The Role of Estuarine Hydrodynamics in the Distribution of Kelp Forests in Kachemak Bay, Alaska  *

G. Carl Schoch  * and Hélène Chenelot  ³

*Kachemak Bay National Estuarine Research Reserve
2181 Kachemak Drive
Homer, AK 99603, U.S.A.

²45 O’Neill Building
School of Fisheries and Ocean Sciences
University of Alaska Fairbanks
Fairbanks, AK 99775, U.S.A.

ABSTRACT


Understanding the circulation and exchange rates of water masses in an estuary is critical to understanding the movement and recruitment patterns of planktonic propagules and how these patterns relate to the distribution and abundance of adults. Forests of bull kelp (Nereocystis luetkeana) are complex three-dimensional habitats that can support tightly linked trophic interactions between primary producers, herbivores, and carnivores. Therefore, the spatial distribution of this important habitat can affect local food webs. Kelp forests in Kachemak Bay, Alaska, were mapped from 2000 to 2002 using low-altitude aerial photography. Over the 3 years, kelp forests were found only in the outer basin, and only a few attached sporophytes were found in the turbid and lower-salinity inner basin. Many biotic and abiotic factors can affect the dispersal and development of kelp. We tested the hypothesis that decreased salinity and light intensity in the inner basin limit the spatial distribution of Nereocystis sporophytes in this system. Transplant experiments were conducted between the marine and estuarine endpoints of kelp forest distribution. These experiments suggest that the growth of Nereocystis sporophytes transplanted from the marine to the estuarine endpoint was impeded, but that they could survive under estuarine conditions. We tested a second hypothesis, that estuarine circulation patterns control Nereocystis sporophyte distribution. Hydrographic measurements and circulation studies suggest that a strong baroclinic jet develops in the late summer and fall and may prevent Nereocystis spore dispersal into the inner basin. The cyclonic surface circulation in the outer basin may contribute to the observed spatial distribution of kelp forests in this system.

ADDITIONAL INDEX WORDS: Nereocystis luetkeana, spore dispersal, distribution, baroclinic currents, fjords, estuarine circulation, salinity gradient, light intensity.

INTRODUCTION

Kachemak Bay is located in the northern Gulf of Alaska (GOA) at about 59°35'N (Figure 1) and is the only fjord in the National Estuarine Research Reserve System (NERRS). The bay has an area of 1,500 km², a shoreline length of over 540 kilometers, and a maximum tidal range of 8 meters. The mountains on the south side of the bay reach over 2,000 meters and are composed of rocky terrains accreted onto the continental plate margin in association with marine plate subduction processes. Seven glaciers discharge into Kachemak Bay and deliver a large volume of freshwater and sediments during the summer that decrease the salinity and increase the turbidity along the axis of the estuary. The bay is separated into two basins (inner bay and outer bay) by a 6-kilometer-long spit extending southeast from the village of Homer (population 5,000). The bathymetry is characterized by deep trenches and holes extending to depths of 200 meters. The benthic nearshore habitat of both inner and outer basins of Kachemak...
Bay consists of rocky headlands, seastacks, and reefs along the south shore. The north shore of the outer basin consists mostly of mixed boulder, cobbled, and sand, but mud flats characterize the north shore of the inner basin. Kelp forests dominate the nearshore of the outer basin in depths less than 20 meters but have not been observed in the inner basin.

The circulation and water mass properties of Kachemak Bay reflect estuarine, oceanic, and atmospheric forcing. Atmospheric conditions are primarily established by the interaction of cyclonic (counterclockwise) storms associated with the Aleutian Low and the coastal mountains surrounding the GOA, leading to very high rates of coastal precipitation (ROYER, 1998; WILSON and OVERLAND, 1986). Much of this precipitation is presumed to enter the ocean relatively rapidly because of the steep terrain, except in the winter season, when it is stored in mountain snowpacks. Coastal freshwater discharge increases gradually through spring and summer because of melting of the snowpack, reaching a maximum in the fall (ROYER, 1998; WEINGARTNER et al., 2002).

Kachemak Bay is strongly influenced by the seasonal and interannual patterns of the Alaska Coastal Current (ACC). Farther offshore, the mean wind field associated with the Aleutian Low drives the cyclonic flow of the Alaskan Gyre. Along the continental slopes of the GOA, this flow includes the broad and relatively sluggish Alaska Current in the eastern and northern Gulf (Figure 1). Over the inner shelf, downwelling favorable winds and freshwater discharge from the coastal mountains drive and maintain the ACC. The ACC originates on the British Columbian shelf and flows counterclockwise around the GOA (ROYER, 1998). Seasonal variations in wind and coastal buoyancy-forcing give rise to large changes in the strength and density structure of the ACC (JOHNSON, ROYER, and LUICK, 1988). October is a transition month, during which time the ACC evolves from its summer to its winter structure as winds intensify and runoff increases. Maximum near-surface currents are typically observed during the fall as winds intensify and coastal runoff reaches a maximum due to the strong baroclinic nature of the current at this time (JOHNSON, ROYER, and LUICK, 1988; STABENO, REED, and SCHUMACHER, 1995). Kachemak Bay communicates with the GOA through a bathymetric trough extending from Kennedy Entrance, through Lower Cook Inlet, and into the bay along the south shore. As the westward-flowing ACC encounters Kennedy Entrance, a portion of this current turns northward into Cook Inlet, and the remainder of the current...
continues west and then southwest through Shelikof Strait. Once in Kachemak Bay, the flow proceeds counterclockwise around the outer basin (Burbank, 1977).

