the main prawn concentration at 70–85 m. A wide size range of munids was observed, ranging from recently settled juveniles to adults of about 3 cm carapace length. In general, large individuals were found below 100 m whereas small munids were found from 80 to 120 m depth. Munids were observed down to the deepest depth surveyed (209 m).

On the evening dive of the third day, 8 October, dying and dead prawns, the latter covered with swarms of amphipods, were observed between 82 and 90 m depth, with most between 85 and 90 m (Table 1). Some live prawns showing disoriented behavior were also observed. Examination of collected live prawns observed to be in poor condition when sampled showed no evidence of disease or
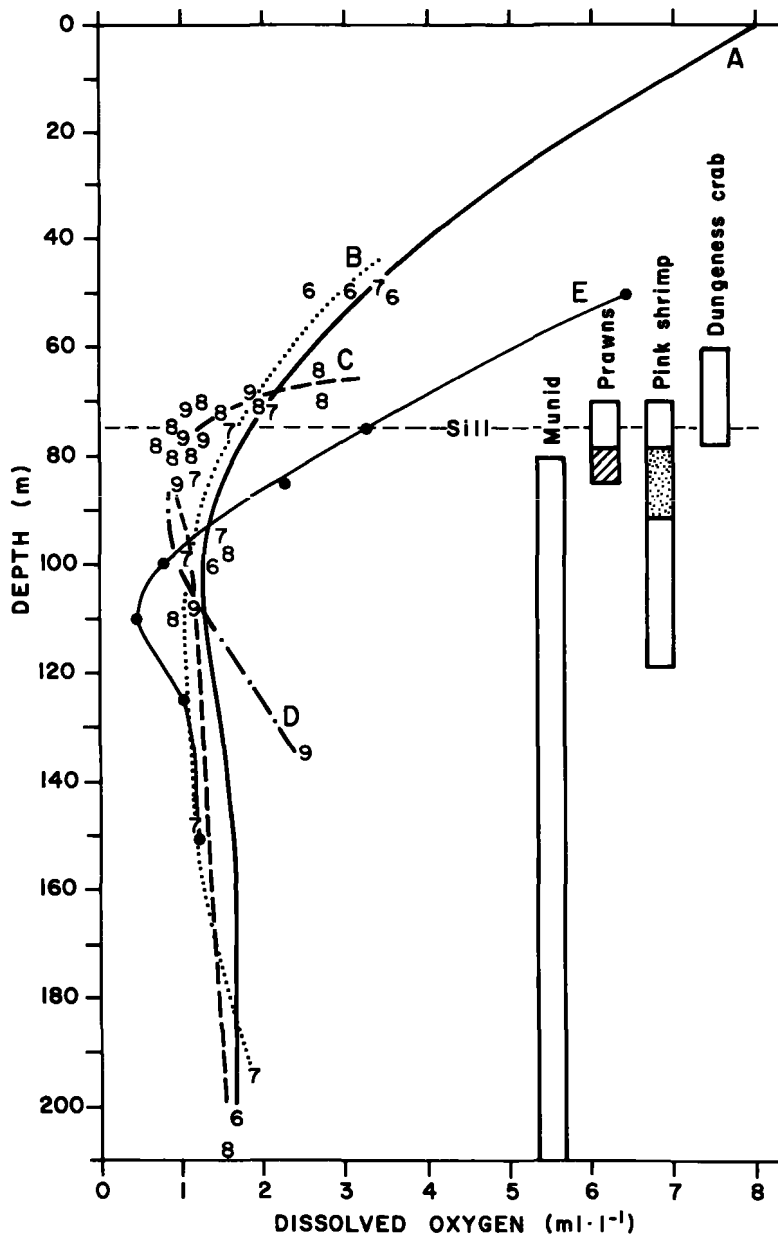
FIGURE 1.—Dissolved oxygen levels (mL · L⁻¹) at depth during each of the 4 days of diving (lines were drawn by eye) and for the UBC sampling, and relative depth distributions of the main abundances of the four large crustaceans observed. Oblique bar = zone of prawn mortality; stipple = area devoid of pink shrimp after low DO₂ water intrusion. Numbers = dates in October 1986. A (——) = 6 October, B (•••) = 7 October, C (——) = 8 October, D (-•-•) = 9 October, E (•—•) = 14 October (UBC profile).

