In Collaboration with
the Netherlands Institute for Sea Research

Journal of Sea Research 50 (2003) 87–95

JOURNAL OF SEA RESEARCH

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Aspects of distribution, transport and recruitment of Alaska plaice (*Pleuronectes quadrituberculatus*) in the Gulf of Alaska and eastern Bering Sea: comparison of marginal and central populations

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Received 25 November 2002; accepted 25 May 2003

Abstract

Shelikof Strait in the Gulf of Alaska appears to be near the extreme warm southern end of the spawning range of Alaska plaice (*Pleuronectes quadrituberculatus*). The spawning location, larval transport, and retention in the nursery area are documented from analysis of historical ichthyoplankton surveys of the region. Data from juvenile and adult trawl surveys were analysed to characterise the nursery areas. Aspects of the spawning distribution, population dynamics and juvenile nursery habitat characteristics in the Gulf of Alaska were compared with those in the primary area of its distribution in the eastern Bering Sea. In the Gulf of Alaska, concentrated spawning appears to be localised on the narrow shelf between 50 to 100 m depth on the north flank of the Shelikof Strait Sea Valley and in several other areas. Larvae drift downstream with prevailing currents. Most juveniles are located in water less than 50 m deep over a mud or sand bottom. Over its range, the mean biomass of plaice is related to the amount of suitable juvenile nursery bottom habitat. The abundance of the marginal Gulf of Alaska population is more variable than the main stock of the eastern Bering Sea. Because the continental shelf in the Gulf of Alaska is narrow and suitable habitat is fragmented, it is proposed that the population of Alaska plaice in the Gulf of Alaska is limited by recruitment to suitable nursery habitat, and that there is a dynamic interplay between the landscape ecology and larval drift due to highly variable currents.
Published by Elsevier B.V.

Keywords: NE Pacific Ocean; Gulf of Alaska; Flatfish; Transport; Nursery; Recruitment

1. Introduction

The linkage of currents during the larval drift period with the landscape of the seafloor, including the topographical and sediment characteristics that determine settlement habitat, is a key feature in the dynamics of flatfishes. Flatfishes often have highly specific habitat requirements for their juvenile and adult stages (Gibson, 1994). Since most marine flatfishes have planktonic egg and larval stages, they drift with currents for periods of weeks to months; larvae depend on features of currents to either retain

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1385-1101/$ - see front matter. Published by Elsevier B.V.
doi:10.1016/S1385-1101(03)00064-9

them or transport them to suitable nursery areas. In regions characterised by a landscape of suitable habitat, fragmented by barriers of unsuitable habitat such as deep sea valleys and canyons, colonisation and recruitment are likely to depend on larval drift rather than movement of juveniles or adults across such barriers.

Alaska plaice is an abundant species in the northern North Pacific Ocean that is lightly harvested, mainly as bycatch in other fisheries. It is a slow-growing and long-lived flatfish that has specific habitat requirements, including availability of certain prey types. Alaska plaice lives on flat mud or sand bottom and feeds on sessile infauna, mainly polychaetes and other worms (Zhang, 1987). The range of Alaska plaice in the east Pacific Ocean is restricted to the Chukchi Sea, Bering Sea and northern Gulf of Alaska (Wolotira et al., 1993). As a consequence of its narrow habitat requirements and limitations on the extent of such habitat, McConnaughey (1994) characterised plaice as a species whose range does not expand with increasing numbers.

The Gulf of Alaska, as a habitat for Alaska plaice, is remarkably different from their main habitat on the eastern Bering Sea shelf, even though they are at the same latitude and are separated only by the narrow land mass of the Alaska Peninsula. The continental shelf of the Gulf of Alaska is narrow (65–175 km) and is swept by the Alaska Coastal Current (ACC) over the shelf and the Alaskan Stream in deeper water (Fig. 1). The ACC is one of the most vigorous and variable coastal currents on the planet, reaching speeds to 100 cm s^{-1}. Sediment types in the region are highly variable, with rocky areas, troughs and sea valleys separating areas of sand and mud bottom. The result is a highly fragmented landscape of habitat for Alaska plaice. By comparison, the continental shelf of the eastern Bering Sea is broad (>500 km) and currents over the middle shelf area are weak (< 10 cm s^{-1}). Most of the bottom habitat types of the inner and middle shelf regions are vast expanses of sand and mud.