The bull kelp (Nereocystis luetkeana) can form extensive kelp forests along the eastern Pacific coast from central California to the eastern Aleutians (Miller and Estes, 1989). Kelp forests are very productive ecosystems in the coastal ocean and are important shallow subtidal habitats. As substantial primary producers, kelp forests support an extensive food web, including invertebrates, fish, seabirds, and marine mammals (for review, see Foster and Schiel, 1985). Kelp forests are the prime feeding grounds for sea otters, a keystone species in this ecosystem (e.g., Duggins, 1980; Estes and Pal misano, 1974; Estes et al., 1998). The structural complexity of kelp forests provides critical refuges and nursery grounds for commercially and recreationally important fish and shellfish species (e.g., Bodkin, 1988; Carr, 1994; Enel ing and Laur, 1985). Nereocystis is the dominant canopy forming kelp in Kachemak Bay. The presence of Nereocystis in Kachemak Bay was documented in the late 1970s (Lees et al., 1980; Trasky, Flagg, and Burbank, 1977), and these reports indicated that Nereocystis plants were not found in the inner basin even though rocky habitat and bladed understory kelps occur there, such as Laminaria bongardiana, Laminaria saccharina, Agar um clathratum, and Pleurophycus gardneri. In this study, we address the overall question of: what limits Nereocystis kelp forests to the outer basin?

Factors that control Nereocystis kelp forest distribution are complex. Kelps, including Nereocystis, undergo heteromorphic alternation of generations (Figure 2). Conspicuous sporophytes produce sori, reproductive structures located on the blades that contain microscopic spores. Sori absi se from the blade and sink to the sea floor, releasing spores into the water column and on the bottom (Amsler and Neushul, 1989). Spores germinate into male and female gametophytes, and the zygotes produced by oogamous sexual reproduction grow into adult sporophytes. The establishment of kelp forests, therefore, requires the successful completion of these different phases of the Nereocystis life cycle. The ultimate distribution of Nereocystis kelp forests depends on biotic and abiotic factors that influence the annual dispersal of detached and drifting sporophytes, sori released by attached or drifting sporophytes, and spores released from sori. Furthermore, physical, chemical, and biological conditions at the settlement site can have a critical impact on the survival, growth, and successful reproduction of the different life stages.

The survival and successful development of spores, gametophytes, and sporophytes can be affected by many intricate processes, including biotic factors such as herbivory, competition for space, shading, fouling, and diseases (e.g., Dayton, 1985; Dayton et al., 1999; Duggins et al., 2001; Foster and Schiel, 1985; Reed and Foster, 1984) and abiotic factors such as nutrient concentrations, salinity, light intensity, temperature, turbidity, and sedimentation (e.g., Dayton, 1985; Dayton et al., 1999; Devinn y and Volse, 1978; Devy sher and Dean, 1986; Foster and Schiel, 1985; Kopczak, Zimmerman, and Krem er, 1991). Kelps, including Nereocystis, are generally restricted to marine habitats and are rarely found in areas of reduced salinity and high turbidity, such as estuaries (e.g., Dayton, 1985; Druehl, 1981). Salinity variation can affect algal growth, respiration, and photosynthetic responses (e.g., Bol ton, 1979; Gerard, Dubois, and Greene, 1987; Herbist and Castenholz, 1994). Few seaweeds are able to adjust their water and mineral contents to survive at low salinities, resulting in a decrease in algal occurrence toward brackish estuarine waters (Druehl, 1981). Light quality and quantity are known to affect photosynthetic responses and metabolic patterns.
The minimal light irradiance required for most kelp is approximately 1% of the light reaching the surface (LUNING, 1981). High turbidity levels can interfere with the penetration of sunlight through the water column, thus limiting the amount of irradiance available to gametophytes and young sporophytes (DREW and JUPP, 1976). The depth at which *Laminaria hyperborea* is found throughout Bantry Bay, Ireland, was found to decrease from the open sea to the head of the bay because of increased turbidity; the density and standing stock of the kelp were negatively correlated with the turbidity gradient (EDWARDS, 1980).