TABLE 1.—Average prawn abundance per observer per 5 m depth increment observed in the depth range 20–124 m during the 4 days of observations, 6–9 October 1986. A = afternoon dive, E = evening dive, numbers in brackets = no. of ascents, no. of observers, < > = dead or dying.

Depth (m)	6 October A (2,1)	6 October E (2,2)	7 October A (1,1)	7 October E (2,1)	8 October A (1,1)	8 October E (3,2)	9 October A (3,2)	9 October E[1] (3,2)
20–24	0	0	0	1.5	0	0	0	—
25–29	0	0	0	1.5	0	0.5	0	—
30–34	0	0	0	3.5	0	0	0	—
35–39	0	0.25	0	4.5	0	0.5	0	—
40–44	0	1.00	0	2.5	0	2.0	0	—
45–49	0	2.0	0	2.0	0	0	0	—
50–54	0	2.5	0	0	0	0	0	—
55–59	0	7.0	0	0.5	0	0	0	—
60–64	0	10.0	1.0	1.0	0	0.5	0	—
65–69	0	14.25	0	5.0	0	1.0	0.6	3.0
70–74	1.0	[2]54.0	38.0	9.0	[2]80.0	2.0	[2]36.0	[2]80.0
75–79	[2]80.0	[2]80.0	0	[2]80.0	0	[2]80.0	[2]80.0 < 8>	[2]80.0
80–84	[2]80.0	[2]36.0	0	0	0	[2]16.0 <[3]18>	0 <[3]12>	[2]36.0 <[3]18>
85–89	0.5	1.0	0	0	0	0 <[3]30>	0 <[3]30>	0 <[3]30>
90–94	0.5	1.5	0	0	0	0 < [3]6>	0 <0.3>	0 <[3]12>
95–99	2.5	0.75	0	0	0	0	0	0 < 4>
100–104	2.0	0.75	0	0	0	0.3	0	0
105–109	2.5	2.75	0	0	0	0	0.25	0
110–114	3.0	4.25	0	0	0	0	0	0
115–119	2.0	0.25	1.0	0	0	1.0	0.25	0
120–124	0.3	1.5	0	0	0	0	0.25	0
Total alive	174.3	219.0	40.0	111.0	80.0	103.8	117.4	199.0
Total dead	0	0	0	0	0	54.0	50.3	64.0
Estimated mortality (%)	0	0	0	0	0	34	30	24

[1] No observations were made above 65 m on the evening of 9 October because of the entanglement of *Pisces* in submerged rope. Recorder equipment failure prevented inclusion of one of the observer's counts of prawn on some of the dives.
[2] Live prawn abundance was estimated >6 m^{-2}, but for purposes of analyses, 6 m^{-2} × 3 m^2 visibility was assumed, giving 18 prawn per meter of water depth.
[3] Dead prawn abundance was estimated >2 m^{-2}, but for purposes of analyses, 2 m^{-2} × 3 m^2 visibility was assumed, giving 6 dead prawn per meter of water depth.

parasitism (S. Bower[1]). Dead prawns, sometimes consisting only of exoskeleton remains, were observed at a density >2 m^{-2} in some areas. Apparently healthy prawns were concentrated in the depth range of 75–80 m at densities >6 m^{-2}. Dead and dying prawns were also observed during both dives on 9 October. By comparing the estimated numbers of dead and living prawns observed in a vertical transect, it was conservatively estimated that approximately 25% of the prawn population observed may have died during this 24-h period, with observations taken over 9 ascents along about 1.5 km of shoreline (Table 1).

Prawn was the only species observed to be dying. Apparently healthy amphipods, munids, and flatfish were observed around the dying prawns. However, coincident with the onset of prawn mortality, the vertical distribution of pink shrimp separated into two groups, one above and one below the depth range of prawn mortality (Fig. 1). No dead pink

shrimp were observed. Only amphipods were observed eating the dying or dead prawns.

