

Decadal-scale dynamics of sea urchin population networks in Fiordland, New Zealand are driven by juxtaposition of larval transport against benthic productivity gradients

Stephen R. Wing*

Department of Marine Science, 310 Castle Street, University of Otago, Dunedin 9054, New Zealand

ABSTRACT: Size structure among 3 genetically distinct populations of the sea urchin *Evechinus chloroticus* was investigated between 1998 and 2007 at 22 study sites distributed in the Fiordland region in southwestern New Zealand. Data on morphology and abundance of the common kelp *Ecklonia radiata* was used as an indicator of the availability of high-quality food among sites. Habitats close to the fjord entrances with relatively high density of *E. radiata* (0.5 ± 0.1 [SE] to 1.2 ± 0.2 m⁻²) supported *E. chloroticus* subpopulations with large average test diameters among years (94 ± 9.3 to 120 ± 2.8 mm) and stable adult modes across the 10 yr period. In contrast those subpopulations in inner fjord habitats with lower *E. radiata* abundance (0 to 0.4 ± 0.1 m⁻²) were characterised by smaller average test diameters (64.3 ± 6.5 to 103.4 ± 1.7 mm) and frequent large pulses of newly emergent juveniles (<60 mm). These patterns in demographic variability were apparent in an index of recruitment, which increased from the kelp-dominated outer coast to the marginal inner fjord habitats. In the 10 yr period, complete adult mortality events were observed at 5 sites in inner fjord habitats, followed by re-colonisation by newly emergent juveniles. The data suggest that population networks arranged across gradients of habitat quality are more likely to exhibit rescue effects and to maintain higher abundance in marginal habitat than are isolated populations. These results highlight the importance of including core source populations in marine reserve networks for regional persistence and stability of marine metapopulations.

KEY WORDS: Fiordland · Marine reserve · Metapopulation · Sea urchin · Sources · Sinks

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INTRODUCTION

Many coastal marine populations are made up of networks of discrete subpopulations of relatively sedentary adults linked by larval dispersal at the meso-scale (10 to 100 km) (Hixon et al. 2002, Kritzer & Sale 2006). Patterns in abundance, and structure of population networks at this scale are strongly influenced by the interaction between hydrodynamic forcing of larval dispersal with patterns in adult productivity and larval production. Consequently, understanding relationships between coastal circulation and recruitment processes has been the focus of a wide range of ecolog-

ical studies on marine invertebrates and fishes (McEdward 1995, Morgan 2001, Underwood & Keough 2001). In this context, several studies have highlighted the structural importance of coastal topography and retention of larvae within the coastal boundary layer (Ebert & Russell 1988, Morgan et al. 2000, Diehl et al. 2007), and the dispersal of larvae within island systems or among estuaries (Jones et al. 1999, Hughes et al. 2000, Almany et al. 2007). These studies have led to considerable insight on the spatial scale of variability within coastal population networks and highlighted the importance of connectivity as a population structuring mechanism in these systems (Fogarty & Botsford 2007).

*Email: steve.wing@otago.ac.nz

The resulting regional-scale population dynamics and persistence within this class of populations is therefore strongly driven by interactions among subpopulations in terms of the source and supply of new recruits and also by spatial variability in vital rates of adults (Wing et al. 2003, Sanford & Menge 2007).

This issue is particularly apparent in topographically complex regions. One such environment is Fiordland, New Zealand where the 15 fjords represent an insular array of marine habitats. Within each fjord there are strong gradients in benthic productivity from abundant kelp forests in the wave-exposed outer coastal habitats to the quiescent inner fjord regions where forest litter dominates the organic matter pool (McLeod & Wing 2007, Wing et al. 2008). This gradient in the quantity and quality of food resources for benthic grazers such as the sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea) within each fjord creates the basis for strong bottom-up controls on growth and reproductive output of adults (Wing et al. 2003, 2008). Mean estuarine circulation driven by a distinct freshwater layer in each of the fjords tends to transport larvae away from relatively fecund populations at the entrances of the fjords towards the less productive habitats in the inner fjords, which results in abundant settlement of *E. chloroticus* in habitats that are marginal for adult growth and survival (Lamare 1998, Wing et al. 2003).

Evechinus chloroticus is endemic to New Zealand and as a subtidal grazer, it has a critical influence on both the composition and productivity of coastal kelp forests and algal reefs (Choat & Schiel 1982, Choat & Andrew 1986, Shears & Babcock 2002). Its distribution includes the Snares, Stewart Island, Chatham Island and Three Kings Islands as well as the mainland North and South Islands (Pawson 1965, Dix 1970b). Dispersal is limited to planktonic drifting and weak ciliary swimming of planktotrophic echinopluteus larvae, which are produced annually with a pelagic existence of 1 to 2 mo (Dix 1969, 1970a, Walker 1984). Juveniles of less than 40 to 50 mm test diameter are usually cryptic, living in rock crevices and under boulders until they emerge as new recruits into the adult population (Shears & Babcock 2002). Within these habitats, growth may be slower and more consistent than among the adult population (Lamare & Mladenov 2000). Because recruitment is typically sporadic and potentially driven by larval supply from distant populations along the coast, the spatial distribution of populations is a critical feature of their regional dynamics.

