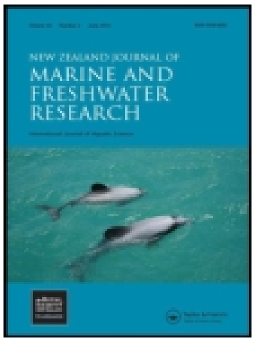

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Louise T. Kregting & Mark T. Gibbs

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Salinity controls the upper depth limit of black corals in Doubtful Sound, New Zealand

LOUISE T. KREGTING*
Department of Marine Science
University of Otago
P.O. Box 56
Dunedin, New Zealand

MARK T. GIBBS
Cawthron Institute
Private Bag 2
Nelson, New Zealand

*Present address: Marine Science Education and Research Centre, University of New England, 11 Hills Beach Rd, Biddeford, Maine 04005, United States. email: lkregting@une.edu

Abstract The New Zealand endemic black coral *Antipathes fiordensis* is found in Fiordland in shallow depths (c. 5m) compared with depths of other black corals worldwide. This is considered to be a result of the low light levels caused by the tannin-rich, surface low-salinity layers (LSLs) of water that are characteristic of the fiords. However, low salinity may also affect the distribution of black corals because of osmotic stress. We found a strong relationship between the upper limit of coral colonies and the salinity gradient along Doubtful Sound and no significant relationship between the upper depth limit of *A. fiordensis* and the underwater light field. This suggests that salinity, rather than light levels, plays a dominant role in controlling the upper depth limit of *A. fiordensis*. This result was supported by a salinity tolerance experiment in which coral colonies were held *in situ* in a range of salinities (6–32 psu). This experiment revealed that corals can tolerate salinities of between 20 and 30 psu for up to 6h as long as lowered salinities were periodically interrupted by higher, less detrimental salinities (>32 psu). Although LSLs may reduce incoming irradiation, the extreme upper limit of *A. fiordensis* in Doubtful Sound appears to be controlled by the salinity field.

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Keywords black coral; distribution; light; salinity; Doubtful Sound; Milford Sound; New Zealand; fiords

INTRODUCTION

Black corals (Order Antipatharia) are almost exclusively observed in deep-water habitats, typically below 100m depth worldwide (Grigg 1965), that are characterised by low current flows and a low light regime. By contrast, a small number of black coral populations have been observed in shallower habitats (>20m) featuring low light levels, such as caves in the Hawaiian Islands (Grigg 1965) or extremely turbid environments in the West Indies (Warner 1981). As both these environments are characterised by low light levels it has been hypothesised that black coral colonies are unable to survive higher light regimes typical of more shallow subtidal environments and that light exerts a dominant influence on the depth distribution of black corals (Grigg 1965).

In the New Zealand fiords, black coral populations of *Antipathes fiordensis* can be found as shallow as 4m, and are possibly the largest population of black corals growing within diving range (<30m) in the world (Grange 1985). Grange & Singleton (1988) suggested that surface low-salinity layers (LSLs) in the New Zealand fiords act to attenuate incoming irradiation, and this in turn leads to the deep-water emergence of antipatharians. The underwater light climate in the New Zealand fiords is low, c. 1–2% of the surface irradiance at 15m depth, owing to a combination of steep narrow walls in the fiords restricting direct light from entering the water column and robust LSLs (Grange et al. 1981; Grange & Singleton 1988). The LSLs act to attenuate incoming irradiation both through scattering light associated with the different refractive indices of the mixing fresh and salt water, and also through light absorption by the humics trapped in the LSLs (Rutherford et al. 2000; Gibbs 2001; Peake et al. 2001).

