

## SPATIAL AND TEMPORAL RECRUITMENT PATTERNS OF DUNGENESS CRAB IN THE NORTHEAST PACIFIC

GLEN S. JAMIESON AND DAVID A. ARMSTRONG

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The Dungeness crab, *Cancer magister*, is the main crustacean species exploited in the northeastern Pacific from central California to Kodiak, Alaska. Abundance along the coast south of British Columbia has fluctuated in a generally cyclical manner which a number of studies have tried to explain, but several unrefuted competing hypotheses currently remain preventing resolution of this question. A combination of mechanisms seems a likely possibility and additional data appears necessary before understanding is achieved. There is general agreement that fluctuation in catch is a reflection of variable year-class strength and recent studies of larval and 0+ crab have investigated the importance of abiotic and biotic factors. Dungeness crab are regionally unique in that while many of their pelagic larvae move tens of kilometres offshore, they must return to shallow water to survive as juveniles. Oceanographic and meteorological conditions seem to be particularly influential in determining the magnitude of dispersal and onshore movement, and the conditions which allow successful settlement off Vancouver Island have now been described. Strong settlement does not necessarily equate with a strong year class at harvesting, though, and biotic factors primarily determine survival of juvenile crab. Finally, there is increasing evidence that the crab population in Georgia Strait and Puget Sound, i.e. in the 'inland sea' inside of Vancouver Island, may be a distinct stock with dispersal, recruitment and population dynamics characteristics unique from the population found on the open outer coast. Comparison of common features between the two stocks is allowing evaluation of the relative importance of major factors influencing population abundance and ultimately, landings. □ *Dungeness crab, Cancer magister, fishery, recruitment, larvae, dispersal, population dynamics, northeast Pacific.*

Glen S. Jamieson, Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, B.C., Canada, V9R 5K6; David A. Armstrong, School of Fisheries, University of Washington, Seattle, WA, USA 98195; 6 July, 1990.

Studies of larval and juvenile stages of commercial Decapoda have generally been done for purposes of describing ecology, reproductive biology, population dynamics, habitat requirements, and predator/prey relationships. While quantitative studies of catch-per-unit-effort (CPUE) and density have been used to estimate the next year's recruitment for incorporation into fisheries management plans, data have been rarely amenable for accurate predictions in excess of one year (Cobb and Caddy, 1989). Although predictive capability is a desirable aspect for management, in the case of Decapoda, this is often frustrated because of high seasonal and spatial variability, as well as tremendous interannual variability, caused by a suite of biotic and abiotic factors (Jamieson, 1986a, b; Botsford *et al.*, 1989). This is particularly the case for quantitative data on larvae, and such data are typically of limited use in definition of stock-recruitment relationships or prediction of ultimate year-class strength in the fishery.

Only a few attempts have been made to esti-

mate adult abundance from measures of larval abundance and female fecundity. Nichols *et al.* (1987) calculated female stock biomass of *Neptrops* lobster in the Irish sea from estimates of larval production and female fecundity and incorporated these data into a multi-species model of lobster and cod interaction. Application of this same technique was used by Nichols and Thompson (1988) to estimate stock size of the edible crab, *Cancer pagurus*. Similarly, Incze *et al.* (1987) accounted for significant differences in interannual densities of larval tanner crab (*Chionoecetes opilio*) based on quantitative changes in number of adult females. However, their suggested relationship did not hold in all years of their study, nor did it apply well to a congener, *C. bairdi*.

Use of indices of juvenile abundance in Decapoda to predict adult spawning stocks or relative strength of fisheries have only been developed successfully in a few instances. Relative year-class strength of juvenile rock lobster (*Panulirus cygnus*), as measured by an index of puerulus

settlement, was correlated to the strength of commercial fisheries four years later (Caputi and Brown, 1986; Phillips, 1986; Phillips and Brown, 1989). A similar approach was used in stock-recruitment analyses of blue crab (*Callinectes sapidus*) populations in Chesapeake Bay (Tang, 1985). A more thorough study was recently presented by Lipcius and Van Engel (1990) based on a thirty year time series of data, from which they concluded that a significant correlation exists between juvenile abundance and spawning stock size.

In this paper, we review recruitment of Dungeness crab, *Cancer magister* Dana, considering all three major life stages: embryo, larvae and juveniles. We define recruitment as abundance change between consecutive life history stages, culminating ultimately in an annual increase in abundance of the fished population since larger crabs only moult once annually. We emphasise recruitment to both larvae and juvenile life history stages, since these are periods of great mortality, and generally the times when relative year-class strengths at recruitment to the fishery are typically established for this species. Events progressively occurring throughout the life history cycle are discussed as these will bear on the abundance of crabs at each successive life history stage leading to recruitment to the fishery. We also consider recruitment in four major geographic regions: 1) the outer coast from San Francisco, California, to Cape Flattery, Washington; 2) off the west coast of Vancouver Island; 3) north of Vancouver Island to Kodiak Island, Alaska; and 4) the Georgia Strait-Puget Sound (GS-PS) complex. These specific locations were selected on the basis of broad-scale oceanographic boundaries, unique oceanographic singularities, and available data on local Dungeness crab population dynamics.

### DUNGENESS CRAB LIFE HISTORY

Dungeness crab ranges from the Pribilofs Islands to Magdalena Bay, Mexico, in the north-eastern Pacific (Hart, 1982; Jensen and Armstrong, 1987) and is commercially exploited from northern California to Kodiak, Alaska. This spatial distribution overlaps generally recognised oceanographic domains (Dodimead *et al.*, 1963; Thomson, 1981; Ware and McFarlane, 1989) for coastal areas of the northeastern Pacific Ocean, and this probably influences observed recruitment patterns and makes causative generalisations inappropriate for the coast as a whole.

Dungeness crab have a relatively long pelagic larval period, with five zoeal stages and one

megalopal stage before settlement to the benthos. Total larval period is about 110 days at ambient temperatures (Poole, 1966; Lough, 1976; Reilly, 1983), with about 28 days spent as megalopae (Hatfield, 1983). It is somewhat unique among nearshore benthic species in that a portion of its larvae is commonly found considerable distances offshore, with later stage zoea and early stage megalopae tending to be found furthest offshore (Reilly, 1983; Jamieson and Phillips, 1988; Jamieson *et al.*, 1989). Late intermoult stage megalopae are found in abundance progressively closer inshore (Hatfield, 1983; Jamieson and Phillips, 1988), but mechanisms which would bring megalopae located more than about 30–40 km offshore to appropriate nearshore locations (<64 m depth) for enhanced survival as juveniles (Carrasco *et al.*, 1985) have not yet been satisfactorily determined (Jamieson *et al.*, 1989). Offshore movement presumably facilitates larval dispersal, but it may be that most nearshore settlement results from those larvae which remained shoreward of region-specific, mostly as yet undetermined, oceanographic boundaries.

Most larval settlement is typically in May and June along the outer coast, with settlement in both estuarine and nearshore locations. Much recent study in Washington (Gunderson *et al.*, 1990) has been focused on the relative importance of some of the region's major estuaries (Willapa Bay and Grays Harbor, Washington), compared with the area shoreward of the 50 m isobath along the outer coast, in terms of their habitat contribution to overall regional recruitment. Juvenile dynamics of Dungeness crab in both these locations have been relatively well described, and it has become evident that considerable annual variation can occur. Female crab extrude their first egg mass as 2 y-olds at about 115 mm, notch-to-notch carapace width (CW), while males are larger than females at puberty and begin mating successfully at about 140 mm CW (3-y olds). Males mostly recruit to the fished population at 3–4 y of age.