In Fiordland, the effect of estuarine circulation on larval dispersal may result in reproductive isolation of populations within some fjords and strong variability in larval supply across the remaining population network (Wing et al. 2003, Perrin et al. 2004). Using microsatellite

markers, Perrin et al. (2003) identified 2 distinct ecotypes of *Evechinus chloroticus* in Fiordland. Ecotype A was restricted to the most wave-exposed habitats on the outer coast and genetically contiguous with other populations around the South Island. Ecotype B was found at fjord entrance sites and in the inner fjord habitats. Further, within Ecotype B, the population in Long Sound was found to be genetically distinct and it is likely that sea urchin larvae rarely disperse into or out of this fjord (Perrin et al. 2003). Therefore, the *E. chloroticus* population in Fiordland consists of 3 distinct classes of populations (Fig. 1). Ecotype A represents an 'open' population with open larval exchange along the coast (Fig. 1d). Ecotype B represents a population network, with satellite populations in the inner fjords (Fig. 1b) linked by larval exchange with populations distributed among entrance sites (Fig. 1a). Finally, the geographically isolated population in Long Sound represents a self-seeding population within Ecotype B (Fig. 1c).

This highlights the interesting question of how these 3 different types of populations (open, isolated, network) are forced by environmental influences on adult growth, survival and recruitment to produce patterns in population structure and abundance. In the present study, the size structure of *Evechinus chloroticus* populations was examined for multiple events over 10 yr from 22 sites distributed across the Fiordland landscape. Measurements of the variability in morphology and abundance of the common kelp *Ecklonia radiata* were used to indicate availability of high-quality food among sites (Wing et al. 2007). Repeated measurements of size distributions of sea urchins were used to investigate demographic variability, as indicated by an index of recruitment, and by variability in average test

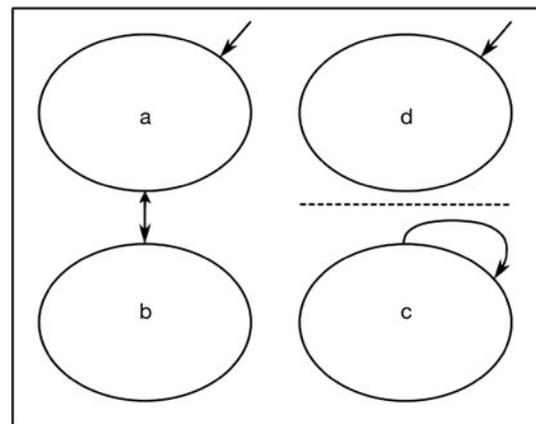


Fig. 1. (a) A core population and (b) a satellite population in a population network; (c) an isolated self-seeding population and (d) an open population. The dashed line indicates a restriction in dispersal; arrows represent larval dispersal among subpopulations

diameter among sites across the region. These data were analysed to test regional patterns in population structure and dynamics across Fiordland with reference to (1) availability of high-quality food, (2) position within the fjords and (3) genetic subdivision of populations within the region. Results of these analyses offer a test of how juxtaposed patterns in recruitment and habitat quality interact to structure and maintain distribution and abundance within and among the 3 populations across this region. This issue has important application to understanding how the newly implemented marine reserve network in Fiordland may influence populations and communities in the system, and specifically how dynamics of subpopulations within marine reserves can be strongly influenced by local habitat quality and by connectivity to populations outside of the reserve network.

MATERIALS AND METHODS

Sea urchin size structure. Size structure information on sea urchins *Evechinus chloroticus* was collected using SCUBA during Fiordland-wide surveys in 1998, 1999, 2002, 2003, 2004, 2005 and 2007 (Fig. 2). The 22 sites were surveyed at least 4 times over this time period (Table 1). Care was taken at each site to collect all sea urchins in a swath 0 to 20 m depth along the shore for 50 to 200 m, depending on density, and search for cryptic juveniles in rubble fields and crevices. At each site, test diameter was measured with Vernier calipers to the nearest mm, and the sea urchins were returned to the seabed. Yearly sample sizes among the 22 sites ranged from 12 to 499 (mean \pm SE, 149 ± 9) and reflected a haphazard accumulation of individuals from each population (Table 1).

Average test diameter (mm) from each of the resulting size distributions and average 'adult' test diameter, individuals >60 mm, were calculated by year and among years for each study site, and SE calculated among years. A recruitment index of the fraction of newly emergent juveniles in the population, animals <60 mm test diameter (Morgan et al. 2000), was calculated for each site and year and an average and SE was calculated among years.

Average size frequency was calculated among years for each site, with SE within each 5 mm size class among years. The average distributions were combined within Ecotype A sites, and within the population network (Ecotype B) for sites from fjord entrance habitats and sites from inner fjord habitats, and for Long Sound. The resulting distributions correspond to population units and major habitat divisions identified by Perrin et al. (2003), with SE among sites stratified among years.