In the central Gulf of Alaska, Alaska plaice appears to be at the warm end of its distributional range. An

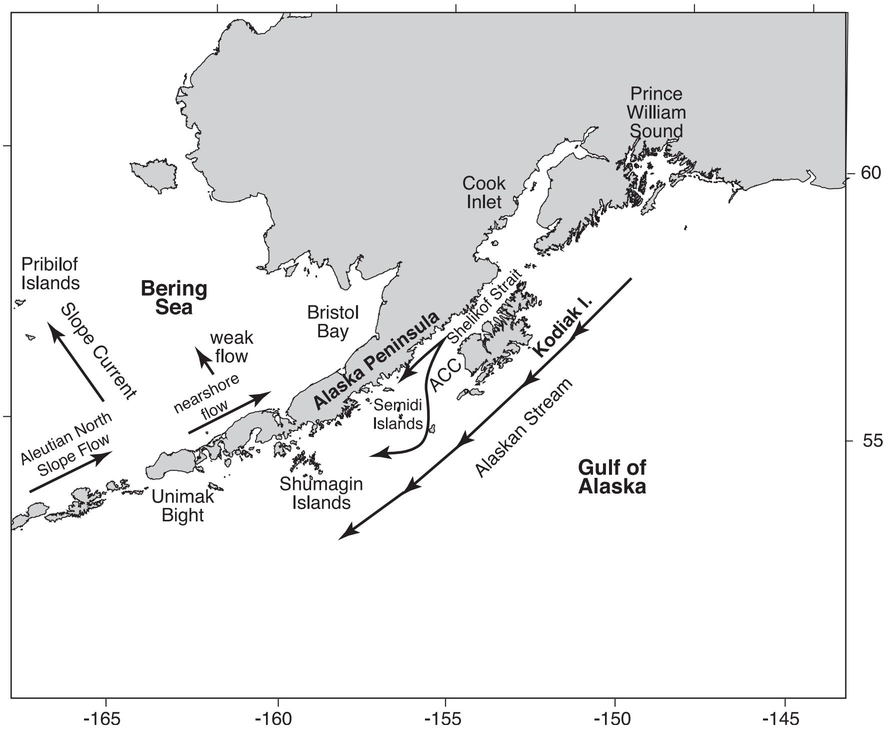

Fig. 1. Currents and physical features of the Gulf of Alaska and eastern Bering Sea.

analysis of trawl survey catches dating back to 1912 showed no catches of Alaska plaice east of about 140°W in the northern Gulf of Alaska (Wolotira et al., 1993). Over the continental shelf in the northern Gulf of Alaska, bottom water temperatures are typically 4–8 °C, but may get as low as 2 °C in some years. By contrast, in the eastern Bering Sea at the centre of its range, plaice commonly live in water colder than 0 °C. These cold bottom water temperatures occur over the middle shelf of the Bering Sea due to formation of a cold water pool (− 1.5° to 2 °C) during winter when surface ice is present and persist through the summer period.

In general, stocks living on the extreme end of their distribution tend to have more variable recruitment and abundance, either due to fluctuating rates of survival in marginal conditions, or due to movement of the population in a changing environment (McCall, 1990; Miller et al., 1991). The discovery reported here of a small spawning stock of Alaska plaice in the central Gulf of Alaska provided a unique opportunity to examine the distribution and dynamics of a population at the margin of its spawning range. We document distributional aspects of the early life history of Alaska plaice in the Gulf of Alaska and compare it to that in the eastern Bering Sea. Juvenile nursery habitat is characterised by depth and bottom sediment type. Population variability across the species' range is examined. Based on our results, we develop the hypothesis that the population abundance and variability of plaice in the Gulf of Alaska is related to the fragmented landscape of narrow shelf habitat that is suitable nursery habitat for juvenile plaice; the recruitment to this habitat by pre-settlement juveniles may vary from year to year depending upon variability in currents and delivery of plaice larvae to the nursery area. This limitation would not appear to be as strong a factor in recruitment of Alaska plaice in the eastern Bering Sea.

2. Methods

Ichthyoplankton data for this study were obtained from a 20-year time series of cruises conducted by the Alaska Fisheries Science Center (AFSC) or jointly with Soviet, Korean and Japanese fisheries research agencies. In the Gulf of Alaska extensive cruises occurred in 1972, 1978, 1979 and 1981 to 1998. Appropriate cruises were selected from our database (ICHBASE) of over 100 cruises based on seasonal and geographic coverage and included 7866 tows. Survey coverage of the eastern Bering Sea included 2744 tows.