However, given the nature of the LSLs, osmotic stress as a result of low salinity is another possible

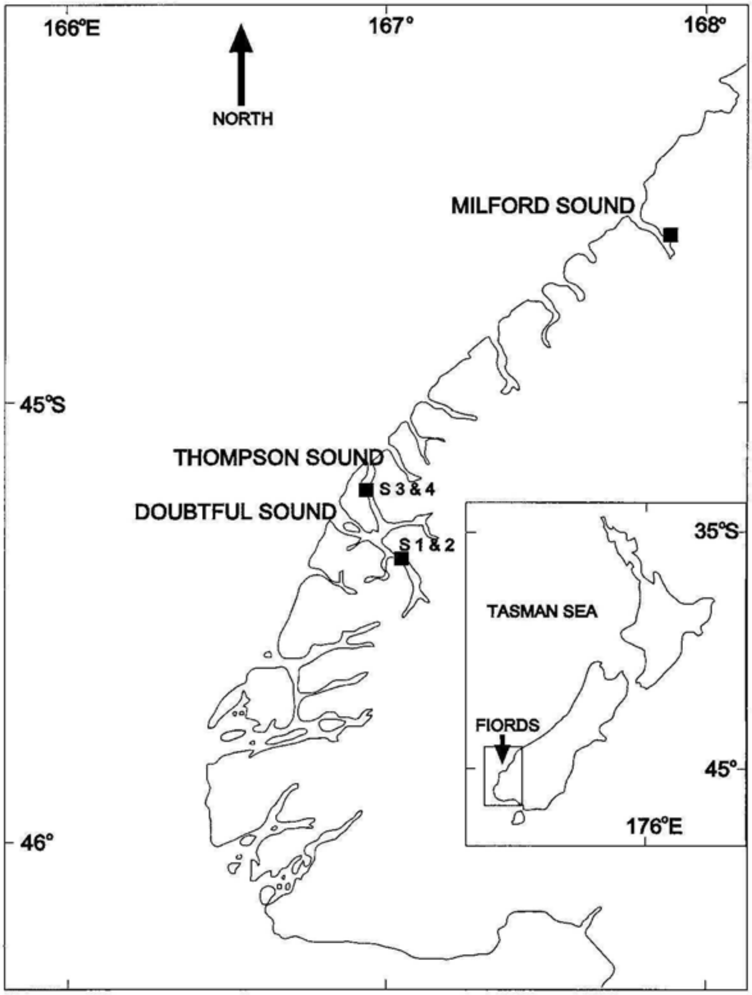


Fig. 1 Map of the southern fiords, Fiordland, South Island, New Zealand. Coral surveys were conducted in Doubtful Sound at the low salinity sites, sites 1 and 2 (S 1 and 2), and the high salinity sites, sites 3 and 4 (S 3 and 4). An *in situ* salinity tolerance experiment was conducted in Harrison Cove, Milford Sound.

factor controlling the upper depth limit of black coral colonies, as salinity may be regarded as a dominant factor in the distribution of organisms in an estuarine environment (Little 2000). Corals, like many marine invertebrates, are osmo-conformers, unable to control their internal fluid chemistry and therefore absorbing water to become iso-osmotic with their surroundings (Rankin & Davenport 1981). Low salinities therefore could cause damage to animal tissue or even death. Animal tissue swelling and damage has been observed for coral colonies of *Acropora formosa* after flood water (Van Woesik et al. 1995), whereas tissue necrosis was observed in anemones exposed to low salinities (Engebretson & Martin 1994). One way osmo-conformers living in fluctuating salinities can minimise physiological stress is by reducing contact with the water (McLusky & Elliott 2004). Reducing surface area to volume ratios by contracting the muscles has been observed in hydroids and annelids (Kinne 1967). In laboratory conditions, *A. fiordensis* was observed to retract tentacles and produce mucus as a physiological response to lowered salinities, with death occurring within 8 h of exposure to salinities <25 psu (Mladenov & Brewin 1996).

The question of the relative roles of light attenuation and salinity tolerance in determining the upper limit of the distribution of *A. fiordensis* is of particular importance in Doubtful Sound, one of the central fiord systems (Fig. 1). The LSL in Doubtful Sound is maintained by a combination of natural environmental inflows (catchment run-off) and an anthropogenic source in the form of a freshwater inflow from the Manapouri hydro-electric power station (Gibbs et al. 2000). The inflow of fresh water from the Manapouri hydro-electric power station enters at Deep Cove, the head of the long (c. 40 km) narrow (c. 2 km) fiord (Fig. 1), and contributes c. 2.5 times more water annually than natural inflows (Gibbs 2001). The anthropogenic inflow plays a strong role in maintaining and controlling the behaviour of the LSL and may potentially control the distribution and abundance of *A. fiordensis* in the near surface waters through alterations to the salinity or light environment. Observations suggest that a light gradient exists across the width of the fiord because of the steep walls within the fiord. The northern side is almost never exposed to direct sunlight, in contrast to the southern side which is regularly exposed to direct sunlight during daylight hours. The fiord is narrow enough so that no cross-fiord salinity gradient occurs (Gibbs 2001). By contrast, strong along-fiord gradients in the near-surface salinity field are a feature of Doubtful Sound so that near the head of the fiord, the LSLs may be several metres deeper than at the entrance of the fiord (Gibbs 2001).