### THE PHYSICAL ENVIRONMENT

#### REGIONAL CIRCULATION

The general surface current pattern over the continental shelf has been described by a number of recent reports, including Hickey (1979, 1989), Freeland *et al.* (1984), and Thomson *et al.* (1989). The west coast of Vancouver Island borders the bifurcation zone of the Subarctic Current, an extensive, albeit poorly defined, zonal flowing, cross-Pacific surface current (Fig. 1). Seaward of the continental shelf, this current

splits into the pole-ward flowing Alaska Current and the equator-ward flowing California Current. Direct observation of a persistent northward near-surface flow off Vancouver Island indicates that the offshore circulation there is dominated by the Alaska Current (Thomson *et al.*, 1989). Dungeness crab occur in two of the three principal oceanographic domains recognised by Ware and McFarlane (1989), namely the Coastal Upwelling and the Coastal Downwelling Domains (Fig. 2). The former extends from Baja California to the northern tip of Vancouver Island and is defined by the normal summer pattern of wind stress curl and Ekman divergence, i.e. upwelling (Parrish *et al.*, 1981). Generally north-west winds from May to September result in a southward-flowing Shelf-Break Current (SBC) centred on the outer margin of the continental shelf. This causes upwelling of intermediate depth, cold water onto the continental margin and offshore transport. Southwest winds dominate this Domain during the winter, causing downwelling, onshore transport and poleward transport of surface waters in a seasonal current called the Davidson Current. The annual transition between the predominantly upwelling and downwelling seasons occurs in the spring (Mar.–Apr.) and fall (Sept.–Oct.) with the seasonal reversal in prevailing alongshore winds and currents (Thomson *et al.*, 1989).

The Coastal Downwelling Domain extends from the northern tip of Vancouver Island northward along the coast of southeast Alaska and then westward along the Aleutian Islands. The Alaska Current flows adjacent to the coast of North America seaward of the coastal margin, being driven by a wind stress curl and augmented by freshwater addition and an along-shore, wind-induced sea level gradient. Freshwater runoff causes a poleward flowing coastal current, extending to about 40 km offshore. The transition in prevailing coastal winds in the spring is weak, but due to the general behaviour of the cyclonic meteorological systems in the region, wind stress tends to augment the baroclinic component of the coastal circulation by confining it close to shore. As a consequence, from central British Columbia north to about Kodiak Island, there is a generally persistent downwelling except for a few months in the summer (Ware and McFarlane, 1989). The southern boundary of this Domain is not sharply defined from a strictly oceanographic viewpoint.

The continental shelf off Vancouver Island, although not a recognised Domain itself, being part of the Coastal Upwelling Domain, has a unique oceanographic feature which for Dungeness crab makes this area intermediate between

the two Domains discussed. The outflow from Juan de Fuca Strait, being of lower density runoff from rivers entering the GS–PS complex, forms the source of the Vancouver Island Coastal Current (VICC). This is a persistent pole-ward flowing coastal current, confined mostly landward of the 100 m isobath on the continental shelf, that extends to about the northern tip of Vancouver Island (Thomson *et al.*, 1989). After the spring transition, this current flows counter to the prevailing northwesterly winds along the outer coast and the Shelf-break Current while after the fall transition, it flows with and merges with the Davidson Current.

#### TOPOGRAPHY

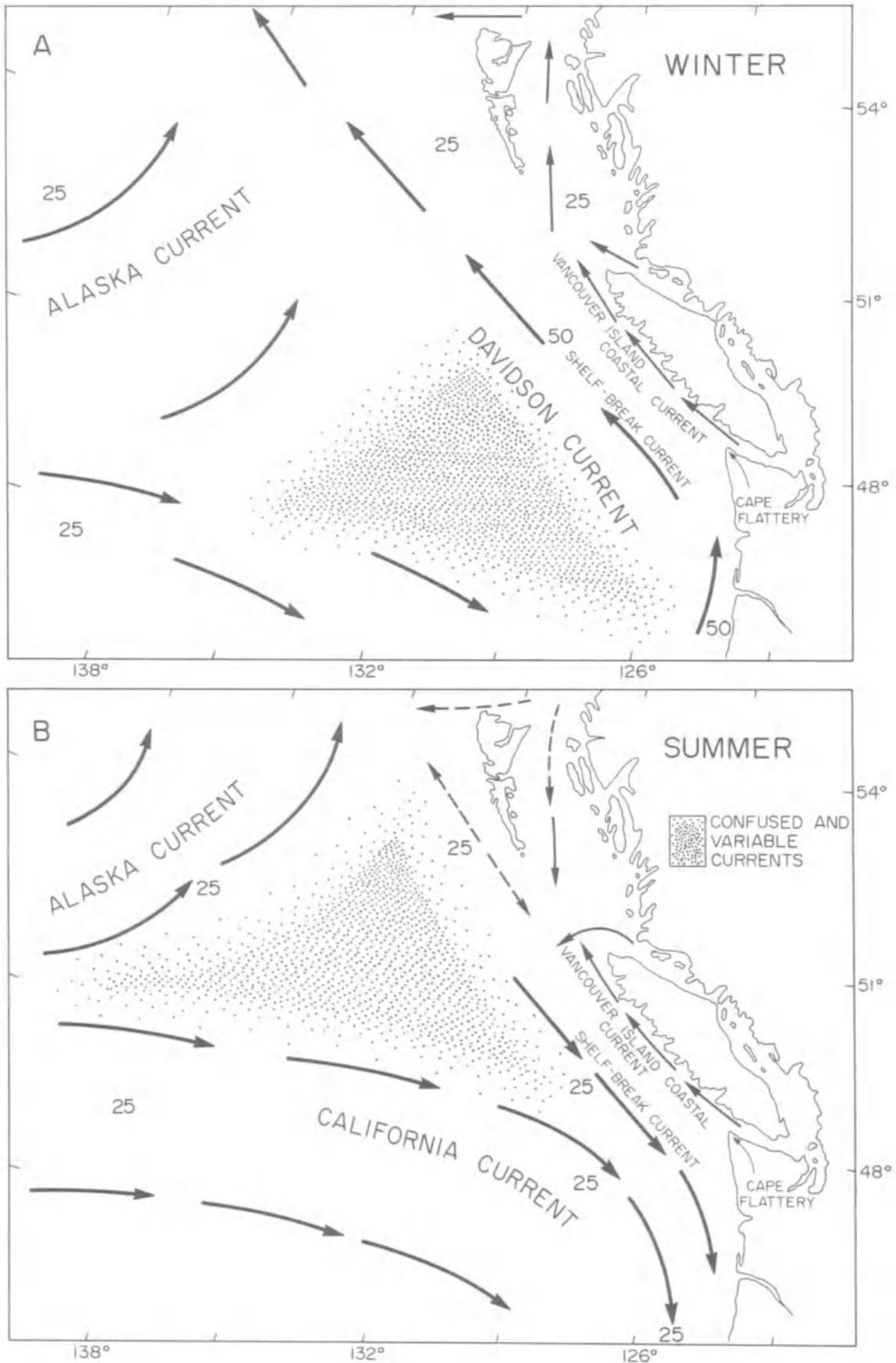
Washington, Oregon and California typically have broad, extensive, sandy beaches extending for scores of kilometres, with few bays or headlands. The coast of British Columbia and southeast Alaska is mostly rocky and fjordal, with many headlands, islands, small bays, and relatively small, crescent-shaped beaches. Dungeness crab most commonly occur in a habitat of extensive sand, and so available optimal habitat is generally less north of Washington State.

Georgia Strait and Puget Sound consist of a variety of habitats, with fjordal inlets predominant on the eastern side in Canada and gently sloping, gravel-sand bottoms predominant in Puget Sound and the southeastern side of Vancouver Island. The Gulf and San Juan Islands are in the middle of this region and have mostly steep, rocky shores, which are of marginal suitability to the Dungeness crab.