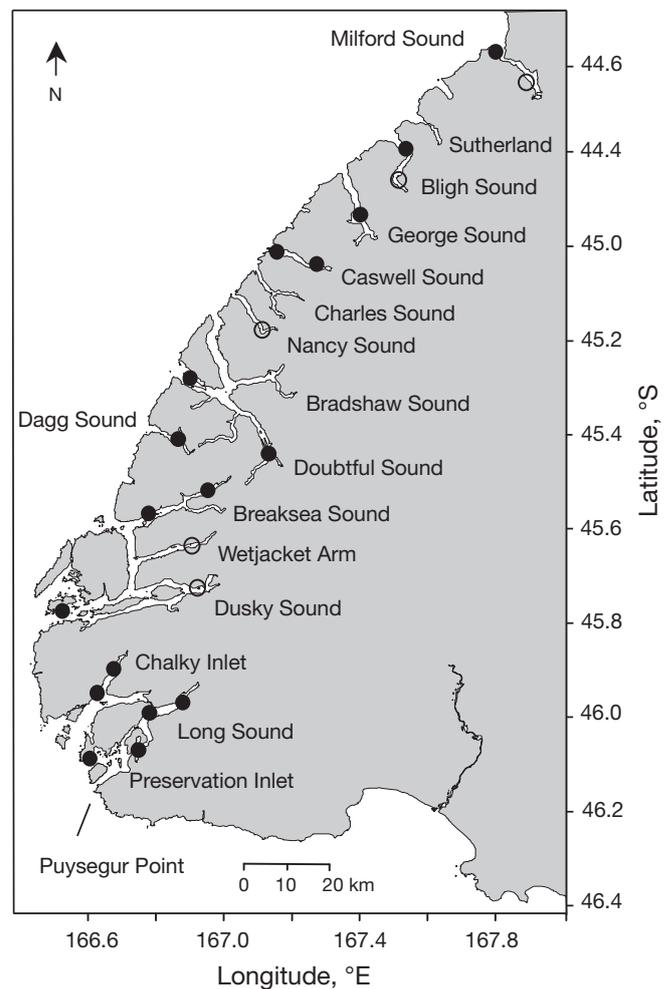


Fig. 2. Distribution of 22 study sites in Fiordland. O: 5 sites where adult mortality events were observed

***Ecklonia radiata* and *Evechinus chloroticus* abundance survey.** A stratified random survey was conducted using 2 m² quadrats at depths of 5, 10 and 15 m during Fiordland-wide surveys in 2003, 2004 and 2006. At each stratum a series of 6 paired quadrats was quantified for *E. chloroticus*, the common kelp *E. radiata* and other conspicuous species of brown algae. For both kelps and sea urchins, if an organism was located on the border of the quadrat, it was counted. At each quadrat position, the first lay of the quadrat was quantified and then the quadrat was flipped horizontally at the same depth stratum for a second count. This resulted in a series of 6 replicate 4 m² quadrats at each depth stratum. Four m² is an appropriate spatial scale for this type of sampling because it averages across a large enough area to resolve local density patterns (Wing et al. 2003). Average density of *E. radiata* at 21 survey sites that matched those with size structure information was calculated among the 3 surveys.

Table 1. Sample sizes for size distribution time series by site and survey. Sites in Ecotype A are in italics, those in Long Sound are in bold, the remaining sites are made up of Ecotype B. Within Ecotype B, sites are designated according to habitat, inner and outer (see Fig. 8)

Site	Apr 1998	Apr 1999	Oct 2002	Nov 2003	Nov 2004	Nov 2005	Feb 2007
Milford inner	308	59	205			252	134
<i>Milford outer</i>		50	144			159	110
Bligh outer		116	90	73		148	103
Bligh inner		35	262	54		167	124
George	210	50	52	57		92	
Caswell inner	289	91	185	114		229	119
Caswell outer		104	101	101		135	120
Nancy inner	340	50	135	102		321	103
Doubtful inner	197	372	158			210	127
Doubtful outer	418	219	125			127	117
<i>Dagg</i>	223	50	106	65	93	100	112
Breaksea inner	499	94	55	41	12	60	
Breaksea outer	185	84	138	37	136	167	95
Wetjacket	177	50	70	27	88	454	118
Dusky inner	106	28	132	86	232	298	
Dusky outer	391	50	117	96	52	83	112
Chalky inner		50	180		183	251	138
Chalky outer	492	50	118		147	223	129
Long inner	125	108	32	94	304	315	110
Long outer			175		76	89	54
Long entrance			256		220	207	123
Preservation outer	418	99	235		117	195	

Morphology of *Ecklonia radiata*. During Fjordland-wide surveys in 2002, 2003 and 2004, morphological data were collected at 5, 10, 15 and 20 m at 17 sites where *E. radiata* was present. Five to 7 mature *E. radiata* individuals were haphazardly collected from each study site and depth. For each individual, frond length and width, stipe length and diameter, secondary blade number, width and length, and frond thickness at intervals of 10 cm along length of the blade from the intercalary meristem to eroding tip were measured (see Wing et al. 2007). Average frond thickness (mm) was used in the present analysis as a proxy for the physiological condition of *E. radiata* (Wing et al. 2007).

Distance to fjord entrance. For each fjord, the distance from study sites to the outer coast was calculated using a geographic information system (GIS) with 50 m horizontal resolution in the inner fjords. In this case, a mean coastline raster line served as a zero line for the distance algorithm 'r.cost' in GRASS 5.3 (Geographical Resources Analysis Support System; ITC-irst). r.cost used a 'knight's move' distance calculation on a square grid to accurately provide distances around complex coastlines (Neteler & Mitasova 2002).

Data analysis. Data on stand density and morphology of *Ecklonia radiata* and average test diameter and density of *Evechinus chloroticus* were used to test relationships between variability of high-quality food with population structure and abundance of sea urchins. Accordingly, the relationship between average frond

thickness (mm) of *E. radiata* and stand density (m^{-2}) was tested using Type II linear regression. Type II linear regression was also used to test the relationship between stand density (m^{-2}) of *E. radiata* and the average test diameter (mm) of *E. chloroticus*. The relationship between stand density (m^{-2}) of *E. radiata* and distance (km) from the fjord entrance was tested using linear regression. Linear regression was also used to test the relationship between density (m^{-2}) of *E. chloroticus* and distance (km) from the entrance of each fjord.

Each time series of size frequency data was examined and significant deviations indicating mortality of the adult population were noted. Linear regression was used to test the relationship between average test diameter (mm) and distance (km) from the entrance of each fjord. Linear regression was also used to test the relationship between distance from the fjord entrances (km) and the index of recruitment. These data were divided into groups of sites representing the 3 genetically distinct populations observed by Perrin et al. (2003), with the population network, Ecotype B, divided into sites from inner fjord and entrance habitats. Differences in fraction of recruits were tested using a Wilcoxon/Kruskal-Wallis test followed by multiple comparisons tests to resolve pairwise differences among these 4 groups of sites (Zar 1999).