Whether light or salinity controls the upper depth distribution of *A. fiordensis* has not been tested *in situ*. The goal of this study therefore was to elucidate the roles of light and salinity on the upper depth distribution of *A. fiordensis* in the New Zealand fiords. This was achieved by determining coral distribution and environmental data, and an *in situ* salinity tolerance experiment.

MATERIALS AND METHODS

Coral surveys

The depth distribution of *A. fiordensis* was determined at two locations within Doubtful Sound (Fig. 1) between August 1999 and August 2000. The first location was midway down Doubtful Sound and was characterised by a thick LSL (<9 m). The second location was near the entrance of Thompson Sound (part of the Doubtful Sound system) and was characterised by a thin LSL (<5 m). The locations were within 200 m of permanent oceanographic moorings (mooring M2 and M4 in Gibbs et al. 2000; Gibbs 2001) allowing the acquisition of site-specific environmental data. Within each location paired sites were chosen, one on the northern side of the fiord which had low light levels because of the steep side of the walls, the other site on the southern side of the fiord which received direct sunlight. Sites one and two were located midway down Doubtful Sound and will be referred to as the low salinity sites, whereas sites three and four were located near the entrance of the sound, referred to as the high salinity sites (Fig. 1).

At each site, nine haphazardly selected 20 (w) × 17 (d) m quadrats were surveyed within a c. 400 m area. A depth of 17 m was chosen for logistical purposes of diving. The top and bottom of each quadrat were defined by deploying weighted ropes from the surface to a depth of 17 m down the steep slopes of the fiord. Each rope was separated by a horizontal distance of 20 m. Depths were referenced against the marked rope and the top of the rope was placed a known distance above the mean spring low water level, so the true depths of the corals could be determined. The tidal range in the Doubtful Sound complex is typically less than 2 m. Divers using SCUBA then measured the depth of each coral within the quadrat by swimming between the end ropes at 0.5 m depth intervals. The depth of each coral was measured using digital depth gauges.

Environmental parameters

Salinity was measured hourly (January–November 1999) at 2 m depth intervals (to 25 m) by the nearby oceanographic moorings. Details of these moorings and analyses of these data may be found in Gibbs et al. (2000) and Gibbs (2001). Data are shown as the number of periods when the salinity was <25 psu, as salinities below 25 psu caused mortality within 8 h because of osmotic stress (Mladenov & Brewin 1996). Comparisons of photon flux density (PFD) at sites one (north face) and two (south face) were determined by deploying two LI-COR 193A spherical quantum sensors on three separate occasions during March and July 2000 for 3 days at a time. Sites one and two were selected midway in Doubtful Sound where the steepest parts of the fiord exist, therefore large differences in light levels between the paired sites were expected. The LI-COR sensors were connected to dataloggers and PFD was recorded every minute. These sensors were deployed at a fixed depth corresponding to the observed upper depth limit of the corals. The depth of the sensors varied between 7 and 9 m depending on the tidal cycle. The weather conditions (fine, variable, or rain) during these deployments were also noted.

Salinity tolerance experiment

To determine the salinity tolerance of *A. fiordensis*, a manipulative experiment was performed in Milford Sound over a period of 16 h (1 September 2000) (Fig. 1). Like Doubtful Sound, Milford Sound also features a robust surface LSL (Gibbs 2001), and was chosen because of the availability of the Milford Sound Observatory mooring floats which allowed the experiment to stay submerged over a tidal period.