### LIFE HISTORY STAGES AND THEIR RECRUITMENT

#### PARENT POPULATION AND FECUNDITY

The extensive pelagic larval duration of Dungeness crab in areas of strong along-shore ocean currents apparently prevents development of discrete, genetically distinctive populations on the outer coast (Soule and Tasto, 1983). There is no evidence to suggest that crab larvae have the navigational ability to 'home' and return to the specific location where they were hatched. In the Coastal Upwelling Domain, larvae hatch in January–February during a period of strong, northward-flowing nearshore currents, which about two months later typically reverse to flow equally strongly in a southerly direction. With an approximately four month larval period, this may result in extensive larval dispersal. Larvae hatching off northern California could theoretically move as far north as British Columbia before currents reverse. Similarly, larvae hatch-



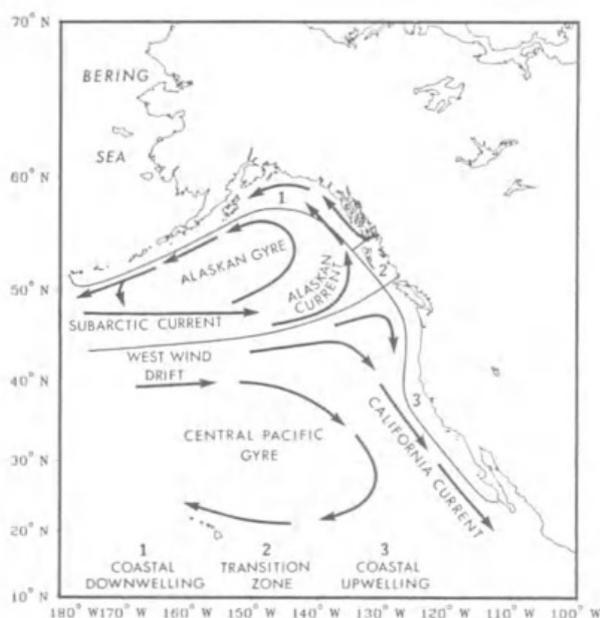


FIG. 2. Approximate areas of oceanic domains and prevailing current directions in the northeast Pacific Ocean (modified from Ware and McFarlane, 1989).

ing near the southern boundary of the Coastal Downwelling Domain could move to its northern boundary, while larvae hatching in the northern part of the Coastal Upwelling Domain could move into the Coastal Downwelling Domain, entirely because of passive transport. The consequence is that considerable mixing of progeny hatched at different sites probably occurs, making it impossible to clearly identify the parent population of juveniles that recruit at any particular location. As discussed by Jamieson (1986a), the extent to which a local population may contribute to local recruitment is unknown, but it appears with available data to be slight.

It is illegal to harvest female Dungeness crab in Alaska, Washington, Oregon and California. Although this can legally be done in British Columbia if females exceed the minimum legal size (MLS) of 155 mm CW (= 165 mm, spine-to-spine carapace width), in practice, few are harvested because of poor market demand, since meat yield is less, and there is a general lack of sufficiently large female crab. The size limit for males, although not known to be based on any documented biological data, presumably allows successful mating to regularly occur since in most locations many female crab caught during the winter carry extruded, fertilised eggs (Jamie-

son and Armstrong, unpubl.). Jamieson (1986a) discussed in detail the available data supporting assumptions relating to crab fecundity, and concluded that if maximising reproductive potential is an identified goal, then insufficient data are presently available to establish what relative level of progeny production is being achieved. Nevertheless, although commercial landings have varied substantially over time (Fig. 3), detailed surveys of larval occurrence (Jamieson and Phillips, 1988; Jamieson *et al.*, 1989; Jamieson, unpubl.) have consistently found widespread high levels of larval abundance over the continental shelf off Vancouver Island and Washington, and in Georgia Strait in the five years studied to date. Annual settlement of larvae has varied substantially during this period (Jamieson *et al.*, 1989), suggesting that factors other than overall larval production are the major determinants in establishing year-class strengths.

#### LARVAL SETTLEMENT

Some Dungeness crab larvae occur at great distances offshore and while this no doubt facilitates and/or is the result of species dispersal, there is always the risk of larval wastage in that many larvae may never return successfully to geographic areas favourable to juvenile survival. It has not been established how far offshore most larvae which do settle and survive have actually gone, but the relative lack of early-stage megalopae, in abundance, in close proximity to shore in outer coast areas, at least off British Columbia and Washington (Jamieson *et al.*, 1989; Jamieson, unpubl.), does suggest that movement in at least the kilometre scale can be expected. Assumed aspects relating to this have been discussed in detail by Jamieson *et al.* (1989), and they, along with Jamieson and Phillips (1988), have demonstrated that juvenile recruitment patterns off the outer coast of Vancouver Island, British Columbia, are substantially different from that off Washington, Oregon and California (Fig. 3).

Outflow from rivers emptying into the GS-PS complex is predominantly through surface outflow in Juan de Fuca Strait, and this outflow, the VICC, subsequently moves northward adjacent to the coast of Vancouver Island. Crab megalopae are virtually absent in this current and are concentrated on its seaward boundary (Jamieson and Phillips, 1988; Jamieson *et al.*, 1989). It thus apparently acts as a barrier to the movement of plankton to shore (Thomson *et al.*, 1989), and

FIG. 1. Prevailing surface circulation off the British Columbia-Washington coast. A, winter. B, summer. Broken arrows indicate uncertain currents. Numbers give speeds ( $\text{cm s}^{-1}$ ) (modified from Thomson, 1981).

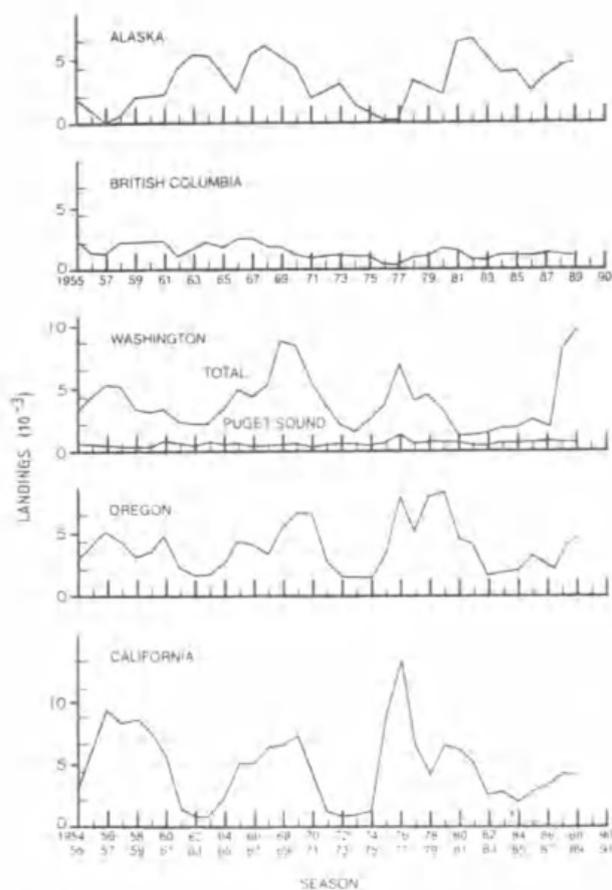


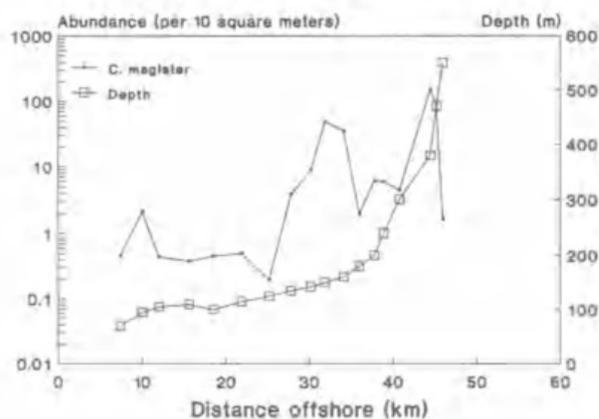
FIG. 3. Dungeness crab landings by political jurisdiction off western North America.

recent study by Jamieson and Thomson (unpubl.) indicates that megalopae are being concentrated in an area of upwelling and/or seaward surface current movement of relatively low velocity ( $1-5 \text{ cm sec}^{-1}$ ) between the VICC and the SBC (Fig. 4). Shoreward movement of surface waters is associated with southerly winds (Fig. 5) but unless sufficiently intense or prolonged, such movement is only to the seaward boundary of the VICC. The presence of the VICC seems to direct most up-welled water offshore, while because of the shallow depth of the nearshore portion of the continental shelf, no shoreward movement beneath the VICC is possible. The only apparent opportunity for substantial movement to the shore is when the VICC temporarily breaks down because of cessation of the surface outflow in Juan de Fuca Strait, which is typically associated with sustained, strong southerly winds. This is accompanied by a rise in mean coastal sea level, enhanced wind and convective mixing of surface waters and the cessation of upwelling — events similar to those which occur during and after the Fall Transition (Thomson *et al.*, 1989). From a crab recruitment,

major recruitment on the west coast of Vancouver Island is thus only possible when appropriate meteorological events occur when megalopae are present and ready to settle, namely May and June (Jamieson and Phillips, 1988). This does not always occur, and since 1983, major crab settlements at Tofino, British Columbia, were only observed in 1983 and 1989 (Smith and Jamieson, 1989a; Jamieson, unpubl.). Little settlement occurred from 1985 to 1987, while there was only limited settlement in 1988.