A general linear model was used to test the relationship between average adult test diameter (mm) among years at each study site and (1) density of *Ecklonia*

radiata (m^{-2}), as a proxy for availability of high-quality food, and (2) the recruitment index, as a proxy for the relative demographic variability in the size distribution, and (3) the interaction between recruitment index and *E. radiata* density. The combined model was used to assess the variability in size that could be statistically explained by these 2 variables among sites across the region. JMP version 7.0 was used for all statistical analyses.

RESULTS

Twelve of the 15 fjords were represented in the analysis with 8 fjords containing multiple sites (Fig. 2, Table 1). Type II linear regression on the relationship between average frond thickness (mm) and frond density ($ind. m^{-2}$) of *Ecklonia radiata* by site demonstrated a significant positive relationship (frond thickness [mm] = 2.64 density [m^{-2}] - 0.13, $R(x) = 0.86$) (Fig. 3a). Type II linear regression testing the relationship between density (m^{-2}) of *E. radiata* and the average

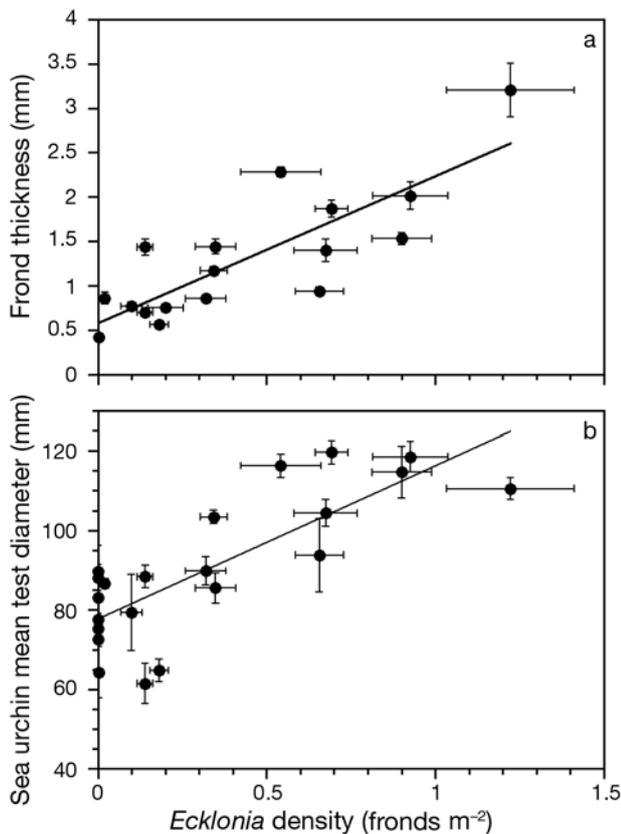


Fig. 3. *Ecklonia radiata* and *Evechinus chloroticus*. Relationship between (a) average kelp frond thickness and (b) average sea urchin test diameter and density of the common kelp. Error bars represent ± 1 SE

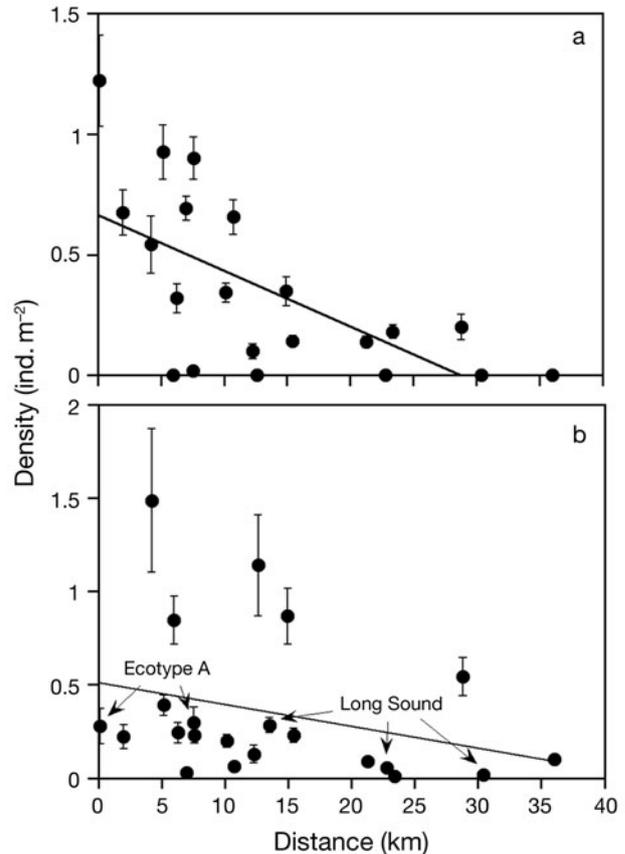


Fig. 4. *Ecklonia radiata* and *Evechinus chloroticus*. Density of (a) common kelp and (b) the sea urchin relative to distance from the fjord entrances. Error bars represent ± 1 SE

test diameter (mm) of *Evechinus chloroticus* by site indicated a significant positive relationship (test diameter [mm] = 70.31 + 61.09 density [m^{-2}], $R(x) = 0.79$) (Fig. 3b).