Ichthyoplankton were sampled mainly with bongo nets (60 cm) and in a some instances Tucker trawls (1 m). A few neuston and Mocness collections were included. All net tows were quantitative and oblique and conducted in a standardised manner using flowmeters. Samples were preserved in 5% formalin and later sorted to species and measured at the Plankton Sorting and Identification Center, Szczecin, Poland.

Data on juvenile Alaska plaice were available from the small-mesh trawl surveys for shrimp conducted by the National Marine Fisheries Service (NMFS) and Alaska Department of Fish and Game (ADF&G) in the Gulf of Alaska from 1953 to 1999. Most surveys were conducted from May to October. A variety of trawls with small-mesh gear were utilised, but from 1972 onward, high-opening trawls with 32 mm stretched-mesh were used. The data base contains information collected on 8996 trawls. Length information on individual Alaska plaice caught in the trawls was not collected. The distribution of juveniles was calculated from catches where the average weight (from the total weight and numbers of all Alaska plaice in each trawl) was less than 0.5 kg, the approximate weight of a 30-cm fish at about the length at sexual maturity (Zhang, 1987). Unfortunately, this criterion tends to exclude catches where juveniles and adults may occur in mixed catches; therefore, the overall distribution of juveniles is conservative. Distribution of Alaska plaice juveniles was also examined from Alaska plaice caught in NMFS groundfish surveys using a variety of trawls, including data from triennial surveys described below. Only fish less than 30 cm were included. The total number of tows analysed for juvenile distribution in the Gulf of Alaska numbered 16 894 and in the eastern Bering Sea numbered 4691.

Data on adult fish distribution were available from the NMFS trawl data described above. For comparisons with the Bering Sea, triennial National Marine Fisheries Service summer groundfish surveys in the Gulf of Alaska from 1984, 1987, 1990, 1993, 1996 and 1999 were used. These surveys represent extensive coverage of the Gulf of Alaska shelf, and included 3846 trawls. The gear used was consistent for between-year comparisons in the Gulf of Alaska (modified poly Nor'eastern net with roller gear and a 32 mm mesh liner in the codend). For comparison of abundances in the Bering Sea, data from the same years were selected from the annual trawl surveys; however, the trawl was an 83–112 eastern trawl with no roller gear. This net configuration is probably somewhat more efficient at catching flatfish. For examination of distribution in the Bering, all annual data, 1971–2001, were used and included 9391 trawls.

3. Results

3.1. Distribution of adults

Based on catches of Alaska plaice in the collection of bottom trawl surveys, the adult distribution in the Gulf of Alaska was mainly centred in bays and in shallow water around Kodiak Island, and in bays and water between the 50–100 m isobaths along the south side of the Alaska Peninsula (Fig. 2a). A few large but highly localised catches have occurred in Kamishak Bay in lower Cook Inlet and near Kayak Island in the eastern Gulf. Small catches have been made in Prince William Sound.

In the eastern Bering Sea the largest catches were broadly distributed in the middle shelf region between 50 and 100 m, although some relatively large catches occurred inshore of the 50 m isobath (Fig. 2b). Catches were generally small in water deeper than 100 m and north of about 62°N.

3.2. Egg and larval distributions

In the Gulf of Alaska, relatively high density and persistent catches of Alaska plaice eggs were located inshore of the 100 m isobath along the north flank of the Shelikof Strait Sea Valley (Fig. 3a). Lower density catches were found along the south flank of the sea valley and in shallow water along the Alaskan Peninsula. Several incidences of large catches were found near the Shumagin Islands and Unimak Pass. These areas may be under-represented in the sampling of eggs due to the timing of surveys. Most surveys of the Alaska Peninsula occurred in May, perhaps later than the main spawning period. No catches of Alaska plaice eggs were found north or east of Kodiak Island.