Four large (c. 1 m height) coral colonies were collected from depths of 25–30 m from Sinbads Cove, Milford Sound (45°37.8S 167°54.4E). The corals were placed in sealed 20-litre buckets underwater and transferred to the Observatory in Harrison's Cove. Small (<20 cm diam.) rocks were also collected along with the corals. Holes were drilled into the rocks and 24 small branches (20 cm) were cut from the c. 1-m colonies using side-cutters and placed into the drilled holes. Colonies were not exposed to air during this operation. The rocks containing the branches were randomly arranged in eight rectangular trays (three replicate rocks per tray) and the trays were kept at a depth of 15 m whilst the colonies acclimatised. The corals remained at this depth for 7 weeks, during which time they were examined weekly to assess their health.

The trays were deployed when the base of the LSL, defined here as 27 psu, was at a depth of 2.5 m. Trays containing three replicate corals were suspended at depths of 2.5, 3.0, 3.5, 4.0, 4.5, 5.0, 7.0, and 15.0 (control) m beneath the water surface under the observatory. Coral vitality was observed by divers every hour for 8 h, then 12 and 16 h after the positioning of the trays. Inspections were made using a magnifying glass and coral vitality was ranked according to the scale developed by Mladenov & Brewin (1996), based on morphology and polyp activity. Polyp activity was determined by touching each replicate coral with a thin wire, using the following ranking system: (1) normal appearance—tentacles clung to wire probe and were translucent and extended; (2) tentacles slightly retracted—some response upon probing, translucent; (3) tentacles retracted—no response upon probing, opaque; (4) swollen polyps—tentacles small, mucus production, and no response upon probing; (5) coral dead—polyps are sloughing off and black skeleton is easily seen.

A conductivity-temperature-depth instrument (CTD; Seabird SBE–19) was deployed every half hour throughout the experiment to measure the salinity profile (2.5 to 15 m). PFD was measured at 1300 h at depths of 3, 5, 7, and 10 m using a handheld light sensor (Li-COR LI–189). PFD measurements were also made on a sunny day before the experiment (29 August 2000) at the same depths as during the experiment for comparison.

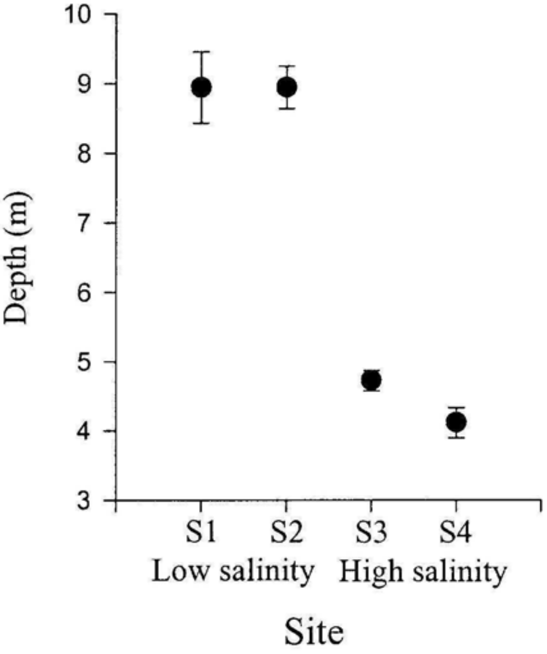


Fig. 2 Mean depth distributions of the shallowest growing black coral *Antipathes fiordensis* colonies from each site in Doubtful Sound. Low salinity sites: NF = S1 (north face, site 1), SF = S2 (south face, site 2); High salinity sites: NF = S3 (north face, site 3) and SF = S4 (south face, site 4). Area = 3060 m^2. ($n = 9 \pm$ SE).

Statistical analysis

To determine the differences in the depth of the shallowest growing black corals between sites (north versus south face) and salinity (high versus low), a two-way ANOVA (general linear model) with salinity and sites as independent factors and coral depth as a dependent factor was used (Zar 1996). Significant differences between treatments groups were compared using the post-hoc Tukey test. To ensure that the assumptions for ANOVA were met, tests for normality (Kolmogorov-Smirnov test with Lilliefors' correction) and equal variance (Levene median test) were carried out before analysis of the data. To compare depth (hence salinity) treatments of the black corals in the *in situ* experiment, a non-parametric Friedman's repeated measures ANOVA on ranks was used as data were not normally distributed (Zar 1996). For all analysis, significance was set at the 5% level ($\alpha = 0.05$). All statistical analyses were carried out using the software package Sigma Stat® 2.03 (SPPS).