There was a significantly higher density of *Ecklonia radiata* toward the entrances of the fjords (density [m^{-2}] = 0.65 - 0.023 distance [km], $r^2 = 0.38$, $p < 0.002$) (Fig. 4a). The relationship between density of *Evechinus chloroticus* (m^{-2}) and distance from the fjord entrance (km) revealed no overall significant trends in abundance with distance (Fig. 4b), though high-abundance sites were only found within the population network, and average abundance within the population network (Ecotype B) was higher than for the other populations across both major habitats.

Examination of time series of size distributions from the 22 survey sites revealed 5 sites with significant mortality events in the adult size distribution and colonisation by a large cohort of juveniles in subsequent surveys (Fig. 2). An example of an adult mortality event is depicted in the size distributions from Wet-jacket Arm with a significant mortality observed between the 2004 and 2005 surveys (Fig. 5).

The relationship among sites between average test diameters (mm) and distances (km) from the entrances of the fjords showed a pattern of large average test diameters on the outer coast and small average test diameters

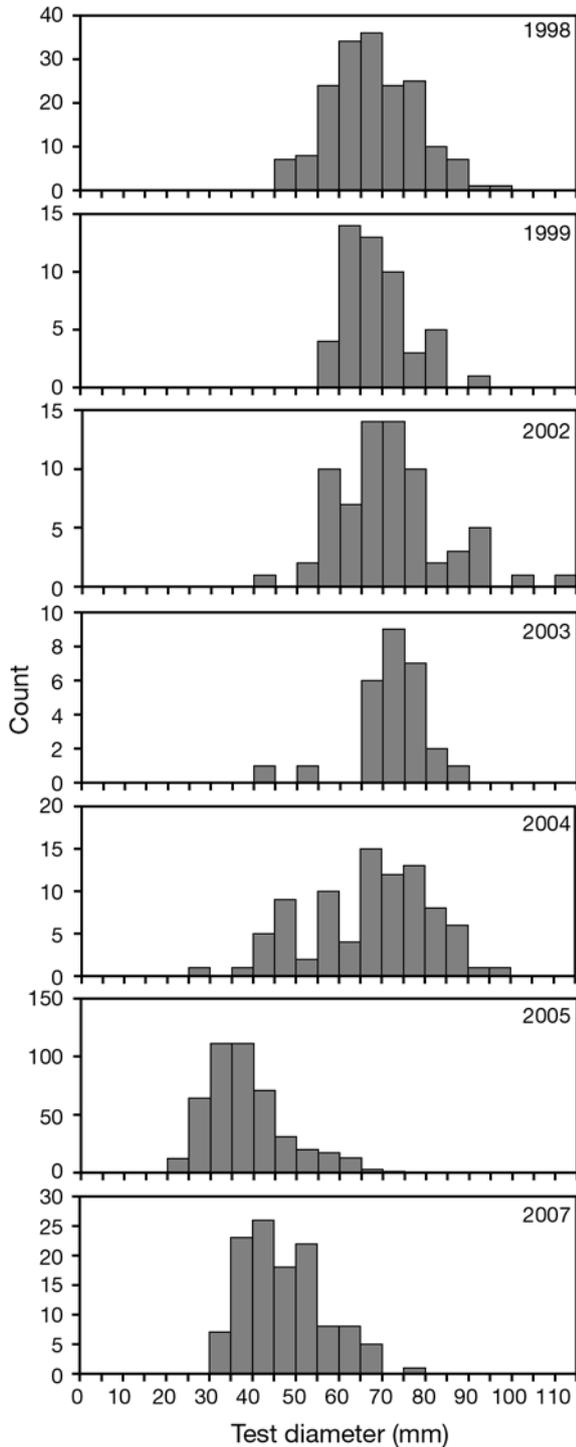


Fig. 5. *Evechinus chloroticus*. Time series of size distributions from Wetjacket Arm showing example of a total adult sea urchin mortality event between the 2004 and 2005 surveys

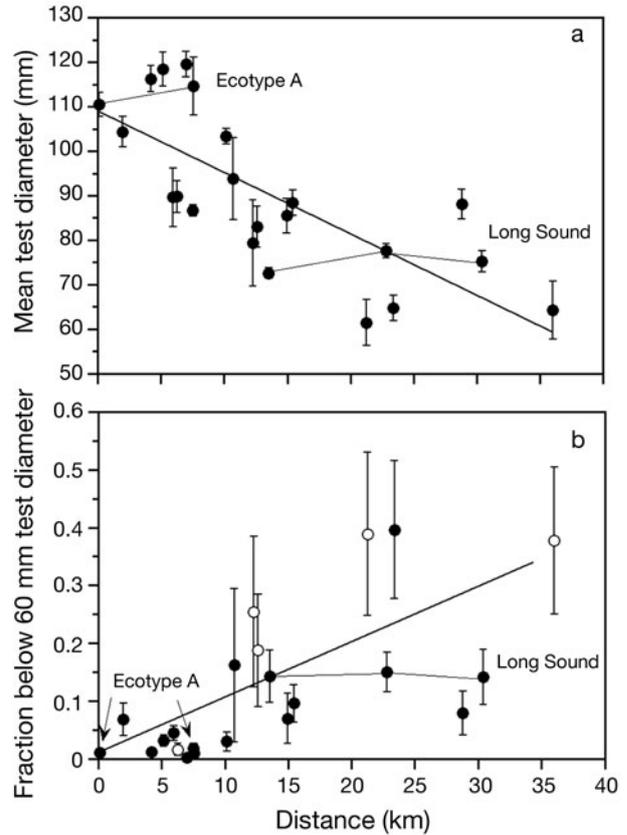


Fig. 6. *Evechinus chloroticus*. (a) Mean test diameter among years and (b) fraction of juveniles in population (sea urchins with <60 mm test diameter) relative to distance from the fjord entrances. Error bars represent 1 SE among years. Open symbols depict populations where adult mortality events were observed between 1998 and 2007