Discussion

Our observations indicate that the tolerance of prawn to low DO$_2$ levels may be less than that reported from laboratory experiments. The tolerance of prawn in a sealed chamber (10°C, 30‰ salinity) to low DO$_2$ levels has been experimentally examined by Whyte and Carswell (1982). Under their experimental conditions, prawns exhibited a reduced metabolic rate at DO$_2$ levels below approximately 2.5 mL · L^{-1} and died at approximately 0.35 mL · L^{-1}. They did not determine how long prawns would survive at dissolved oxygen levels below 1 mL · L^{-1} since their experimental design included only a fixed amount of oxygen. Our study suggests that minimum tolerance occurs at around 1 mL · L^{-1} since at levels below this, death occurred. Oxygen stress in munids has been reported (Burd 1983) to coincide with a loss of equilibrium similar to the disoriented locomotor behavior we observed for

[1] S. Bower, Pacific Biological Station, Nanaimo, B.C., V9R 5K6, pers. commun. October 1986.

prawns. Based on our observations, we further note that prawns appear to be less tolerant to low DO_2 levels than many of the other species found in the same depth range. However, published data on tolerance to hypoxic conditions for the species present exists only for munids, which have been shown to tolerate hypoxic conditions as low as 0.1–0.15 mL $\cdot$ L^{-1} (Burd 1983; Burd and Brinkhurst 1984, 1985).

All benthic species observed, except prawn, had a relatively large depth range over which individuals were found in abundance. Those species apparently more tolerant to low DO_2 levels were found from about 85–210 m. It is unknown why in contrast to other species observed, prawns were concentrated in a narrow depth range at 70–85 m water depth, so close to lethal water conditions. Most prawns were apparently prevented from going deeper by intolerance to low DO_2 concentrations, although a few individuals were below this low DO_2 layer and, for the short term at least, were apparently surviving. At night, there was little change in the observed general depth preference of the main prawn concentration, although more prawns were observed at shallower depths. Prawns were not observed moving vertically on the cliffs in a directed manner, and so prawns observed at shallower depths at night may have been hidden there during the day.

With the sudden movement of low DO_2 water into the depth range occupied by prawns, it is unknown why prawns did not simply walk upwards on the cliff, away from the low DO_2 area, and stay in a tolerable environment, as did the pink shrimp. The distance prawns would have had to travel was <10 m in the 70–75 m depth range. Some vertical movement of prawns may have occurred, since in the afternoon dive prior to the evening dive in which dead prawns were first observed, the depth range in which prawns were abundant was narrow (5 m) and at its shallowest depth (70–75 m).

Two oceanographic factors apparently caused the observed prawn mortality: the existence of a low DO_2 water mass in close proximity to the prawns and some event which caused this water mass to intrude suddenly into the prawn habitat. As indicated earlier, the presence of oxyclines in Saanich Inlet is well documented, although the close proximity of prawns to this lethal environment had not previously been described.

We offer two possible explanations that could account for sudden intrusion of the anoxic layer: 1) change in the amplitude of oscillations of the oxycline, or 2) an overall change in level of the mean oxygen surfaces, perhaps related to a change in subsurface properties. With respect to the first, Thomson et al. (in press) showed that in Saanich Inlet, there are regular, peak-to-peak oscillations in DO_2 level of the order of 2.5 mL $\cdot$ L^{-1} at 100 m depth. These oscillations were found to occur over a period of hours, with a standard deviation and range of effective vertical isopycnal displacement estimated to be 2.0 and 9.6 m, respectively. Thomson et al. (in press) collected their data in April 1987, when the mean DO_2 level at 100 m was 4.8 mL $\cdot$ L^{-1}. If similar oscillations of the oxycline occurred during our observations, when DO_2 levels were much lower, then with a moderate change in oscillation amplitude, prawn could suddenly experience lethal DO_2 levels for time periods up to approximately 6 hours. The causal mechanism generating the oscillations and changes in amplitude of oscillation of the pycnocline, and hence oxycline, is currently unknown, but is probably due to internal gravity waves propagating within the inlet (R. Thomson[2]).

The second explanation involves a rapid change in average depth of the oxycline caused by changes in vertical density profile of the water column. Intermediate depth waters outside Saanich Inlet are most dense in the fall, and intrusion of this denser water over the sill into the inlet typically occurs at this time (Pickard 1975). Such intrusions are often caused by strong tidal influxes, and fluctuations in depth of the pycnocline and oxycline subsequently propagate down the inlet as a density intrusion (Holbrook and Halpern 1982). Any intrusion has the potential of suddenly altering oxygen concentrations at various depths. The observation of mortality beginning in late afternoon on 8 October is in agreement with that expected based on the daily and hourly timing of tidal action seen during the study period.