South of Cape Flattery, located at the southern, seaward end of Juan de Fuca Strait, the absence of a 'barrier' current adjacent to the coast means that settlement is not physically impeded by nearshore currents, although years of excep-

### Line G, June 1989



### Line E, June 1989

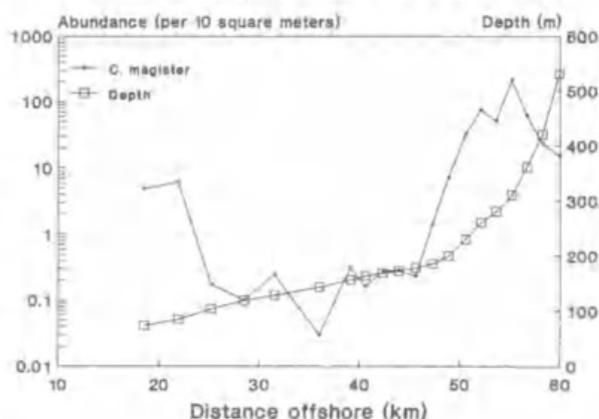


FIG. 4. Abundance of Dungeness crab megalopae in across-shelf transects in relation to depth. The north-flowing Vancouver Island Coastal Current is mostly shoreward of 100 m depth, with the south-flowing Shelf-Break Current on the seaward side.

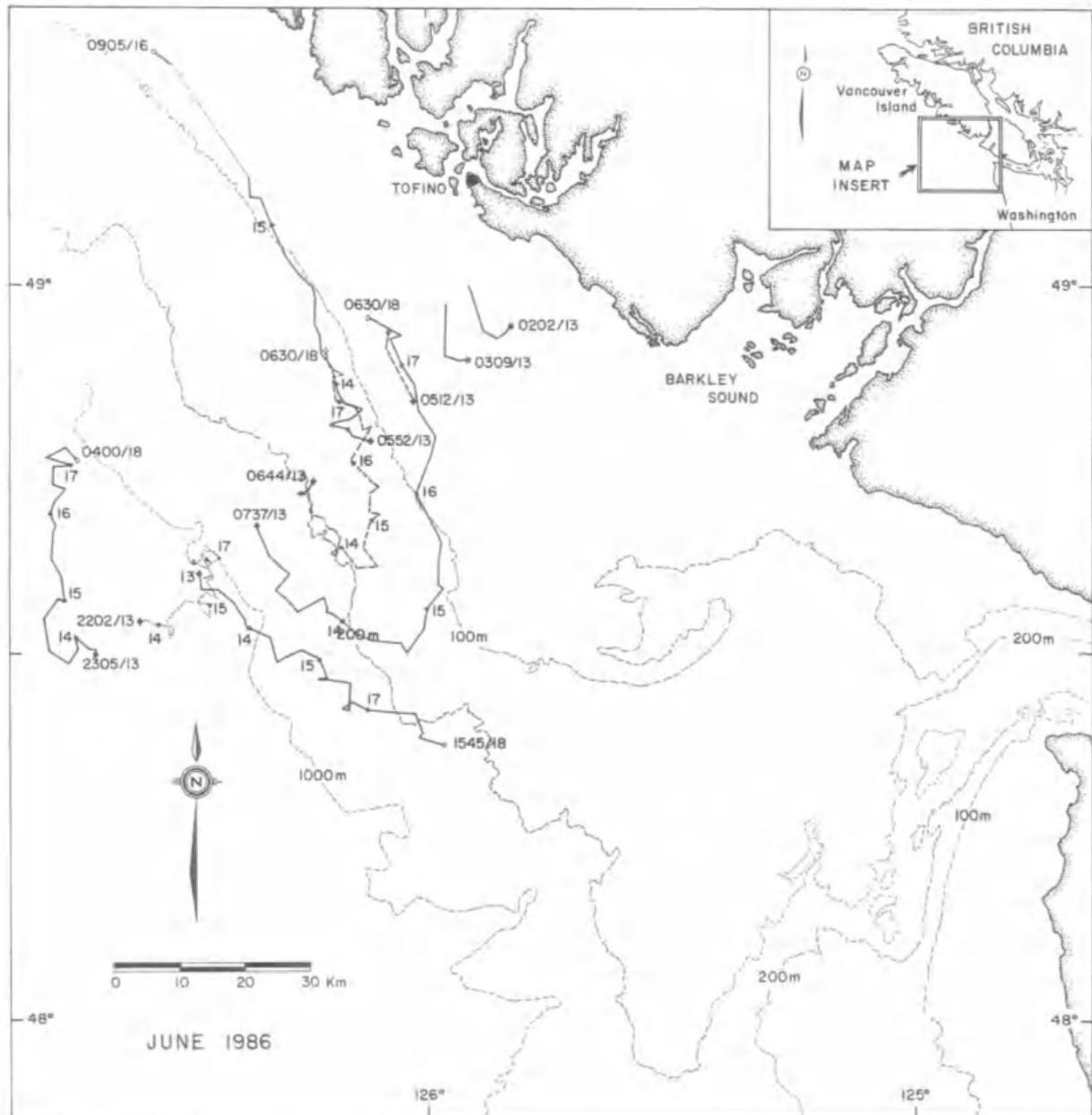


FIG. 5. Tracks of 9 drifters deployed along a transect off Tofino, British Columbia, on June, 1986. Marks along each track indicate the position of each drifter at noon on the day (the adjacent 2-digit number) indicated. Four-digit numbers refer to the hour the drifter was deployed and/or retrieved (from Jamieson *et al.*, 1989).

tional settlement are also typically sporadic. The temporal pattern of settlement along the American coast has shown an annual variability in magnitude of about ten-fold, with no obvious similarity to that off Vancouver Island. Major landings have occurred about every 9–10 y (Fig. 3) and causative mechanisms have been hypothesised and discussed extensively (Jamieson, 1986a; Methot, 1989; Botsford *et al.*, 1989). A satisfactory explanation has yet to be fully established. While larvae have been observed in abun-

dance over most of the continental shelf, some data suggest (R.A. McConnaughey, Univ. Washington, Seattle, WA, pers. comm.) that in years of major settlement off Washington, most larvae may never move far from shore. This, coupled with that area's extensive favourable habitat, increases larval survival at settlement.

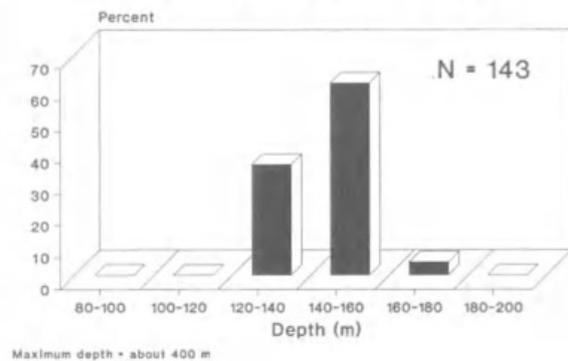
There have been no studies of relative larval distribution and abundance off Alaska. Annual commercial landings (Fig. 3) do not show the same pattern evident off British Columbia or

further south, but this may be because, like the crab fishery in British Columbia (Jamieson, 1985), regional landings are the composite of a number of distinct regional fisheries (Koeneman, 1985; Kimker, 1985; Merritt, 1985; Eaton, 1985). Recruitment patterns in each region may be largely disconnected, giving no clear pattern for the region as a whole.