diameters in the inner fjords (test diameter [mm] = 108.9 - 1.37 distance [km], $r^2 = 0.55$, $p < 0.0001$) (Fig. 6a). Regression analysis of the relationship between the recruitment index and distance (km) from the outer coast resulted in a significant positive relationship (recruitment index = 0.002 + 0.0089 distance [km], $r^2 = 0.46$, $p < 0.0005$) (Fig. 6b). This analysis demonstrated a distinct pattern with low numbers for the recruitment index at sites near the outer coast and increased variance among sites toward the inner fjord habitats. The variance among years also increased with distance from the outer coast with a distinct trend for higher demographic variability in the inner fjord habitats. Results of the Wilcoxon/Kruskal-Wallis test for differences in the recruitment index among the genetically distinct populations identified by Perrin et al. (2003) and grouped by habitat (entrance, inner fjord) indicate significant differences (indicated below by different superscripts) among habitats within the population network ($\chi^2 = 10.53$, $df = 3$, $p = 0.0145$, Ecotype A^{ab}, Long^{ab}, entrance^b, inner fjord^a) (Fig. 7).

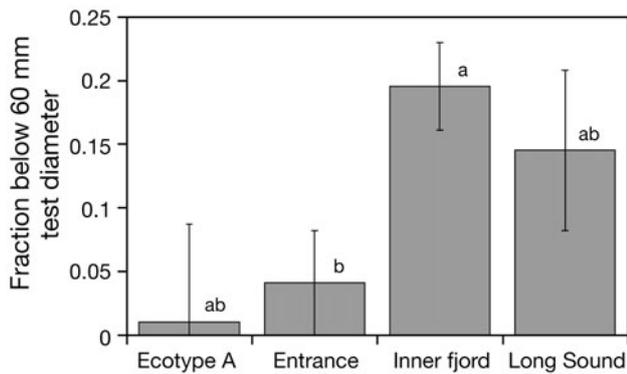


Fig. 7. *Evechinus chloroticus*. Average of recruitment index among sites from Ecotype A, entrance, inner fjord, and Long Sound. Error bars indicate ± 1 SE. Groups not connected by the same letter are significantly different

Table 2. Results of a general linear model for average adult sea urchin test diameter (mm), individuals > 60 mm, among sites with density of *Ecklonia radiata* (m^{-2}) and the recruitment index. Summary of fit: $r^2 = 0.82$, RMSE = 7.15, $p < 0.0001$, $n = 22$

Term	Estimate	SE	T ratio	Prob > t
Intercept	93.68	3.74	25.06	<0.0001
Density of <i>E. radiata</i> (m^{-2})	23.80	7.52	3.16	<0.0054
Recruitment index	-60.77	19.20	-3.17	<0.0054
Recruit index \times Density of <i>E. radiata</i> (m^{-2})	-19.93	74.32	-0.27	0.79

Results of combining size distributions among years and across sites reveal several distinct patterns (Fig. 8). The open population representing Ecotype A has a distinct large mode of test diameter, centred at 112 mm with a low proportion of individuals at smaller size classes (Fig. 8a). The portion of the population network from the entrance kelp-dominated sites has a similarly large mode with average test diameter of 105 mm and a moderate proportion of new recruits in the smaller size classes (Fig. 8b). The portion of the population network from the inner fjord sites has a smaller mode centred at 79 mm test diameter with larger and more variable proportions of newly emergent animals in the size distribution (Fig. 8c). The isolated population in Long Sound has a distinct mode centred at 75 mm test diameter with a large proportion of new recruits (Fig. 8d). Results of the general linear model on average test diameter among sites indicate a significant relationship, with 82.4% of the variance in average adult test diameter statistically explained by combined variability in density of *Ecklonia radiata* and the recruitment index (Table 2). In this combined model, the interaction between density of *E. radiata* and the recruitment