Weather patterns, local wave dynamics, and current velocities may play a significant role in the ultimate spatial distribution of kelp forests, especially in high-latitude ecosystems. For example, storms can increase the dispersal range of individual spores (REED, NEUSHUL, and EBELING, 1991), and the export of detached sporophytes from kelp beds on open coasts can also be significant. HARROLD and LISIN (1989) estimated export rates of *Macrocystis pyrifera* from Monterey Peninsula forests at 130,000 tons per year. Once detached from the substrate, reproductive sporophytes can drift with the wind and currents, potentially dispersing large numbers of spores over relatively long distances. This mechanism may assist in maintaining these species' geographic ranges as well as increasing genetic exchange between isolated populations (HARROLD and LISIN, 1989; LADAH, ZERTUCHE-GONZALEZ, and HERNANDEZ-CARMONA, 1999; VAN DEN HOEK, 1987). Although the dispersal of kelp spores is thought to be limited to a short distance around the parent plants, spores of some kelp species (e.g., *Macrocystis* spp.) have been observed to remain viable in the water column for several days (BRZEZINSKI, REED, and AMSLER, 1993; REED, AMSLER, and EBELING, 1992) and may be carried long distances by currents (e.g., NORTON, 1992; REED, LAUB, and EBELING, 1988; VAN DEN HOEK, 1987).

The spatial and temporal dynamics of kelp forests in Kachemak Bay have not been studied, and a better understanding of factors limiting the distribution of *Nereocystis* sporophytes to the outer bay would benefit our understanding of how this important habitat affects local food webs. In this study, we quantified the spatial distribution pattern of *Nereocystis* kelp forests for a 3-year period and focused on two hypotheses to help explain the absence of kelp forests in the inner basin of Kachemak Bay:

**H1:** Decreased salinity and light intensity of estuarine conditions determine *Nereocystis* sporophyte distribution.

**H2:** Estuarine circulation patterns determine *Nereocystis* sporophyte distribution.

The first hypothesis was tested by performing a transplant experiment of *Nereocystis* sporophytes between two sites along the salinity and turbidity gradient of the bay and by investigating the effects of estuarine conditions on their growth. The second hypothesis was evaluated by studying the hydrography of Kachemak Bay with water column profiles, the dispersal of drift cards, and the trajectory of satellite-tracked drifters.

**METHODS**

**Determining Interannual Variability of *Nereocystis* Sporophyte Distribution**

To quantify the interannual spatial variability of kelp forest distributions in Kachemak Bay, polygon maps were produced annually from 2000 to 2002. The coastline of the entire bay was flown, and aerial photographs were obtained of all *Nereocystis* kelp beds in late summer when plant growth was near maximum but before winter storms could dislodge mature sporophytes. Images were acquired with a Hasselblad 501CM camera (Gothenburg, Sweden) using ISO 100 color print film from an altitude of 200 meters during an extreme low-tide cycle and when the sun angle was near zenith. These images were individually rectified to digital orthophoto quadrangles. Each kelp bed was delineated by a polygon and incorporated into a Geographic Information System (GIS) vector data layer. Polygons were analyzed using analysis of variance (ANOVA) for among-year differences in size and density. Distributions from 2000 were used to define the estuarine limit of *Nereocystis* sporophytes.

**H1:** Decreased Salinity and Light Intensity of Estuarine Conditions Determine *Nereocystis* Sporophyte Distribution

Two study sites were chosen along the estuarine gradient of Kachemak Bay (Figure 3A). The sites were similar in terms of wave exposure (based on fetch for the prevailing westerly winds), current velocity, and substrate type. Port Graham (PGE: 59°22.270’ N, 151°53.728’ W) is located toward the open sea and is characterized by clear oceanic water. The kelp forests in Port Graham were dense...
and continuously distributed along a narrow band within the 20-meter bathymetric contour. In early July 2001, the blades and pneumatocysts of most plants were visible at the surface in 5 meters of water during low tide. Many juveniles about 1 meter long were distributed among the larger plants. Halibut Cove (HCE; 59°35.866' N, 151°16.141' W) is located in the inner basin, near the narrows formed by the spit, and characterized by more brackish water. The experiment site was located adjacent to an exposed rocky headland. The *Nereocystis* plants at this site in July formed a small (ca. 5 × 20 meters), patchy aggregation with no plants visible at the surface in 5 meters of water at low tide, and only a few scattered juveniles were observed among the larger individuals. This site

---

Figure 3. Generalized circulation pattern in Kachemak Bay, Alaska. (A) The location of experiment and sample sites. (B–D) Polygons representing the annual spatial distribution and areal extent of kelp beds from 2000 to 2002.
was selected because it is at the distribution limit of *Nereocystis*.

A transplant experiment was conducted in July and August 2001 to determine the effects of lower salinity and light intensity on the growth pattern and survival of *Nereocystis* in estuarine conditions. Four ground lines were placed end to end at a depth of 8 meters from mean lower low water (MLLW) at each site as shown in Figure 4. A total of 24 *Nereocystis* juveniles were collected from a 100-meter-diameter area surrounding PGE, and 12 juvenile plants were collected near HCE. The selected transplants had an average stipe length of 47.8 centimeters (± 1.3 centimeters; n = 36). The holdfast of each transplant was carefully woven through a soft nylon line and secured with cable ties on each side. This technique minimized abrasion on the stipes and holdfasts. The nylon line was secured to a small, labeled float equipped with a snap hook. This design had several advantages, because it standardized the substrate on which the holdfasts were secured (the small float). The flotation lifted the ground lines off the seafloor, thus preventing sea urchin grazing and potential effects of sedimentation. This design also minimized the handling of transplants underwater, because each float could easily be clipped onto the ground lines using the attached snap hook. On each ground line, plants were attached at intervals of 50 centimeters to mimic natural densities (Lees *et al*., 1980), with 12 from Port Graham and 12 from Halibut Cove at HCE, and 12 plants from Port Graham at PGE.