Larval settlement patterns in the GS-PS complex are different from those along the outer coast. Megalopae settle in abundance mostly later in the year (August-September), are smaller in size, and show some minor, although perhaps significant, morphological differences (DeBrosse *et al.*, 1990). Recent studies of megalopal spatial and vertical distribution (Jamieson and Phillips, unpubl.) in Georgia Strait indicate that in July, megalopae are found in high abundance throughout the Strait but that their vertical distribution during daylight seems to differ from that found off the outer coast (Fig. 6). In the Strait, megalopae appear to descend to depths of about 150 m while offshore, they are seldom found in quantity below about 40 m (Jamieson *et al.*, 1989). While megalopae have been caught below 100 m on the outer coast (Jamieson, unpub. data), they have been late intermolt stage, suggesting they may have been in the process of settling. Dungeness crab megalopae have been caught as deep as 273 m in coastal inlets in epibenthic sled tows (Jamieson and Sloan, 1985), a depth where they are unlikely to survive as juveniles.

This difference in megalopal diel migration behaviour has interesting consequences, particularly if zoea from the two regions show similar differences as well. Since summer water temperatures below about 50 m in most of the Strait are 7-8°C (Thomson, 1981) [temperatures on the outer coast at 25-50 m depth are about 12-14°C (Thomson *et al.*, 1989)] and daylight in July is about twice as long as darkness, growth rate would be reduced, thereby probably extending the larval period and possibly resulting in their smaller size at settlement. It also could result in stock isolation, since the surface water of Juan de Fuca Strait, the main connection between the GS-PS complex and the Pacific Ocean, flows predominantly seaward (Fig. 7) while water below about 80-100 m flows predominantly shoreward (Thomson, 1981). Georgia Strait megalopae, which may spend most of their time at depth, would thus tend to be retained within the GS-PS complex while outer coast megalopae, which are mostly near the surface, would generally be prevented from entering the Strait. Sustained southerly winds can, though, temporarily stop the outflow of surface water in

### Megalopal Day Depth Distribution Georgia Strait, July 19, 1989



### Megalopal Day Depth Distribution Outer coast, May and June, 1987

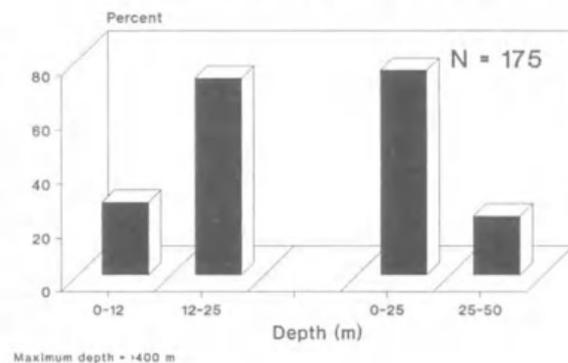


FIG. 6. Daytime depth distributions of megalopae off the outer coast (modified from Jamieson *et al.*, 1989) and Georgia Strait. Data collected with Tucker trawls in 1987 and 1989, respectively.

Juan de Fuca Strait and the penetration of outer coast water (Fig. 8), sometimes containing megalopae (P. Dinnel and D. Armstrong, unpubl.), has been documented (Thomson, 1981; Thomson *et al.*, 1989). However, for reasons described later, this is mostly on the American side of the Juan de Fuca Strait and relatively few outer coast megalopae would seem likely to penetrate into the Canadian waters of Georgia Strait.

#### JUVENILE SURVIVAL

**UPWELLING DOMAIN:** Megalopae settle to the benthos and metamorphose to first instar juvenile crabs primarily between May and June along the coast from Northern California through Washington State (Botsford *et al.*, 1989). Most studies of juvenile crab populations in this area have been descriptive portrayals of distribution and abundance, growth and size-at-instar

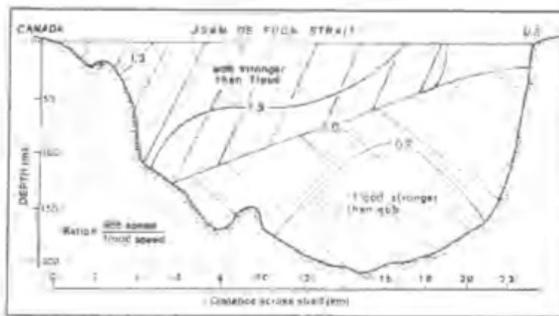


FIG. 7. Average direction of water flow in cross-section of Juan de Fuca Strait from Pillar Point (USA) to Port Renfrew (Canada). Shaded is a seaward flow, no shading is a landward flow (from Thomson, 1981).

(Cleaver, 1949; Poole, 1967). There have been few quantitative surveys that provided estimates of mortality or indices of year-class strength, but those done indicate that considerable differences in survival occur within a region, depending on both abiotic and biotic factors. It is important to briefly discuss these factors in considering how recruitment is mediated.

Although larvae may occur in abundance offshore, juveniles for the most part seem to survive only in nearshore locations, in water generally

shallower than 40 m (Gotshall, 1978; Carrasco *et al.*, 1985). Estimated density increases approximately 20- to 50-fold as depth decreases from 41–70 m to 16–40 m (Carrasco *et al.*, 1985; McConnaughey and Armstrong, unpubl.). Even inside of the 40 m isobath, density of 0+→0+ crab fluctuates appreciably because of substrate type. It is highest on well sorted sand and lowest on gravel-cobble (Fig. 9). Trawl samples off Grays Harbor, Washington, in 1985 showed 0+ crab densities as high as 30,000 crab/ha on sand, compared to only about 200/ha on gravel. Post-settlement crab growth on the outer coast from June through September is typically relatively slow, and young-of-the-year are only usually about third instar (13 mm CW) by September (Fig. 10; Gunderson *et al.*, 1990). This is due in large part to bottom water temperatures of less than 10°C in this upwelling system. As a consequence of small size, crab mortality is high, since they remain susceptible to many predators (Reilly, 1983) through the winter. Even numerically strong year-classes at settlement, such as that of 1985 (Gunderson *et al.*, 1990), can have their abundance depleted sufficiently through their first winter to become unexceptional at recruitment to the fishery.