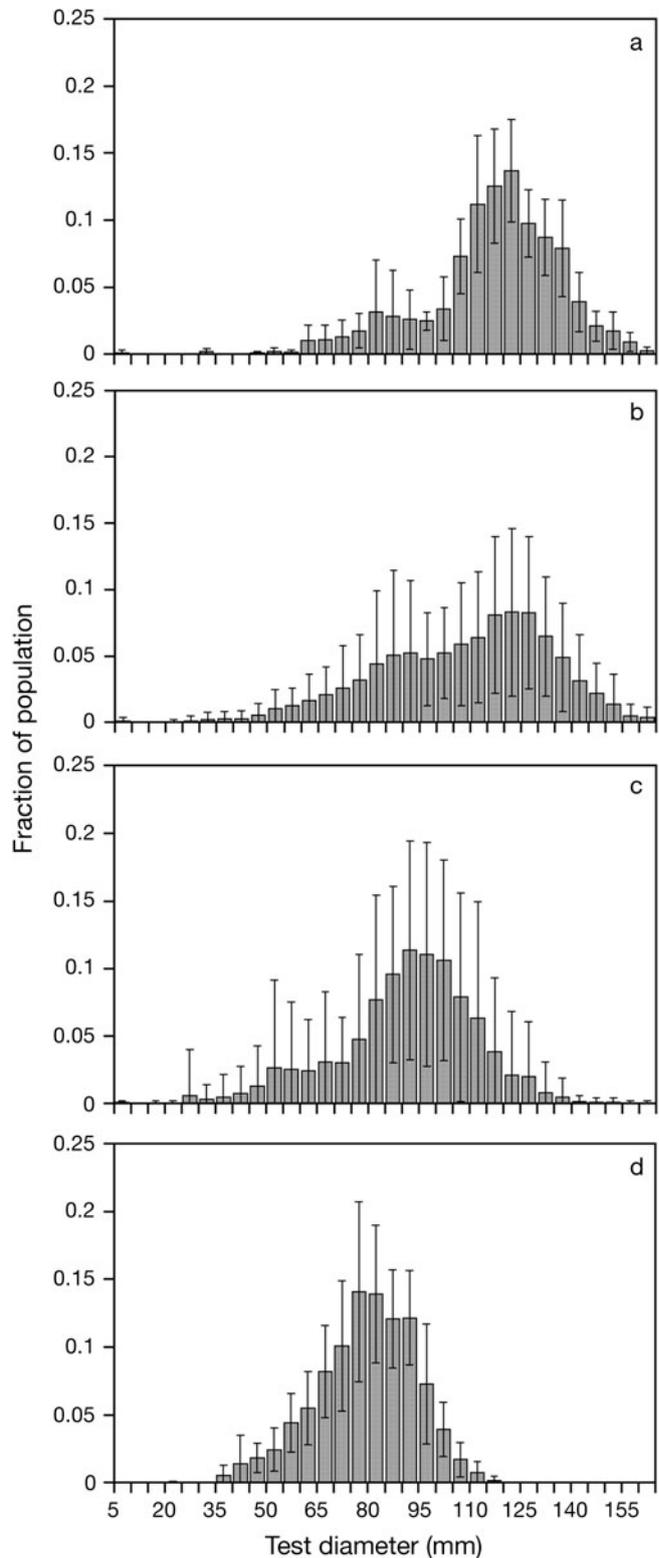


Fig. 8. *Evechinus chloroticus*. Long-term average size frequency of sea urchin populations from (a) Ecotype A ($n = 1212$), (b) entrance ($n = 6063$), (c) inner fjord ($n = 8632$) and (d) Long Sound ($n = 2288$). Error bars depict SE among years stratified within SE among sites for each size class

index was not significant. The recruitment index alone statistically explained 54 % of the variability in average adult test diameter (adult test diameter [mm] = $105.7 - 91.8$ recruitment index, $r^2 = 0.547$, $p < 0.0001$), while density of *E. radiata* alone statistically explained 65 % of the variability in average adult test diameter (test diameter [mm] = $83.1 - 34.5$ density of *E. radiata* [m^2], $r^2 = 0.657$, $p < 0.0001$).

DISCUSSION

The results of this study indicate that metapopulation dynamics and size structure of sea urchins in Fiordland are influenced by the effects of availability of high-quality food on adult growth and survivorship, and the effects of estuarine circulation on recruitment. The resulting strong spatial and temporal variability in population size structure distributed within each of the fjords demonstrates that populations at the fjord entrances are characterised by stable size distributions of large individuals with evidence of gradual recruitment. Populations in the inner fjord marginal habitats more regularly undergo total mortality events and recolonisation by large recruitment events. This pattern results in greater demographic variability within subpopulations in the inner fjord habitats. Further analysis of genetically distinct populations, identified by Perrin et al. (2003), indicates that the open population on the outer coast (Ecotype A) displays less demographic variability than the isolated population in Long Sound. The larger population network (Ecotype B) within the fjords has connected subpopulations displaying a range of demographic variability according to where they are located across the major habitat gradient between outer coast and inner fjord regions within each of the fjords.

Within the inner fjord habitats occupied by the population network (Ecotype B), average densities of adults are high (0.35 ± 0.12 [SE] m^{-2}) relative to those in similar habitat within Long Sound (0.12 ± 0.23 m^{-2}). Similarly, average densities of adults within Ecotype A were low (0.25 ± 0.28 m^{-2}) relative to those in the population network in similar habitats (0.49 ± 0.15 m^{-2}). This pattern demonstrates that sites in the population network contained areas of relatively high abundance compared to those in the open and isolated populations occupying similar habitats. A comparison of the recruitment index among populations identified by Perrin et al. (2003) reveals a high recruitment index within Long Sound (0.14 ± 0.06) relative to the recruitment index in the Ecotype A population (0.009 ± 0.07). This pattern suggests different influences on demographic variability between the 2 populations, consistent with independent dynamics. Comparisons of the recruit-

ment index across the remaining population network demonstrates the relatively large influence of recruitment on the size distributions of populations in the inner fjords (0.20 ± 0.03) relative to those at entrance sites (0.04 ± 0.04). There was also a high degree of demographic variability within the network related to local habitat quality, specifically the presence or absence of high-quality macroalgal food.

Density of *Ecklonia radiata* served as an effective proxy for the availability and quality of food for *Evechinus chloroticus*. *E. radiata* growing under conditions of light limitation, and flow-mediated limitation of mass transfer, generally have a wide and thin thallus, while in well-illuminated and wave-washed conditions, they develop a thick and relatively narrow frond (Wing et al. 2007). We observed a strong relationship between variability in morphology as indicated by frond thickness (mm) and stand density (fronds m^{-2}). Accordingly, across the wave-exposure and irradiance gradients within Fiordland (Wing et al. 2007), we observed a strong relationship between density of *E. radiata* and average test diameter of *E. chloroticus*, indicating the influence of food quality and availability on growth and survival of sea urchins (Lamare & Mladenov 2000, Wing et al. 2003, 2008).