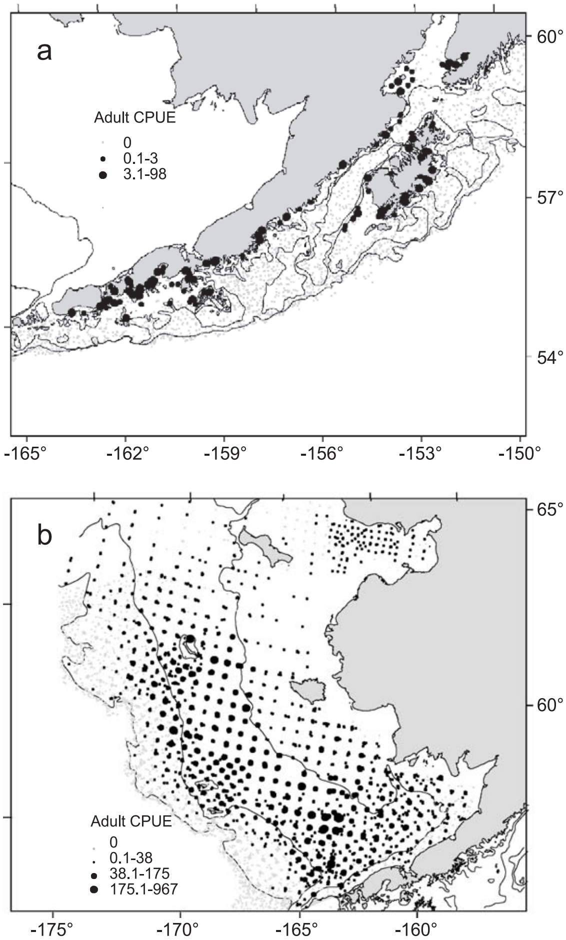

Fig. 2. Distribution of all Alaska plaice from NMFS triennial bottom trawl surveys. (a) Gulf of Alaska, 1984 to 1999. Also shown are the 100 and 200 m isobaths. (b) Eastern Bering Sea, 1971 to 2001. Also shown are the 50, 100 and 200 m isobaths. CPUE is kg/distance fished (km).

In the eastern Bering Sea, eggs are spawned in the middle shelf region between the 50 and 100 m isobaths, and at several locations along the northern side of the Alaska Peninsula near the 50 m isobath (Fig. 3b).

The highest catches of Alaska plaice larvae were located along the northern flank of the Shelikof Strait

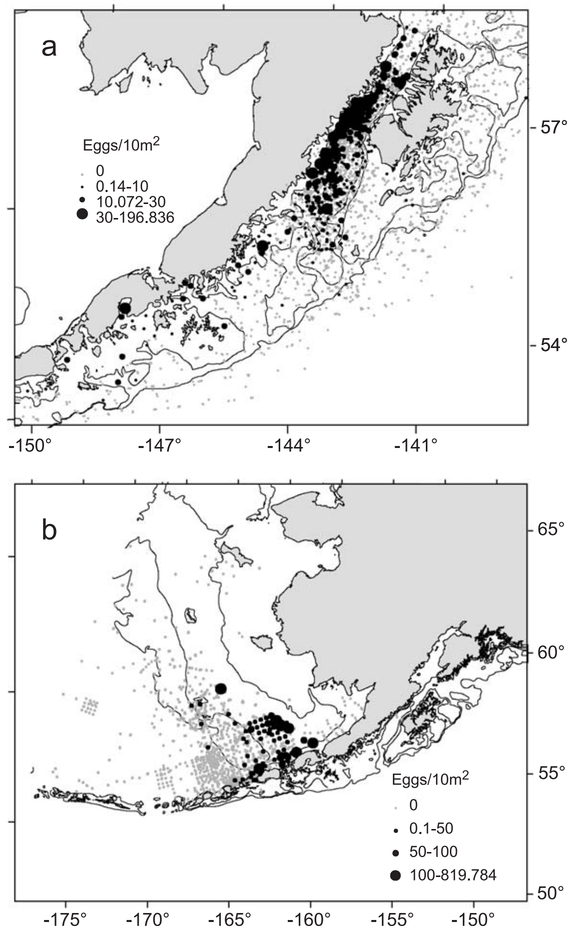

Fig. 3. Distribution of Alaska plaice eggs in NMFS ichthyoplankton surveys conducted from 1972 to 1998 during the period from March 1 to May 15 (a) in the Gulf of Alaska, (b) in the eastern Bering Sea.

Sea Valley, extending into the centre of the sea valley (Fig. 4a). Relatively small catches of plaice larvae were found downstream of the Semidi Islands, and only one catch of plaice larvae was recorded east of Kodiak Island despite extensive survey coverage.

Analysis of the mean size (mm SL) of larvae by region shows that the smallest plaice larvae were located in the Shelikof Strait Sea Valley, consistent with our interpretation of the main spawning region from egg distributions. Currents in this region are strong, with persistent eddies in the sea valley which may retain larvae for a period; in the lower sea valley there are several locations where the current penetrates onto the shelf. Plaice larvae were consistently found to be larger as distance from the spawning region increases, indicating downstream transport. The largest mean sizes were found in shallow water along the Alaska Peninsula, over the Trinity Islands shelf on the south end of Kodiak Island and in deep water offshore, indicating three transport pathways from the main spawning area.