Prawn mortality as described would thus appear to be an episodic, but perhaps not an uncommon, event in Saanich Inlet. It is probably a fall phenomenon, for the oceanographic reasons described above and since in other years, this was when the hypoxic layer was shallowest (Richards 1965; Tunnicliffe 1981; Burd and Brinkhurst 1984). Our observations clearly demonstrate that sudden catastrophic mortality can occur on a scale which may noticeably affect species abundance in an area. If undocumented, such episodic mass mortality may confound an understanding of species population dynamics. For fishermen in the area, mortality of prawn is a concern and may explain why seasonal landings may

not meet expectations. Understanding the timing and likelihood of such events can improve management, and since the geographical occurrence of such mortality may often be quite localized, increased harvest in specific locations prior to high natural mortality events might be justified.

Acknowledgments

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MORPHOLOGICAL DIFFERENCES BETWEEN TWO CONGENERIC SPECIES OF PLEURONECTID FLATFISHES: ARROWTOOTH FLOUNDER, *ATHERESTHES STOMIAS*, AND KAMCHATKA FLOUNDER, *A. EVERMANNI*

The two flatfishes of the genus *Atheresthes* (family Pleuronectidae) are commonly caught in the eastern Bering Sea commercial trawl fishery. From 1977 to 1983, they comprised an estimated 10.03% of the total flatfish catch by the foreign trawl vessels in the Bering Sea/Aleutian Islands region (data compiled from U.S. Foreign Fisheries Observer Program, Northwest and Alaska Fisheries Center). However, these two species, the arrowtooth flounder, *A. stomias*, and Kamchatka flounder, *A. evermanni*, are morphologically similar and hence difficult to distinguish. As a result, fisheries workers in the field often lump the two species or misidentify them. Because the two species may have biological differences not presently known, it is important for management considerations and stock assessments to distinguish the species in fisheries surveys. The objective of this paper is to describe gross morphological differences between the two species more explicitly, so that the two can be accurately identified in the field.

Norman (1934) thought that these two species of *Atheresthes* were so similar that eventually they were shown to be identical. However, based on electrophoretic evidence, Ranck et al. (1986) concluded that *A. stomias* and *A. evermanni* are valid species. Wilimovsky et al. (1967) previously had reached this same conclusion by using a special morphological character index to separate the two species. This index is a function of caudal vertebrae number, gill raker number, distance from anterior eye margin to dorsal origin, and eye diameter. Unfortunately, the index is too complex to use in the field because it is based partly on characters that cannot easily be evaluated by gross external examination. This study describes a simpler method for differentiating the two species based on previously described external morphological characteristics and two new morphological characters.

Methods

Collections were made in the eastern Bering Sea in an area between lat. 54° and 59°N, long. 163° and 174°W (Fig. 1) aboard the National Marine Fisheries Service RV *Chapman* in summer 1984.

Specimens were unselectively sampled in the field from trawl catches containing *A. stomias* and *A. evermanni*. The fork length and sex of the fish along with location of sample were recorded, and each specimen was preserved in 3.7% seawater/formaldehyde solution.

In the laboratory, the following characteristics were examined:

1) Upper eye position: Specimens were first classified according to the position of the upper eye, following Norman (1934). If the orbit of the upper eye interrupted the profile of the head (Fig. 2A), the specimen was classified as *A. stomias*. If the upper eye did not interrupt the profile of the head (Fig. 2B) and was completely on the right side of the head, the specimen was classified as *A. evermanni* (Norman 1934; Wilimovsky 1967).

2) Gill raker counts: After initial separation of the specimens on the basis of the upper eye position, the four gill arches of the eyed side were removed and the gill raker count of each of the four arches recorded. Counts of the upper and lower limbs were recorded separately and the two counts were separated by a plus sign (for example, 4+12 means 4 rakers on the upper limb and 12 on the lower limb). If a gill raker straddled the angle of the arch, it was included in the count of the lower limb. In this study, only the lath-shaped structures were counted as gill rakers; the rudiments were not counted.

Results

A total of 251 fish was examined. Based on the upper eye position, 170 specimens were classi-