RESULTS

Coral surveys

There was a significant difference in the upper depth limit of black corals between the low and high salinity sites (two-way ANOVA $F_{1,35} = 194.3$, $P = 0.001$). Corals growing at the high salinity sites near the entrance of the fiord were found at an average depth of 4.4m, which was significantly shallower than corals at the low salinity sites further up the fiord at an average depth of 8.9m (Tukey test $P < 0.001$)(Fig. 2). There was no significant difference in the upper depth limit of corals between the sides of the fiord (north face versus south face) within the high and low salinity sites (two-way ANOVA $F_{1,35} = 0.885$, $P = 0.354$) (Fig. 2). There was also no significant interaction between salinity (high versus low) and site (north face versus south face) (two-way ANOVA $F_{1,35} = 0.885$, $P = 0.354$).

Environmental parameters

The annual mean salinities at 4m at the high salinity sites and 9m at the low salinity sites were almost identical at 29.58 and 28.39 psu, respectively (Table 1). The number of periods when the salinity was less than 25 psu was also similar at the high and low salinity sites (Table 1). By contrast, light levels were considerably higher at site two on the south face of Doubtful Sound by comparison with site one on the north face of Doubtful Sound (Fig. 3), with the differences occurring over a range of weather conditions. In particular, the maximum PFD recorded at site two during March 2000 was 425.7 μmol photons m^{-2} s^{-1} compared with 31.5 μmol photons m^{-2} s^{-1} at site one (Table 2). During July, light levels were considerably lower and maximum PFD recorded was 266.9 μmol photons m^{-2} s^{-1} and 38.8 μmol photons m^{-2} s^{-1} for site two and one, respectively (Table 2).

Salinity tolerance experiment

The greatest changes observed in the vitality of *A. fiordensis* colonies occurred within the first 6h for all treatments (Fig. 4), and after 6h there was no change in the vitality of any of the coral colonies (Fig. 4). The black corals varied in response to the different depth (salinity) treatments (Friedman's rank test $P < 0.001$). Visual signs of osmotic stress

Table 1 Frequency when the salinity was continuously <25 psu for 1, 6, 12, 24, 48, and 72h at the upper depth limit (4m at the high salinity sites, sites 3 and 4, and 9m at the low salinity sites, sites 1 and 2) of *Antipathes fiordensis* during 1999. Mean annual salinity values at 4 and 9m depth are also shown.

	Frequency where salinity <25						Annual
	1h	6h	12h	18h	24h	48h	salinity
High salinity	783	179	75	42	24	2	29.58
Low salinity	673	207	78	34	17	0	28.39

Table 2 Comparison between mean and maximum photon flux density (PFD) from site 1 (S1, north face) and site 2 (S2, south face) in Doubtful Sound, New Zealand (2000) (μmol photons m^{-2} s^{-1}), and percentage increase in PFD that site 1 receives compared with site 2 based on maximum values.

	S1 mean	S1 max.	S2 mean	S2 max.	% more PFD that S 1 receives compared to S 2 based on max. values
7 March	7.5	23.2	151.7	425.7	94.5
8 March	11.6	31.5	–	189.3	83.3
9 March	11.9	23.2	–	87.9	73.6
18 July	7.3	7.3	61.3	148.5	95
19 July	6.5	N8.2	95.9	266.9	96.9
20 July	14.5	25.1	23.9	61.6	59.3
25 July	1.8	15.2	1.8	17.0	10.9
26 July	4.5	7.3	15.1	29.0	74.8
27 July	–	38.8	–	52.8	26.5