Quantitative data of sufficient 0+ → 0+ y-class

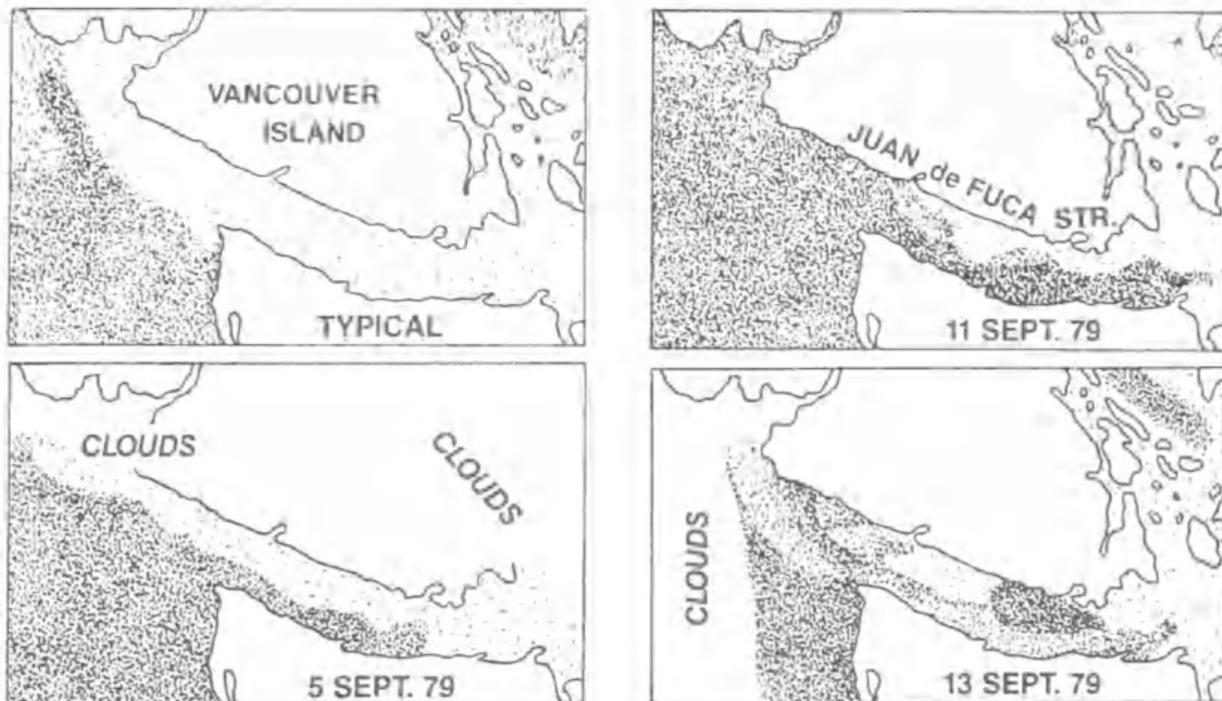


FIG. 8. Drawings based on infrared satellite images of sea-surface temperatures, showing a sequence of warm-water intrusion (heavy stippling) into Juan de Fuca Strait from the Pacific Ocean in September, 1979. Intrusion was confined to the southern half of the Strait and reached a maximum of 135 km from the entrance. Four days after the cessation of the causative southwest winds, the seaward estuarine circulation was reestablished and the intrusion began to be advected out of the Strait (from Thomson, 1981).

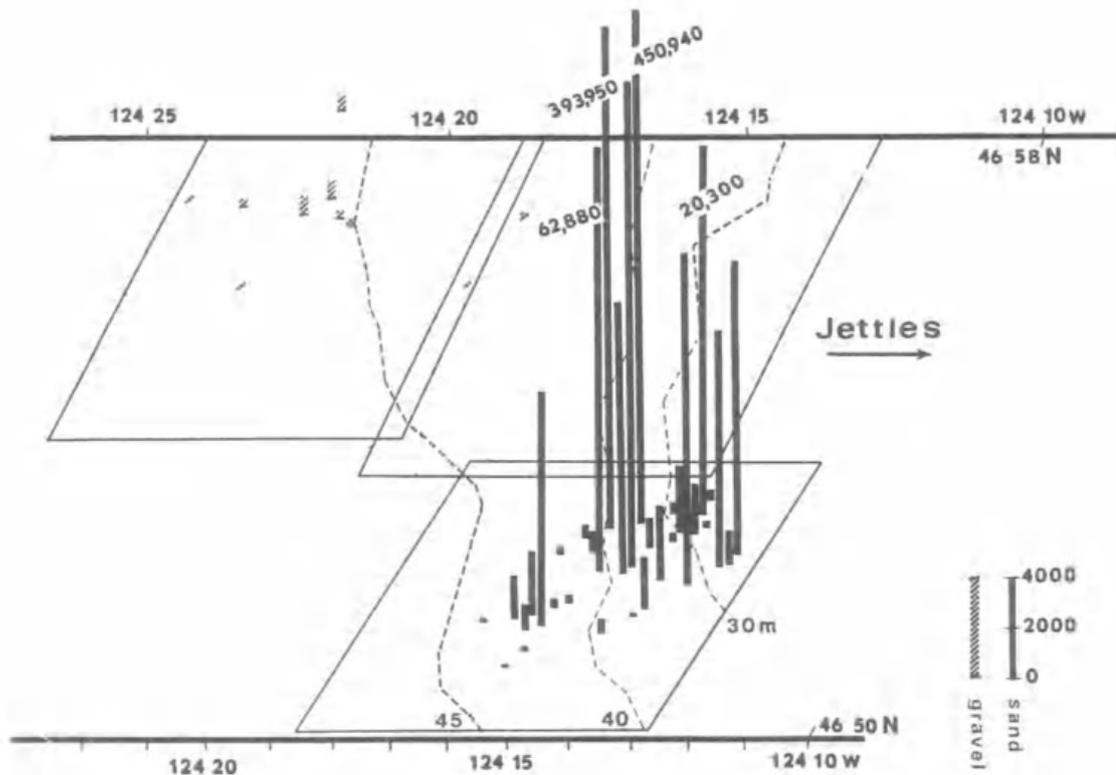


FIG. 9. Dungeness crab density (number  $\text{ha}^{-1}$ ) offshore of Grays Harbor, WA, June 1985.

survival over sequential years to construct indices of year-class strength and determine spawner-recruit relationships are non-existent. Gotshall (1978) found no correlation between an index of 0+ crab abundance and commercial landings 3.5 y later, based on cursory coastal and estuarine surveys in northern California. However, Warner (1987) measured 0+ crab density in fall trawl surveys off northern California from 1972 through 1985 and noted that a 20-fold greater density for the 1972 year-class subsequently resulted in a near-record commercial fishery in 1976 (11,300 t). Tasto (1983) and Reilly (1983), who estimated the abundance of benthic juveniles and larvae in central California, respectively, both observed relatively strong year-classes in 1975 and 1977, which were consistent with an increase in commercial landings for California in 1978–80 (Methot, 1989; PMFC, 1989).

The most comprehensive study of 0+ Dungeness crab recruitment and survival has been done along the southern Washington coast between 1983 to 1989 (Armstrong and Gunderson, 1985; Gunderson *et al.*, 1990). While they found that high interannual variability in estimated abundance of 0+ crab did not equate well to the strength of future fisheries, measures of 1+ y-old crabs did. The high abundance of 1+ crab in 1985

(1984 year-class; Fig. 11) led to a record high fishery in excess of 10,000 t in 1987/88 and 1988/89 (Fig. 3). Unique to the 1984 year-class was unusually rapid growth of the coastal cohort (Armstrong and Gunderson, 1985), which re-

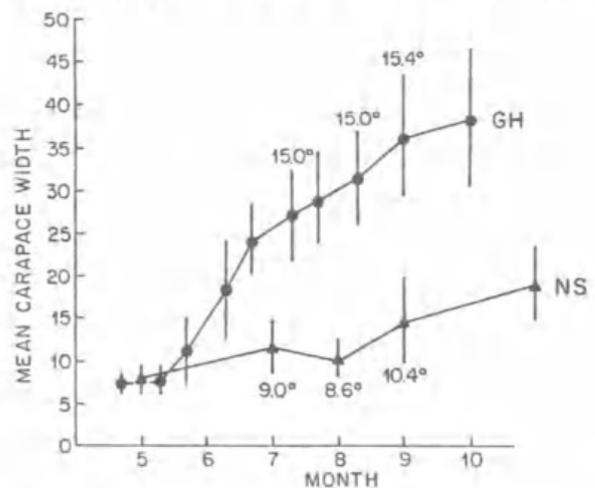


FIG. 10. Comparison of 0+  $\rightarrow$  0+ Dungeness crab growth during their first summer inside an estuary (Grays Harbor, GH) and on the outer coast in near-shore waters near the estuary (NS). Numbers indicate mean bottom water temperature ( $^{\circ}\text{C}$ .); bar = 1 SE (from Armstrong and Gunderson, 1985).

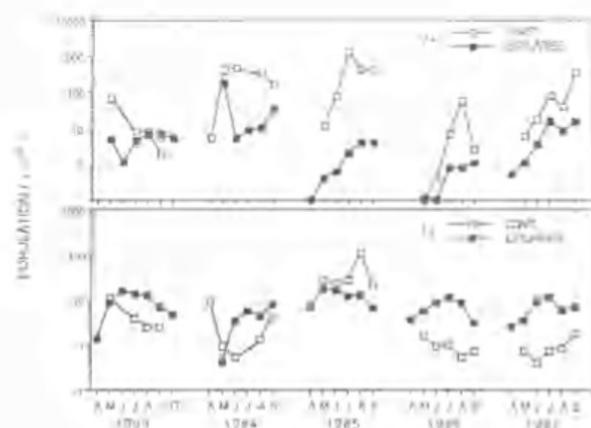


FIG. 11. Population estimates for  $0^+$  and  $1^+ \rightarrow 0^+$   $1^+$  Dungeness crab by month and year on the outer coast and adjacent estuaries off Washington. Estuarine data for 1983–84 are for Grays Harbor only, but include Willapa Bay for 1985–87 (from Gunderson *et al.*, 1990).

sulted in a mean size, by fall, of about 22 mm CW. Gunderson *et al.* (1990) speculated that the more rapid growth of this year-class increased survival over fall and winter and, in turn, a strong  $1^+$  cohort in 1985 (Fig. 11). The cause of more rapid growth in 1984 seemed to be a combination of early settlement and unusually warm bottom water temperatures in May and June, 1984, compared to other years during the study.