Water column profiles of salinity and downwelling photosynthetically active radiation (PAR) were conducted monthly (n = 3) near the Port Graham and Halibut Cove experiment sites using a caged Seabird SBE 19plus conductivity-temperature-depth (CTD) profiler (Bellevue, Washington) and a Licor Model LI-192SA quantum sensor (Licol, Lincoln, Nebraska). The salinity data were compiled into 1-meter depth bins and plotted. Salinity and PAR attenuation with depth relative to surface values were compared between sites using a t test.

Water samples were collected in July and August near each experiment site for analyses of nitrate (NO₃⁻), a major nutrient required for kelp growth. Considering the stratified summer water column in Kachemak Bay, on each occasion, three samples were collected from the surface water (1 meter below the surface) and three from the bottom water (1 meter above the bottom, at a depth of 8 meters at MLLW). Samples were filtered through a 0.45-micrometer disk filter and stored at −20°C until analyzed using standard methods (Armstrong, Stearns, and Strickland, 1967). A time series of light intensity and water tem-
perature was measured at each site during the experiment using data loggers attached to the ground lines (8 meters MLLW). Light intensity (Onset StowAway, Falmouth, Massachusetts) was measured hourly, and temperature (Onset Hobo, Falmouth, Massachusetts) every 15 minutes. The mean and maxima daily light values and the mean daily temperature values were compared between sites using a t test for paired samples. An additional time series of salinity was provided by the NERRS System-Wide Monitoring Program with instruments deployed in the outer basin near the village of Seldovia and in the inner basin near the end of the Homer spit (Sanger et al., 2002). YSI 6600 data loggers (Yellow Springs Instrument Company, Yellow Springs, Ohio), deployed 1 meter above the bottom in 8 meters of water, measured conductivity and recorded salinity at 30-minute intervals. The variation in daily mean salinity during the field experiment was compared between sites using a t test for paired samples.

Underwater stipe measurements were conducted weekly for 6 weeks using SCUBA. On each sampling event, the total stipe length was measured as the distance between the holdfast and the pneumatocyst. This technique of measuring the stipe length and elongation rates of kelp as a way of evaluating its development has been used in several other studies (Duncan, 1973; Maxell and Miller, 1996; Miller and Dorr, 1994; Nicholson, 1970). In this paper, only total stipe length for the 6-week transplant experiment will be reported. Other results will be detailed in another manuscript. A two-way ANOVA for repeated measures, followed by a Tukey test, was used to determine differences in stipe lengths among sites and origins (SAS Institute Inc., 1999).

H2: Estuarine Circulation Patterns Determine Nereocystis Sporophyte Distribution

Hydrographic data were collected along a north-south transect in the outer basin during the spring and fall to compare seasonal differences in vertical and horizontal structure of the water column (Oikonen and Howell, 2003). A 20-kilometer transect line was sampled every 2 kilometers using a caged Seabird SBE 19plus conductivity-temperature-depth (CTD) profiler. The temperature and salinity data were compiled into 1-meter depth bins and then plotted using Matlab (Mathworks, Inc., 2001).

To investigate the trajectory of dominant surface currents, we first used drift cards as a low-cost means to study and infer regional surface currents. Over 1,000 7- × 10-centimeter plywood drift cards were deployed near Port Graham along a 5-kilometer transect, perpendicular to shore, on three separate excursions in May, September, and March (3,000 cards total). We relied on the public and community volunteers to collect and report stranded cards, and in October 2001, a bay-wide beach walk by community volunteers provided a spatially comprehensive survey of stranded cards prior to the onset of winter storms.

We deployed satellite-tracked drifter buoys (Technocean, Cape Coral, Florida) near floating rafts of detached kelp on three separate occasions at approximately 2-week intervals during August and September to better understand the path and duration of successive trajectories. These buoys were released from the same approximate location in the outer basin near Port Graham. The drifters had a surface float with a global positioning system (GPS) receiver for positioning and telemetry electronics for communicating with the Argos satellite (Service Argos, Largo, Maryland). At regular intervals, the drifters communicated with the Argos satellite and uploaded hourly GPS positions, which were plotted on a map.