A break in the larval mean size occurs over the shelf between the Shumagin and Semidi Islands (indicated by a lighter shading of blocks in Fig. 5). The smallest larvae in this grouping were located

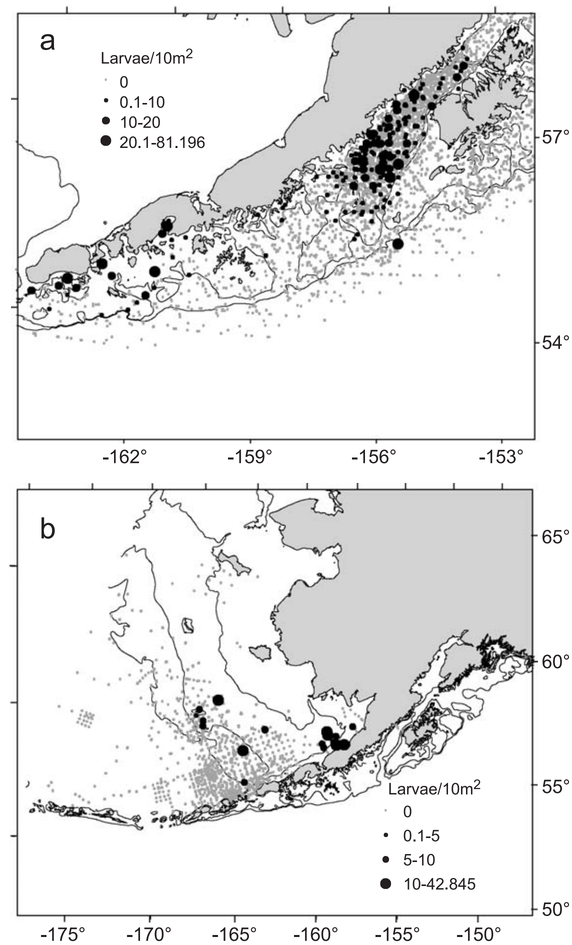

Fig. 4. Distribution of Alaska plaice larvae in ichthyoplankton surveys conducted from 1972 to 1998 (a) in the Gulf of Alaska, (b) in the eastern Bering Sea.

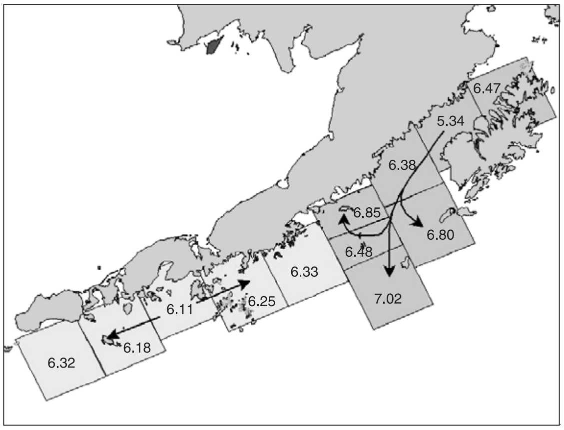

Fig. 5. Mean size (mm SL) of Alaska plaice larvae by region in the Gulf of Alaska. The potential dispersal routes of larvae are shown by the heavy lines with arrows.

around the Shumagin Islands, which we interpret to be the centre of another spawning region. As currents are weak in the shallow water of the shelf in this region, dispersal of larvae may not be strongly directional and may spread to either side of the spawning region.

Ichthyoplankton survey coverage in the eastern Bering Sea is less extensive, and in particular the middle shelf has not been thoroughly surveyed. However, larvae appear to be relatively rare there. Some larvae have been found somewhat northwest of the middle shelf spawning area near the Pribilof Islands. There is another aggregation of larvae that has apparently drifted from the spawning area towards outer Bristol Bay (Fig. 4b).

3.3. Juvenile distribution and nursery characteristics

Both the ADF&G small mesh trawl surveys and the NMFS bottom trawl surveys showed the same patterns in juvenile distribution, so catches were combined (Fig. 6a). The highest density catches were located around Kodiak Island and along the inner shelf of the Alaska Peninsula downstream of the Shelikof Strait Sea Valley. Large catches of juvenile plaice were also found along the Alaska Peninsula near the Shumagin Islands and in lower Cook Inlet. Relatively small but persistent catches were seen in Prince William Sound and in the northern Gulf.