Another aspect of settlement along the open coast in the Upwelling Domain is direct recruitment of juveniles to coastal estuaries (Fig. 12). Settlement there can be high in both intertidal and subtidal areas, although in the subtidal, mortality is relatively high and newly settled crab quickly disappear (Dumbauld and Armstrong, 1987; Gunderson *et al.*, 1990). Optimal habitat in the intertidal has a large quantity of bivalve shell, notably of cultured oyster (*Crassostrea gigas*) or wild softshell clam (*Mya arenaria*) (Armstrong and Gunderson, 1985; Dumbauld and Armstrong, 1987). Estuarine crab also benefit from higher temperatures and accelerated growth (Fig. 10). By September, estuarine  $0^+$  crab are approximately 35 mm CW, in contrast to the approximately 13 mm CW of outer coast juveniles. During the summer, intertidal crab gradually move to the subtidal, where they are now able to avoid most predators by virtue of their greater size (Reilly, 1983). However, despite high intertidal estuarine abundances of  $0^+$   $1^+$  crab abundance, annual  $1^+$  y-old subtidal estuarine populations are fairly constant and fluctuate only about two-fold (Fig. 11; Gunderson *et al.*, 1990). This had led to speculation that estuaries provide a relatively stable recruitment

source to the fishery, representing a significant proportion of the long-term average landing in coastal fisheries. Contrary to original hypotheses of Armstrong and Gunderson (1985), estuaries may thus not be the source of particularly strong year-classes that cause peaks in cycles of fisheries landings (Fig. 3). Such peaks instead seem to be the result of high survival of  $0^+$  crab that settle and recruit directly in outer coast areas (Gunderson *et al.*, 1990).

**DOWNWELLING DOMAIN:** As previously noted, this region is topographically quite different from most of the Upwelling Domain region. General life history and fishery information on the species has been summarised by Koeneman (1985) for southeast Alaska. There is no reason to assume that aspects of life history and habitat requirements are any different for Dungeness crab in this area, but the timing of seasonal life cycle events is different. Settlement of larvae is later and typically occurs in August and September. Although fisheries landings do not show cycles of the same magnitude as reported along the coast from Washington to California, substantial fluctuations in catch probably reflect variability in year-class size, attributable to the same suite of biotic and abiotic factors hypothesised to affect the species elsewhere in its range (Botsford *et al.*, 1989). The downwelling features of this area, as previously described, may serve to retain larvae nearshore rather than encourage long distance transport in the Alaska Current. Larvae may thus be produced and retained in a smaller geographical scale and progeny may recruit to areas near where they were hatched. No systematic, quantitative long time series of data exist for juvenile Dungeness crab recruitment and survival in this Domain.

**GEORGIA STRAIT/PUGET SOUND:** As noted earlier, oceanographic features in the inland sea of the GS-PS complex, which extends across the border between Canada and the United States, lead to unusual conditions that may result in maintenance of a separate stock distinct from that on the outer coast. Based on timing of settlement and size of first instar juveniles, P. Dinnel and D. Armstrong (unpubl.) have defined at least two cohorts of  $0^+$  crab recruiting to Puget Sound in May through September. The first cohort settles in May and June and juveniles are approximately 7–8 mm CW, comparable in size with outer coast crab juveniles (Gunderson *et al.*, 1990). This outer coast cohort is identical in size to cohort 'a' reported by Orensanz and Gallucci (1988). Coastal zoeae or megalopae apparently enter the GS-PS complex through the Strait of Juan de Fuca, probably either in surface waters when surface outflow temporarily ceases (Fig.

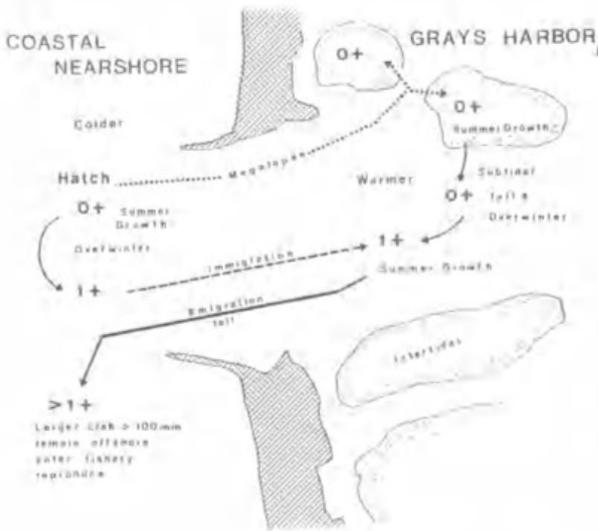


FIG. 12. Schematic of generalized movement and distribution of megalopae, 0+ and 1+ y-old juvenile crabs between the nearshore coast and Grays Harbor estuary.

8), as discussed earlier, or at depth in the compensating inward flow of more dense water. Because of the across-Strait tilt in the boundary line separating net seaward flow at the surface and net landward flow in the lower layer (Fig. 7) due to the combined effects of the Coriolis force and channel curvature (Thomson, 1981), outflow favours the Canadian side and inflow the American side. This explains why most settlement of outer coast crabs in the Strait and GS-PS has been observed in American waters.

The second cohort identified by P. Dinnel and D. Armstrong (unpubl.) settles in late July and August and is substantially smaller, with a first instar size of <5 mm CW. Because of settlement later in the summer, this 'Puget Sound' cohort (synonymous with cohort 'b' of Orensanz and Gallucci, 1988) grows relatively little in its settlement year and typically overwinters in the intertidal. Settlement by the Puget Sound cohort two months after the 'outer coast' group is probably due to slow growth caused by cold water temperatures in the central part of the GS-PS complex. Tidal flow among the American San Juan Islands and Canadian Gulf Islands brings to the surface the denser, colder lower water layer, and this vertical mixing of the water column results in surface water temperatures which are colder there than found on the outer coast. Such conditions do not apply in the central part of Georgia Strait and in the southern, low current parts of Puget Sound.

As occurs along the outer coast, juvenile crab predominantly occur in shallow water habitats

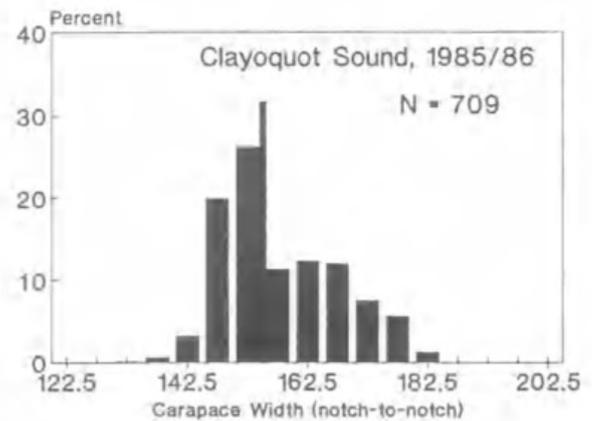
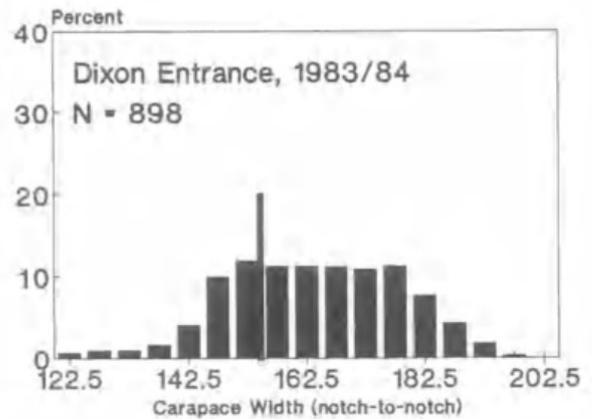
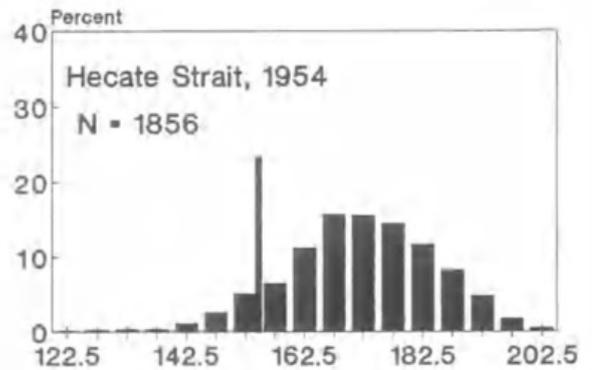