The recruitment index, fraction of the population comprising animals <60 mm test diameter, was used as a proxy for the relative influence of new recruits within the size distribution. Because test diameter of adults is strongly influenced by food quality and quantity among sites (Wing et al. 2008), it is very important to base the recruitment index on newly emergent individuals. Individuals with a test diameter <60 mm represent newly emergent recruits that are 3 to 4 yr old and have been previously living under boulders and in crevices during their cryptic phase (Lamare & Mladenov 2000). During this time they feed on algal films and drift algae and have generally depressed and consistent growth rates, as indicated by the goodness of fit of a Richard's growth function (Lamare & Mladenov 2000). Analyses of size distributions indicate that these individuals make up transient cohorts, rather than static growth-depressed size classes within each of the habitat types. The frequency of large modes of these new recruits in size distributions reflects the dual influence of relatively high adult mortality and high larval recruitment in the inner fjords, and highlights the importance of estuarine circulation for retaining larvae within these marginal habitats.

Lamare (1998) proposed that the predominant estuarine circulation within Doubtful Sound retained distinct cohorts of *Evechinus chloroticus* larvae. This work was corroborated by a study of spatial variability in growth, per-capita gamete production, and larval settlement by Wing et al. (2003), which indicated a

source-sink structure within the Doubtful Sound population. A 3-dimensional hydrodynamic model was used to test the likely source and supply of larvae within Doubtful Sound. Results indicated that populations within the inner fjords likely received a large proportion of larvae from the more productive entrance regions, and that the population was characterised by a strong reproductive source-sink structure.

Further, Wing et al. (2008) used stable isotope analysis to examine the carbon inputs to sea urchin populations along the nutritional gradient between the entrance of Doubtful Sound and the habitats at the head of the fjord, where inputs of forest litter dominate the carbon pool. Abundant kelp forests at the entrances of the fjords corresponded with high rates of assimilation of diet, particularly *Ecklonia radiata*, high growth rates, and large average test diameter of sea urchins. In the inner fjord habitats, these high-quality food sources were replaced with a community of estuarine algae, benthic diatoms and forest litter made available by microbial recycling. Isotopic analysis indicated that low rates of assimilation of diet in these regions corresponded with low growth rates and small average test diameters in the size distributions.

The patterns observed in the present system-wide study were consistent with these more detailed studies within Doubtful Sound. Over the 10 yr study period and across the 22 study sites there were clear relationships between quantity of *Ecklonia radiata* and size structure of local populations of *Evechinus chloroticus*. The relationship between abundance and morphological variability of *E. radiata* indicated that more wave-exposed sites toward the entrances of the fjords, where conditions are less limiting for algal growth, supported a larger quantity of this high-quality food source (Wing et al. 2007, 2008). Accordingly, at sites with abundant *E. radiata*, populations of *E. chloroticus* were characterised by adult modes in their size distributions with relatively large mean test diameters (94 ± 9.3 [SE] to 120 ± 2.8 mm). At sites without abundant populations of *E. radiata* in the inner fjord habitats, there were more prominent cohorts of new recruits, as indicated by the recruitment index, and there were relatively frequent total mortality events in the adult population. Causes of these mortality events, such as disease or physiological stress, may be associated with the poor nutritional status of sea urchin populations inhabiting inner fjord habitats. In the inner regions of Long Sound, which likely contains a reproductively isolated population, demographic variability was reduced. A corollary is that connectivity within the population network may result in a strong rescue effect, greater demographic variability and potential for higher average abundance for populations in the inner fjord marginal habitats, relative to abundance in reproductively

isolated populations in similar habitat, such as that observed in the marine reserve in Long Sound.

These combined environmental and demographic influences on size structure of *Evechinus chloroticus* were reflected in the results of the general linear model for mean adult test diameter, individuals >60 mm test diameter, within size distributions at the site level. Results indicated that variability in mean adult size among sites was strongly linked with a proxy for availability of abundant and high-quality food, density of *Ecklonia radiata*, and with a proxy for relative influence of newly emergent juveniles in the population, the recruitment index. These 2 variables statistically explained 82% of the variance in mean adult test diameter among sites.

The present data and analyses provide a rare comparison of regional-scale dynamics within a marine population network, with those in an isolated population and an open population, for a single species. Recently the Fiordland Marine Management Act 2005 established formal spatial management within this system in the form of 14 commercial exclusion zones within the inner fjord habitats for a total area of 46 002 ha (59% of inner fjord habitat) and 10 marine reserves with a total area of 10 241 ha (13% of inner fjord habitat) including the 3670 ha Te Tapuwae o Hua marine reserve comprised of Long Sound (Wing et al. 2004). The results of the present study have important implications for understanding population dynamics of sea urchins within this new spatial management scheme.

Sea urchins play a critical role in the structure of rocky reef communities and are important grazers on macroalgae and benthic invertebrates. Accordingly, their population dynamics have important consequences for maintenance of biodiversity within this system. In the context of spatial management the present study highlights the critical dependence of sea urchin subpopulation dynamics on local habitat quality and on supply of recruits from productive kelp forest habitats outside the marine reserve network (Wing et al. 2004). Because the most demographically stable and productive segments of the sea urchin population network fall outside the spatial management scheme, this leaves the regional population vulnerable to exploitation, or changes in food web structure in those outer coastal habitats. This could be partially ameliorated by inclusion of more kelp forest habitat in the marine reserve network, which would likely lead to greater stability of the regional sea urchin population, and other populations linked to kelp forest habitats (Rodgers & Wing 2008). This system highlights the important influence of connectivity of subpopulations for maintenance of abundance and distribution across gradients in habitat quality, which has important general consequences for understanding the effects of

spatial management of both fisheries and biological diversity within Fiordland and other coastal systems.

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