RESULTS

Determining Interannual Variability of Nereocystis Sporophyte Distribution

The distribution of kelp forests from 2000 to 2002 is shown in Figure 3B–D. Polygons representing the annual spatial distribution and areal extent of canopy kelp forests were analyzed for among-year differences. For the purposes of this analysis, a kelp forest was considered to be an aggregation of six or more Nereocystis sporophytes with a separation distance of no more than 5 meters. The number of aggregations varied from year to year (2000: 168; 2001: 138; 2002: 140). The areas of the smallest and largest aggregations were (respectively) in 2000: 139 m² and 64,008 m²; 2001: 294 m² and 41,261 m²; and in 2002: 181 m² and 40,819 m². Among-year density differences of individual kelp forests fluctuated significantly (2000: 3.86 plants/m²; 2001: 2.32 plants/m²; 2002: 3.77 plants/m²; p < 0.001). Kelp forests were more dense on the south shore than the north shore of the outer basin (south shore: 3.51 plants/m²; north shore: 1.22 plants/m²; p < 0.001). Over the entire bay, kelp forests were found consistently in the
same location during the 3-year study, but the total areas among years were significantly different (2000: 177,903 m$^2$; 2001: 146,073 m$^2$; 2002: 197,858 m$^2$; $p < 0.001$). The one exception where a major kelp forest was entirely absent over the 3-year study occurred off the end of the Homer Spit in 2001 (Figure 3C). This was the primary reason for the significant decrease in total area that year and is explained by the onshore migration of a very large sandbar that temporarily buried the rocky habitat (Adams et al., 2004). Although individual Nereocystis sporophytes and small patches of a few plants were observed on rocky reefs near Halibut Cove, kelp forests were not observed in the inner basin during this study.

**H$_2$: Decreased Salinity and Light Intensity of Estuarine Conditions Determine Nereocystis Sporophyte Distribution**

The water column profiles showed that PAR measured at the surface varied from 2,020 to 297 $\mu$mol/s/m$^2$ depending on cloud cover and time of day, and PAR measured at 10 meters varied between 314 and 40 $\mu$mol/s/m$^2$ and 59 and 12 $\mu$mol/s/m$^2$ at PGE and HCE, respectively. In terms of relative attenuation, only 8.7% ± 0.8% of surface PAR reached a depth of 10 meters at HCE, whereas 19.9% ± 1.5% of surface PAR was available at 10 meters at PGE (Figure 5A). The difference in PAR attenuation between the two sites was significant ($t$ value = 6.69; $p < 0.001$; $n = 11$). The mean summer salinity profile (Figure 5B) shows that surface salinities at Port Graham (30.1 ± 1.0 psu) were considerably higher than at Halibut Cove (24.9 ± 1.0 psu), but at 10 meters the salinities were very similar (Port Graham: 31.38 ± 1.0 psu; Halibut Cove: 31.30 ± 1.0 psu). The difference in salinities between the two sites was significant ($t$ value = 2.56; $p = 0.015$; $n = 11$). Furthermore, the halocline was at 2 meters near Port Graham and at 4 meters near Halibut Cove, suggesting that the plants at Halibut Cove were subjected to lower salinities at shorter stipe lengths than the plants at Port Graham.

The water samples collected in July and August at the surface (1 meter depth) and bottom (8 meters depth) were analyzed for nitrates (NO$_3^-$), and the mean values (± 1 standard error [SE]) are shown on Figure 5C. The difference in nitrate concentration between the two sites was significant ($t$ value = 6.75; $p < 0.001$; $n = 12$). Nitrate concentrations in the outer basin bottom water near Seldovia (5.10 ± 1.2 $\mu$M) were about twice the concentrations in the inner basin near Homer (2.16 ± 0.5 $\mu$M), and for the surface water, the nitrate concentrations in the outer basin near Seldovia (3.78 ± 0.5 $\mu$M) were about five times the concentration.
near Homer (0.66 ± 0.5 μM). These data suggest that the entire water column of the inner basin is nutrient diminished relative to the outer basin, but in particular the surface water in the inner basin is nearly depleted of nitrates.

The time-series measurements of water temperature and total light at each experiment site and salinity at the NERRS monitoring site showed consistently lower light and salinity in the inner basin, but little difference in mean (± 1 SE) water temperature between the inner and outer basins. The daily mean bottom water temperatures (Figure 6A) at PGE (9.8 ± 0.1°C) and HCE (9.7 ± 0.1°C) were not significantly different (t value = 1.92; p = 0.062; n = 38). However, HCE had significantly lower mean daily minima (8.4 ± 0.1°C) and higher daily maxima (11.7 ± 0.1°C) than PGE (9.5 ± 0.1°C and 10.0 ± 0.1°C, respectively). As a result, the daily variation was greater at HCE than at PGE (t value = 14.45; p < 0.001; n = 38).

Synchronous fluctuations in daily mean levels of total light between PGE and HCE suggest the overall pattern was dictated by similar variations in cloud cover and sun angle (Figure 6B). HCE received less than 74% of the light intensity measured at PGE. The summer daily mean light levels were 0.81 ± 0.03 log lumen/m² in Port Graham versus 0.68 ± 0.3 log lumen/m² at HCE (t value = 9.71; p < 0.001; n = 40). The same pattern was observed when comparing averaged daily light maxima (t value = 6.24; p < 0.001; n = 40). Salinity differences were found to be significant between basins (Figure 6C), with the mean salinity in the inner basin (31.39 ± 0.05 psu) lower than the outer basin (31.89 ± 0.02 psu; t value = 11.02; p < 0.001).