FIG. 13. Commercial catch size distributions of Dungeness crab, showing the reduction in relative proportion of large crabs as fishing has intensified over time. The narrow vertical bar indicates the minimum legal size limit, modified to show the notch-to-notch measurement. Hecate Strait data modified from Butler (1960); remaining data modified from Smith and Jamieson (in press).

characterised by sand and small cobble, often with eelgrass (*Zostera marina*) or overlying mats of algae such as *Ulva* sp. At a number of intertidal locations throughout Puget Sound, Dinnel *et al.* (1987) reported high densities of 0+ crab in cobble-sand, with densities highest if macrophytes were present (Dinnel *et al.*, 1986). Predictably, refuge availability is an important element determining the carrying capacity of an area, but in contrast to the outer coast where bivalve shell is important (Armstrong and Gunderson, 1985), algae and eelgrass provide most cover in the GS-PS complex. As measured by trends in the fishery, overall recruitment and survival of juvenile stages appears to be more constant and stable within the GS-PS complex compared to the outer coast, and is probably limited in magnitude to a great extent by availability of appropriate refuge habitat for early juvenile instars at settlement.

#### PRE-RECRUIT SURVIVAL

Pre-recruits are defined here as the size cohort that will recruit to the exploitable cohort in the next subsequent year, and for Dungeness crab, this implies male crab in the size interval of about 130–159 mm CW (Smith and Jamieson, 1989b). The conventional assumption is that since male crab greater than 140 mm show evidence of previous matings by abrasion marks on their chelipeds (Butler, 1960; Smith and Jamieson, *in press*), current minimum size limits (155–159 mm CW, depending on jurisdiction) should protect many crab from capture for at least one breeding season prior to their recruitment to the exploitable size range. The rationale and data used to justify existing size limits were never documented, but in the early 1900s when size limits were first introduced, it is hypothesised that most crab populations were less heavily exploited than at present and that a relatively large proportion of crab significantly exceeded the minimum size limit adopted. In 1954, the mean size of crab sampled by Butler (1960) in Hecate Strait, the location of the largest fishery at that time, was about 173 mm CW, with many crab exceeding 190 mm CW (Fig. 13). Crab this size are seldom caught today in any significant fishery in British Columbia (Fig. 13), although large crab are caught on the outer coast of Washington [mean = about 175 mm CW (S. Barry, Washington State Dept. Fish., Montesano, WA, pers. comm.)] and even larger crab are caught in Alaska. Merritt (1985) reported that the mean CW of commercial crab caught at Bluff Point, Cook Inlet, AK, from 1973–75 ranged from 190–200 mm, but that the very large crab (230+ mm CW) caught when the fishery first began

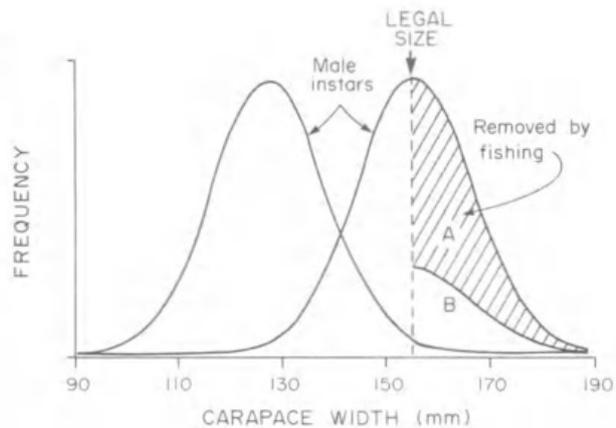


FIG. 14. Diagrammatic depiction of a male crab instar size distribution in relation to the minimum legal size limit, and the effect of fishing removal on the apparent instar composition of a size frequency distribution. Two instars from Clayoquot Sound, 1985–86, are shown: adjacent  $\mu = 129$  mm CW ( $\pm 12$  mm CW) and  $\mu = 156$  mm CW ( $\pm 13$  mm CW) instars (from Smith and Jamieson, 1989b).

there in 1973 had disappeared. Crab landed in Kachemak Bay, adjacent to Bluff Point and which has been exploited for most of the century, averaged 15% smaller than Bluff Point crabs between 1978–83.

In an intensive study of the Tofino, British Columbia, crab fishery, Smith and Jamieson (1989a, b) reported that the recruiting instar size distribution was nearly halved by the minimum legal size (MLS) (Fig. 14). Forty-two percent of this cohort were pre-recruits, and hence unavailable to the commercial fishery that year. What was surprising, though, was that there was considerable evidence (Smith and Jamieson, 1989a) that these pre-recruits had a high natural mortality ( $M=2.9-4.5$ ), with less than 10% ultimately surviving to legal size. Thus, about 40% of this recruiting cohort apparently never recruited.

It is not known if this was a phenomenon unique to the relatively small geographic area involved (about 60 km<sup>2</sup>) and/or that particular time period (1985–86). Further study, both at Tofino and elsewhere, is currently under way, but because of a lack of settlement at Tofino in recent years and logistic difficulties in conducting an appropriate study in a larger geographic area, these results have not been confirmed elsewhere to date. Smith and Jamieson (1989a) suggested this apparently high mortality might be a result of having recruits being removed from the population in this year-round fishery virtually as fast as they recruit ( $F=5.1-6.9$ ); only 9–16% of recruits are expected to survive more than 90 days. Continuous trapping and release of

pre-recruits while fishing for recruits (current escape port size is not optimal; Jamieson, unpubl.) may have increased their mortality substantially, or there may be some, as yet undetermined, biological explanation.

A final consideration is the growth history of the recruiting cohort. In the Tofino instance described above, the MLS divided the recruiting cohort almost equally, but this may not always occur. In some years, mean instar sizes may be such that the MLS falls between distinct, adjacent instars, rather than over one instar specifically, resulting in almost the entire pre-recruit instar recruiting with its next moult. Any scenario between the above two extremes may occur, resulting in up to a two-fold difference in recruitment of year-classes of similar absolute abundance. This may mostly explain the large average size of recruited crab in the outer coast Washington fishery (175 mm CW) relative to that in the Tofino fishery (about 165 mm CW; Smith and Jamieson, 1989a).

#### SUMMARY

The prediction of relative year-class strength at recruitment to the fishery for Dungeness crab, and probably for most species, is not a trivial matter. Limited mobility, pronounced spatial differences in abundance, and a variable environment result in sufficient unpredictability that future estimation of year-class abundance of Dungeness crab to a fishery can only be made with acceptable accuracy from 1+ y-olds. Female abundance, in the absence of any fishery for them and little data on their occurrence because of the use of escape ports, is unavailable. The ultimate settlement location of larval production is also unknown. Consequently, traditional stock-recruitment relationships are effectively meaningless for management and have not been determined for this species. Research emphasis is currently focusing on determining and describing the critical environmental conditions (currents, temperature, winds, refuge availability), behaviour (larval distribution in the water column), and population dynamics (growth rate, survival and causes of mortality) in coastal areas having significant regional fisheries.

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