In the eastern Bering Sea, large catches of juveniles were located north of Bristol Bay near the 50 m isobath and shallower, and some small catches have been made near the 100 m isobath close to the Pribilof Islands (Fig. 6b).

The inner shelf regions of the Gulf of Alaska and eastern Bering Sea were mapped for sediment characteristics and depth to compare with juvenile plaice distribution. The area of the shelf that was composed of mud and/or sand shallower than 50 m depth is shown as the shaded area in Fig. 7. Large catches of

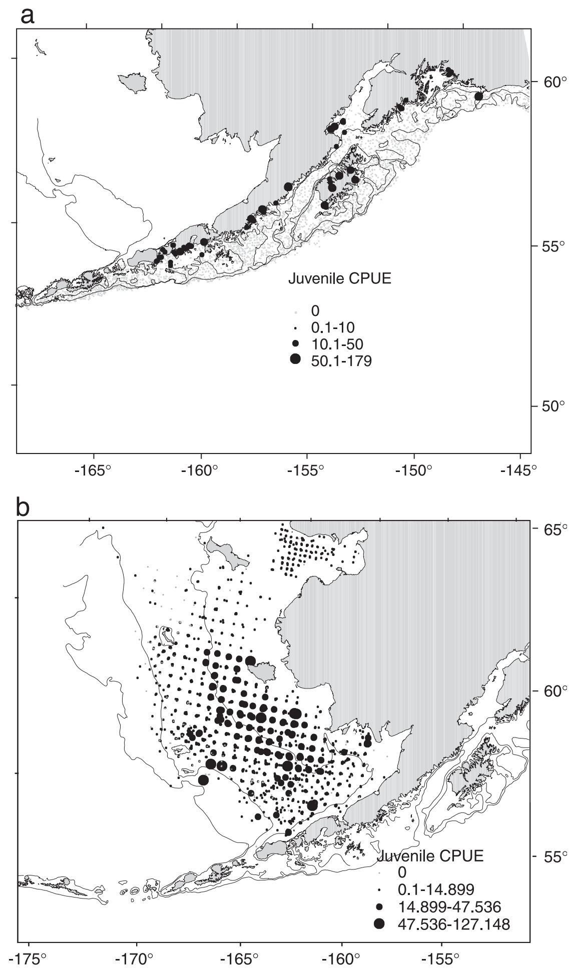

Fig. 6. Distribution of juvenile Alaska plaice (< 30 cm length) in trawl surveys conducted by ADF&G and NMFS, 1953 to 1999, (a) in the Gulf of Alaska, (b) in the eastern Bering Sea. CPUE is kg/distance fished (km).

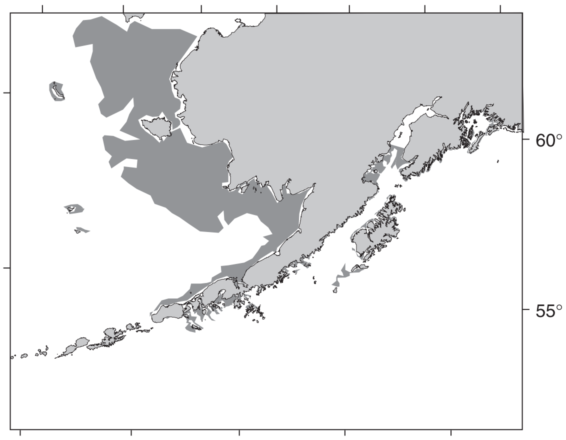

Fig. 7. Habitat characterised as mud and/or sand sediment in water shallower than 50 m depth in the eastern Bering Sea and Gulf of Alaska (hatched areas).

juvenile plaice were concentrated in the shallow mud/sand habitat. The sediment characteristics of the Bering Sea were also examined and the area of suitable nursery habitat was defined as above for comparison to the Gulf of Alaska. By comparison, the area of suitable juvenile habitat is continuous and extensive in the eastern Bering Sea.