Kelp transplants were selected for size similarity and condition (47.6 ± 1.1 centimeters; F = 3.19; p = 0.082). Six weeks after being transplanted, the longest individual stipe measured 456 centimeters for a Halibut Cove transplant to HCE (the length was 48 centimeters when transplanted), and the shortest stipe was 43 centimeters for a Port Graham transplant to HCE (the length was 35 centimeters when transplanted). After 6 weeks, the total stipe lengths of Halibut Cove plants transplanted to HCE were the longest (228.2 ± 30.1 centimeters; n = 12), and Port Graham plants transplanted to HCE were the shortest (91.2 ± 16.6 centimeters; n = 10) (Figure 7). At HCE, Port Graham transplants grew relatively little compared to Halibut Cove transplants, and the difference between the two sets of plants was visible after only 2 weeks (46.6 ± 2.9 centimeters for Port Graham plants and 78.1 ± 4.5 centimeters for Halibut Cove plants on week 2; ANOVA; df = 1; p < 0.001 for weeks 2, 3, 4). After 6 weeks, plants collected from Port Graham and transplanted to HCE (91.2 ± 16.6 centimeters) were significantly shorter than Port Graham plants transplanted to PGE (170.1 ± 22.4 centimeters) (ANOVA; df = 1; F = 8.01; p = 0.011). Some Port Graham transplants died at both PGE and HCE over the course of the experiment, resulting in a sample size decrease from 12 to 10.
**H₂: Estuarine Circulation Patterns Determine Nereocystis Sporophyte Distribution**

Hydrographic transects were conducted in the spring and fall along the line shown in Figure 3A. The spring CTD profiles across the axis of the outer basin show the water column to be relatively well mixed (Figure 8A), with the north side of the bay being slightly more stratified than the south side. The fall profiles show the development of a strong gradient across the axis of the outer basin caused by less saline water stratified at about 15–20 meters within about 5 kilometers from the north shore (Figure 8B). This south-to-north density decrease will drive a westward-flowing geostrophic baroclinic current along the north shore of the bay. These data suggest that estuarine flow is maximized in the late summer and fall coinciding with peak freshwater discharges from the surrounding rivers, glaciers, and snowfields, and resulting in a westward-flowing baroclinic jet trapped against the north shore by Coriolis deflection.

The drift cards released from the outer basin were consistently not transported (i.e., recovered) into the inner basin during spring, fall, or winter. Figure 9A shows the release and recovery locations for all deployments. About 38% of the cards were recovered from the spring and summer deployments, but only 1% were recovered from the winter deployment. About 3% of the recovered cards were found on islands near the south shore, and 90% of the recovered cards were stranded on the north shore of the outer basin. About 5% of the recovered cards were found north in Cook Inlet, and less than 2% were found far to the south in Shelikof Strait.

Satellite-tracked drifter buoys were deployed on three successive occasions in August and September. None of the buoys entered the inner basin. All of the buoys followed a trajectory similar to Drifter #39,994 released on August 23 for a 2-week
The Role of Hydrodynamics in Kelp Distribution

Figure 9. (A) Recovery locations of drift cards released from a transect in the outer basin on three separate occasions in May, September, and March. Most of the cards stranded on the north shore of the outer basin, and some were advected out of the bay. No cards were transported into the inner basin. (B) Trajectory of one of three satellite-tracked drifters (Buoy 39,994) deployed in August. The results of these studies suggest that the circulation of Kachemak Bay may limit the exchange of surface water between the outer and inner basins. A density-driven surface current flows out of the inner basin, strengthening during the late summer and fall when freshwater runoff reaches a maximum. This provides a likely mechanism preventing drifting rafts of dislodged sporophytes from entering the inner basin. Deep-water (>20 meters) exchange still occurs at tidal frequencies, and kelp spores may be advected into the inner basin at depth.

DISCUSSION

Our study of interannual variability of Nereocystis kelp forests in Kachemak Bay showed that the total area of kelp forests varied significantly and that individual kelp beds varied in size and density. However, with the exception of one major kelp forest habitat that was overwhelmed by migrating sand, the kelp forests were consistent in terms of where they occurred from year to year. Kelp forests occurred along the south shore in narrow dense bands that reflect the steep bathymetry. The shallower bathymetry along the north shore of the outer basin provides more habitat, resulting in very large, but less dense, kelp forests. No kelp forests were observed in the inner bay during the 3-year study, although a small and sparse kelp aggregation was observed every year of the study at Halibut Cove. The kelp forests in Port Graham were continuous and considerably denser than the aggregations in Halibut Cove. We first tested the hypothesis that decreased salinity and light intensity of estuarine conditions determines Nereocystis sporophyte distribution.