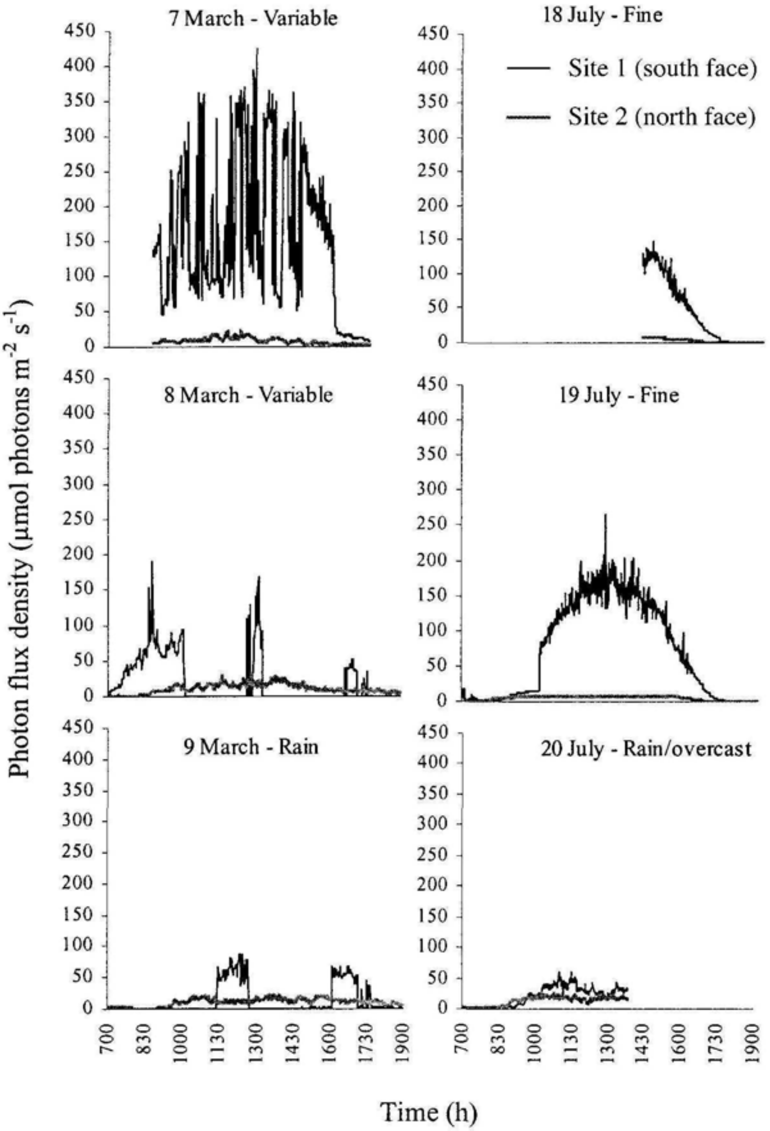


Fig. 3 Daily variation in photon flux density (μmol photons m^{-2} s^{-1}) from the north (site 1) and south (site 2) face, from 7–9 March and 18–20 July 2000 in Doubtful Sound, New Zealand. Weather conditions on each day are indicated on each graph.