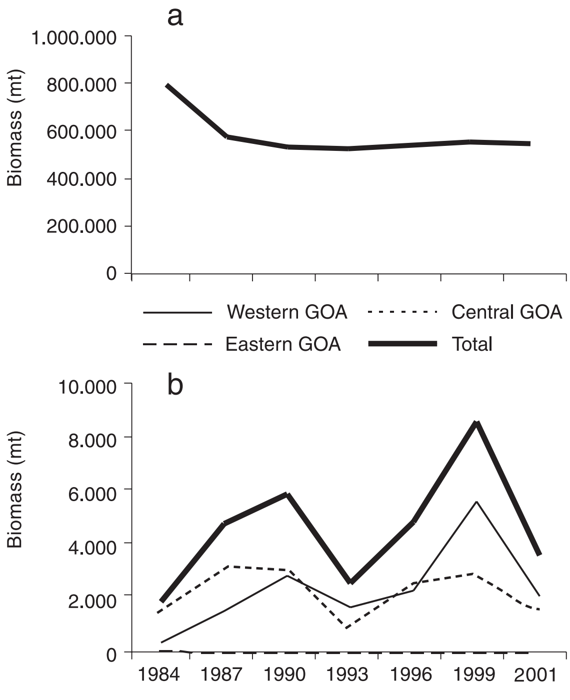

Fig. 8. The abundance of Alaska plaice in NMFS research trawl surveys for the same years: (a) in the eastern Bering Sea, and (b) regions of the Gulf of Alaska. Note: the biomass for the eastern Gulf of Alaska is near the axis.

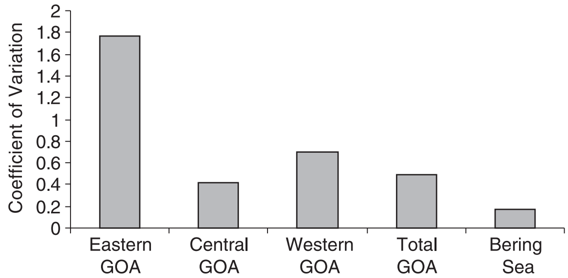

Fig. 9. Coefficient of variation of stock biomass of Alaska plaice over the same years in different regions.

3.4. Macro-ecology

Comparison of stock biomass estimates from NMFS triennial surveys over the same years shows that the Alaska plaice stock in the Bering Sea is about 2 orders of magnitude greater than the total stock in the Gulf of Alaska (Fig. 8a, b). The western and central Gulf of Alaska regions have similar size populations, while the eastern Gulf population is minimal. A comparison of the coefficient of variation shows that the eastern Gulf of Alaska population is extremely variable, while over the same period the Bering Sea population has been very stable (Fig. 9).

The average stock biomass in different regions was compared to the amount of suitable juvenile habitat within each area. There appears to be a strong

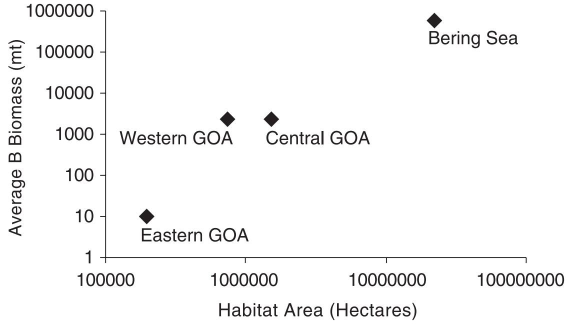

Fig. 10. Relationship between stock biomass and available nursery habitat for juveniles in regions of the Gulf of Alaska and eastern Bering Sea.

relationship between the average stock biomass and the area of suitable juvenile habitat (Fig. 10).

4. Discussion

Alaska plaice in the northern Gulf of Alaska spawn mostly on the northern side of the Shelikof Strait Sea Valley. Most large catches of eggs were caught over water depths of 50–100 m. Larvae drift downstream in the near-shore portion of the ACC and over the shelf region near the Semidi/Sutwik Islands; however, a large number of larvae were distributed in the middle sea valley, apparently being transported away from shallow nursery areas, and presumably into unfavourable outer shelf habitats or into the Alaska Stream. In spite of potential flushing of larvae, spawning persists along the north flank of the Shelikof Strait Sea Valley. The high productivity of that locality, coupled with the successful delivery of a sufficient portion of the larvae to suitable settlement habitats inshore, is likely to favour the area as a spawning ground for plaice. Juveniles are found around Kodiak Island and downstream along the southern shelf of the Alaska Peninsula. The widespread distribution of the population in summer surveys and the broad distribution of juveniles downstream combined with the highly localised spawning region, as determined by the distribution of eggs, indicate a potential spawning migration to the northern side of the Shelikof Strait Sea Valley.