The results of our Nereocystis sporophyte transplant experiments from Port Graham (the oceanic endpoint) to Halibut Cove (the estuarine endpoint) suggest a negative effect on growth. The transplants from Port Graham to the Halibut Cove experiment site grew less than the transplants from Port Graham to the experiment site in Port Graham. However, Port Graham transplants in Halibut Cove appeared healthy and robust and showed no signs of herbivory. The light levels (PAR in μmol/s/m² and total light in log lumens/m²) measured at the study sites showed that less light penetrates through the water column in Halibut Cove than in Port Graham, suggesting that the
slower elongation of oceanic plants in Halibut Cove compared to plants in Port Graham may be due in part to light attenuation (e.g., Dean and Jacobsen, 1984; Han and Kain, 1996; Luning, 1981). Lower salinity and lower nitrate levels may also have affected the performance of Nereocystis sporophytes in the inner bay. Although most transplants in Halibut Cove survived throughout the experiment, it is possible that those plants and the surrounding natural population were stressed by the estuarine environment and were more susceptible to other negative factors. By the end of the summer, sori were appearing on some transplants at PGE, although the transplants were behind compared to the natural population in Port Graham. Halibut Cove plants were still not reproductive in October during our final visit to the experiment site.

Conversely, higher salinity and light intensity in Port Graham were anticipated to promote kelp growth. But interestingly, the Halibut Cove transplants to the experiment sites at Halibut Cove grew faster than the Port Graham transplants at either site. These results suggest that plants from different origins may be adapted to grow best under the conditions at their original site. Several studies suggest that salinity and light levels different from where the individual grew have a negative impact on algal growth (Bolton, 1979; Duncan, 1973; Gerard, Dubois, and Greene, 1987), but it is difficult to disentangle the cause of phenotypic variability, especially in a wild population of unknown genotype, because both polygenic and environmental factors can be responsible.

Nereocystis stipe elongation is complex and is affected by many different factors, including light quality and quantity and nutrient availability (Duncan, 1973; Duncan and Foreman, 1980). Monitoring stipe length is an easy way of evaluating the influence of environmental factors, but it may not be directly related to productivity or reproduction success of kelp. The results of this study suggest that plants from different origins respond differently to estuarine conditions. Although Halibut Cove plants grew tall, they were not observed to develop to sexual maturity. More research is needed to determine the fitness level of estuarine plants. It is possible that Halibut Cove plants have adapted to grow faster to maximize exposure to the higher-quality light available only at the surface. Although this would be an intriguing direction for further research, for the purposes of this study, the estuarine conditions encountered in Halibut Cove were not sufficiently detrimental to prevent Nereocystis sporophytes from growing.

We also tested the hypothesis that estuarine circulation patterns determine Nereocystis sporophyte distribution. The hydrographic data from the CTD profiles confirmed the intensification of a baroclinic jet along the north shore of the outer basin in the late summer and fall. This current starts in the inner basin where most of the freshwater accumulates from glacial runoff. The jet intensifies in the narrows formed by the Homer Spit, and then Coriolis deflection forces the jet north against the north shore of the outer basin. The drift card recovery locations concur with these observations on the regional surface circulation. All drift cards deployed in the outer basin were recovered in the outer basin or were advected out of the system. None of the released cards were found in the inner basin. This was consistent with theArgos drifter trajectory, which followed the south shore until it was repeatedly rejected from the inner basin, and then advected with the baroclinic jet along the north shore.

These results suggest that the strong estuarine flow from the inner basin is a mechanism restricting surface water exchange between the outer and inner basins of Kachemak Bay. This mechanism may prevent rafts of dislodged Nereocystis sporophytes from dispersing into the inner basin. At this latitude, Nereocystis sporophytes mature in late summer or early fall, coinciding with the intensification of winter storm systems over the GOA. Many of the large sporophytes cannot withstand the drag imposed by higher waves and break free from their holdfasts. Important causes of detachment for large kelp sporophytes include actual removal by storm waves; weakening of aging holdfasts, which increases the potential for detachment during storms (Harrowd and Lisin, 1989; McPeak, Glantz, and Shaw, 1988); and grazing on the stipe by snails (Lacuna vinca; Duggins et al., 2001). Spores can be dispersed over great distances when rafts of free-floating sporophytes are carried by the prevailing circulation pattern (Harrowd and Lisin, 1989; Ladah, Zertuche-Gonzalez, and Hernandez-Carmona, 1999; van den Hoek, 1987). However, drifting rafts of reproductive sporophytes carried with the prevailing currents in Kachemak Bay may not be able to penetrate the barrier imposed by the strong estuarine flow conditions, and instead they are swept along the north shore by the baroclinic jet, similar to the trajectory of the Argos drifter. Yet this is not con-
sistent with the observed kelp aggregation at Halibut Cove. A possible explanation for this persistent patch is that the baroclinic jet may occasionally weaken under conditions of low freshwater input to the inner basin, and this may allow an episodic supply of reproductive drifting sporophytes to be advected into the inner basin. Spores may also be advected into the inner basin below the surface jet in the more tidally dominated subsurface flow. However, if this were a dominant process of connecting outer and inner basin kelp populations, then we would expect to see more kelp forests occupying the rocky reefs of the inner basin. Because the Halibut Cove transplants were not observed to reach the reproductive stage of development, it is possible that the local reproductive output is not sufficient to maintain and expand a large bed. It is likely that this population relies on an outside source for local recruitment. A sporadic and limited source of propagules for the inner bay may increase the chances of genetic isolation of the Halibut Cove aggregation. Further research into the genetic differentiation of Nereocystis populations between the inner and outer basins may reinforce this explanation.