Other spawning areas in the Gulf of Alaska are located around the Shumagin Islands and in the Unimak Bight. In limited surveys in the northern Gulf of Alaska, plaice eggs have not been found, but based on the occurrence of juveniles, small spawning populations may exist in Prince William Sound and in the eastern Gulf of Alaska.

By comparison, in the eastern Bering Sea, spawning occurs across the broad middle shelf between 50–100 m and along the Alaska Peninsula near the 50 m isobath based on egg distributions. Data on larval plaice are less extensive, but from surveys conducted since the reports of Zhang (1987), most plaice larvae are caught in outer Bristol Bay and near the Pribilof Islands. Eggs and larvae along the Alaska Peninsula are transported into outer Bristol Bay by a near-shore coastal current. Transport in the middle shelf region is weakly towards the north, carrying larvae onto the northern inner shelf region.

There is only restricted information on the distribution of small post-settlement juvenile plaice. In surveys of several bays around Kodiak Island and limited coverage of the Alaska Peninsula, B. Norcross (University of Alaska Fairbanks, pers. comm. summer 2002) reported finding young juvenile plaice in bays on the north side of Kodiak Island. From the distribution of larger juveniles (<30 cm) from RACE trawl surveys and from ADF&G small mesh trawl surveys, it appears that almost all juvenile plaice are caught in waters <50 m depth over mud and/or sand sediments. The area of the shelf comprised of this nursery habitat type is fragmented and restricted in extent, and consequently represents a small target for drifting larvae. The mud and sand bottom type is fractured by numerous sea valleys, troughs and rocky bottom that are likely barriers to dispersal of the benthic post-settlement stages of plaice.

In contrast, the area of suitable habitat over the eastern Bering Sea shelf is continuous and much greater than that of the Gulf of Alaska. According to Zhang (1987), Alaska plaice in the eastern Bering Sea are almost entirely distributed in waters <110 m, spawning occurs in spring over depths of 75–100 m, and juveniles <20 cm are located in water <25 m. From examination of RACE trawl catches, juveniles <30 cm are located in water near the 50 m isobath or shallower, although there is a group of juvenile plaice in deeper water near the Pribilof Islands. The presence of larvae in outer Bristol Bay, in conjunction with the apparent absence of older juveniles, indicates either active or passive (with currents) movement towards the northwest shelf.

The time trend of plaice stock biomass in the Gulf of Alaska is highly variable compared to that in the centre of its distribution in the eastern Bering Sea. This result presents an interesting exception to the species range hypothesis, which states that variability in recruitment of flatfishes should be least near the centre of the species range, highest at northern latitudes, and intermediate at southern latitudes (Miller et al., 1991). In the case of Alaska plaice, latitudes of the Bering Sea and Gulf populations are essentially similar, while the temperature, landscape and currents are greatly different. Leggett and Frank (1997) also found that recruitment data for several flatfish species were inconsistent with the species range hypothesis, arguing for density-independent control of recruitment, dominated by environmental factors operating on a local scale. For Alaska plaice, available habitat and larval delivery appear to be critical in examining species population variability. Availability of suitable juvenile nursery habitat corresponds to mean stock and (inferred) recruitment levels, as found for other flatfish species (Rijnsdorp et al., 1992). The interplay of the landscape ecology of nursery habitat with larval delivery further complicates latitudinal comparisons. In the Gulf of Alaska, the landscape of suitable juvenile habitat is fragmented by troughs, sea valleys and rocky areas. Delivery of larvae into suitable nursery areas is unpredictable due to the highly variable ACC. A large portion of larvae may be swept through the Shelikof Strait Sea Valley into the Alaskan Stream. In the Bering Sea, juvenile plaice habitat is continuous and currents are either weak (over the middle shelf) and favouring retention or are strongly directional towards suitable juvenile habitat (along the Alaska Peninsula). We propose that larval delivery to nursery grounds in the eastern Bering Sea is not as variable or as critical a factor in recruitment compared to the Gulf of Alaska.

Alaska plaice in the Gulf of Alaska appears to be living at the edge of its distribution range. As such, plaice in this region are likely to be more vulnerable to factors affecting population fluctuations than their counterparts in the eastern Bering Sea. In particular, the effects of subtle changes in climate, such as warming episodes (1–2 °C) due to El Niño or low frequency decadal oscillations (Pacific Decadal Oscillation), are likely to be pronounced at the population level and could contribute to stock variability due to variations in survival or distribution shifts; therefore enhanced monitoring of these marginal populations may be instrumental as harbingers of climate change.

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