CONCLUSIONS

There are many biotic and abiotic factors that act individually or in complex combinations to ultimately affect the spatial distribution of kelp forests. This study provides evidence that the distribution of Nereocystis kelp forests in Kachemak Bay is not solely limited by the negative effect of the estuarine environment on the growth of Nereocystis sporophytes. Furthermore, the distribution may be influenced, at least in part, by the circulation patterns causing surface water to be deflected from the inner basin by a strong surface current (i.e., baroclinic jet) leaving the inner basin during periods of high freshwater runoff. This surface current is sufficiently strong and consistent to prevent drifting debris, such as rafts of dislodged sporophytes, from entering the inner basin. However, spore dispersal by drifting rafts of sporophytes is only one of many mechanisms for spore dispersal. Recent work on the causes of spatial variation on the recruitment of benthic algae (Macrocystis pyrifera) suggest that spore dispersal rather than drifting fertile sporophytes may allow kelp recruitment from distant populations (Reed, Schroefer, and Raymond, 2004). If sinking sori or spores can penetrate the halocline in Kachemak Bay, thereby escaping the surface current, the tidally dominated subsurface currents could readily provide a transport mechanism into the inner basin.

Although the lower light, salinity, and nitrate concentration of the inner basin did not affect Nereocystis sporophytes sufficiently to prevent growth, the experiment did not evaluate these effects on productivity and reproductive output of sporophytes or on other stages of the kelp life cycle. Microscopic stages of kelp are known to suffer high mortality rates and are commonly considered the bottleneck phase of the kelp life cycle (Fletcher and Callow, 1992; Santelices, 1990). The germination of Nereocystis spores collected from Port Graham was observed to be impeded by low salinity, suggesting that spores may be more sensitive to estuarine conditions than sporophytes. These findings will be documented in another manuscript. Further work on the effects of salinity, light, and temperature on gametophyte development, gametogenesis, and sporophyte production would help determine other critical factors that ultimately dictate the distribution of Nereocystis kelp forests in Kachemak Bay.

The significance of our finding that the development of a seasonal baroclinic jet may impede the exchange of surface water relates to the importance of nearshore coastal habitats to juvenile and early life stages of many species of fish, invertebrates, and marine mammals. It is coastal and estuarine environments, such as Kachemak Bay and Lower Cook Inlet, that have been most affected by natural and human-induced sedimentation, contaminant delivery, and infrastructure development. Kachemak Bay has experienced the collapse and closure of several fisheries over the last 100 years, and interestingly, several of these exploited fisheries have been closed for over a decade but show little evidence of recovery. These include King crab (Paralithodes camtschaticus), Pacific herring (Clupea pallasi), shrimp (Pandalus spp.), urchins (Strongylocentrotus spp.), Dungeness crab (Cancer magister), and Tanner crab (Chionoecetes bairdi). Elders in the native village of Seldovia have noted the long-term decrease in density and size of Nereocystis kelp forests. Therefore, understanding the circulation and exchange rates of water masses is critical to understanding the movement and recruitment patterns of planktonic propagules and how these patterns relate to the distribution and abundance of adults. For example, the cyclonic circulation observed in the outer basin of
Kachemak Bay could be extremely important for localized movement of nutrients, drift debris, and planktonic organisms. This study provides evidence suggesting that the strongly stratified estuarine circulation patterns in Kachemak Bay result in a surface circulation pattern that favors planktonic propagule export over retention. Our findings in this study lead to a new hypothesis that weak retention of planktonic propagules in Kachemak Bay may explain the slow rates of recovery for adult populations, which are vulnerable to rapid depletion following a disturbance. The interacting physical and biological processes controlling species abundances and distribution in Kachemak Bay warrant further study to improve our understanding of variability in populations and community structure and our ability to manage economically important species.

ACKNOWLEDGMENTS

Steve Baird and Jenny Cope rectified the aerial photos and digitized the kelp beds. Steve Okkonen provided the CTD data with funding from the Coastal Marine Institute of the University of Alaska Fairbanks and Cook Inlet Regional Citizens Advisory Council. The satellite-tracked drifters were provided by Mark Johnson, who also graciously provided the trajectory plot, with funding from the Coastal Marine Institute of the University of Alaska Fairbanks and Cook Inlet Regional Citizens’ Advisory Council. We are very grateful for the support provided by these organizations and individuals. We thank the anonymous reviewers for comments that greatly improved an early version of this manuscript, and we sincerely appreciate the efforts of Michael Kennish for editing this special issue of JCR.

LITERATURE CITED


Journal of Coastal Research, Special Issue No. 45, 2004