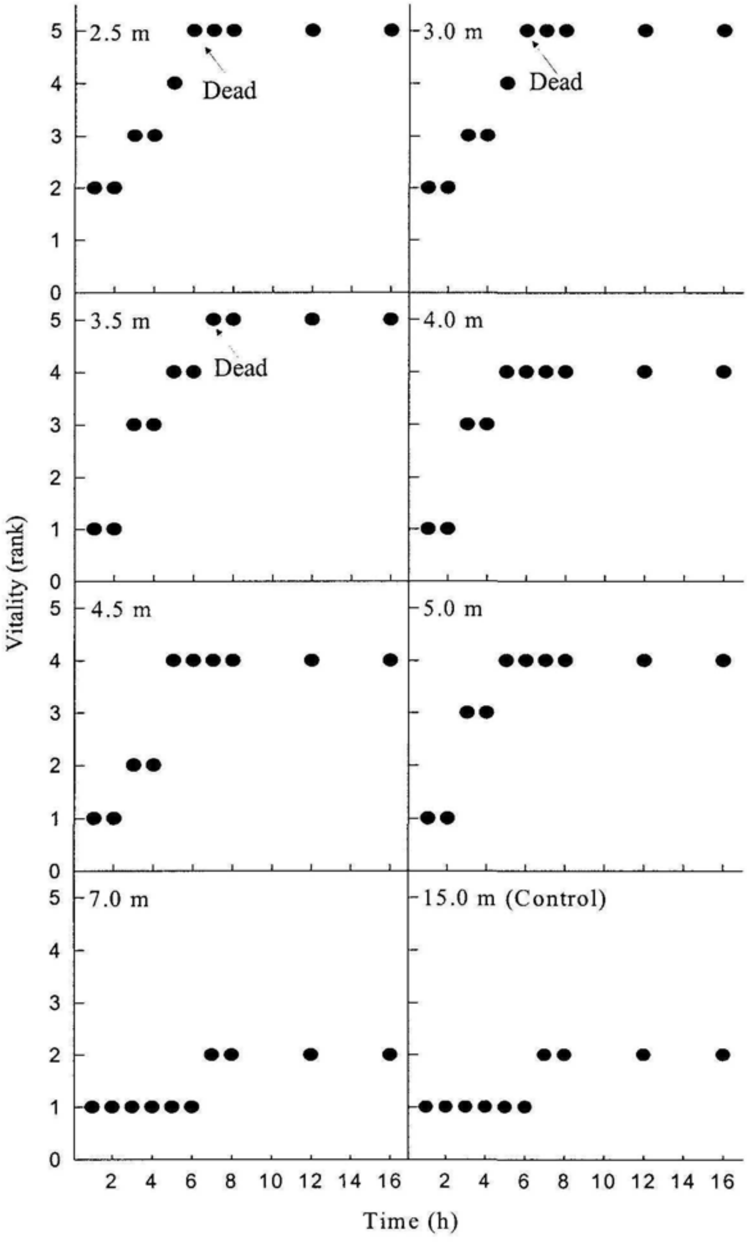
were evident within the first hour for corals at 2.5 and 3.0 m (Fig. 4). The results from the transplant treatments may be summarised as follows.

Corals above 3.5 m were exposed to salinities ranging from 6.3 to 30 psu (2.5 m), 6.6 to 32 psu (3.0 m), and 7.8 to 32 psu (3.5 m) from 0 to 5 h. Within 1 h at these depths, osmotic stress was evident with tentacles becoming unresponsive, their size declining and swollen, with mucus production evident. After 5–6 h corals at 2.5, 3.0, and 3.5 m were classified as dead (Fig. 4).

Corals at 4.0 and 4.5 m were unresponsive to a wire probe after 4 h (Fig. 4) and were exposed to minimum salinities of 12.9 psu (4.0 m) and 25 psu (4.5 m). Throughout the remainder of the experiment (12 h) tentacles retracted to the point where polyps were indistinguishable from the main axial skeleton. Salinity values from 4 h onwards fluctuated between 24–30 psu (4 m) and 25–32 psu (4.5 m).

Corals at a depth of 5.0 m had a reduction in tentacle size within 2 h, having been exposed to salinities of c. 32 psu. After 6 h, mucus production was evident and the polyps became very small and difficult to define. The colonies stayed in this state for the remainder of the experiment (10 h) with salinities fluctuating between 30 and 33 psu.

Fig. 4 Coral vitality ranked from 1 to 5 (1, healthy; 5, dead), of the black coral *Antipathes fiordensis* suspended at 2.5, 3.0, 3.5, 4.0, 4.5, 5.0, 7.0, and 15.0 (control) m, over 16 h at the Underwater Observatory, Milford Sound, New Zealand, October 2000. (*n* = 3 ± SE) (error bars smaller than points).



Coral colonies at 7.0 and 15 m depth remained healthy with tentacles fully extended, translucent and responsive to the wire probe for the first 6 h of the experiment. At 6 h, a slight reduction in the vitality of the corals was evident with tentacles slightly retracted and they remained this way for the remainder of the experiment. Salinity values at 7.0 and 15 m were 32–33 and >34 psu, respectively.

The structure of the LSL, and hence the distribution of salinity with depth, changed throughout the day of the experiment (Fig. 5). Large physical disturbances of the LSL were recorded at 4 and 6 h of the experiment. The base of the LSL varied between c. 1 and 5 m from the surface during the day with no difference in salinity between 7 and 15 m (data not shown). At the start of the experiment (Time = 0 representing

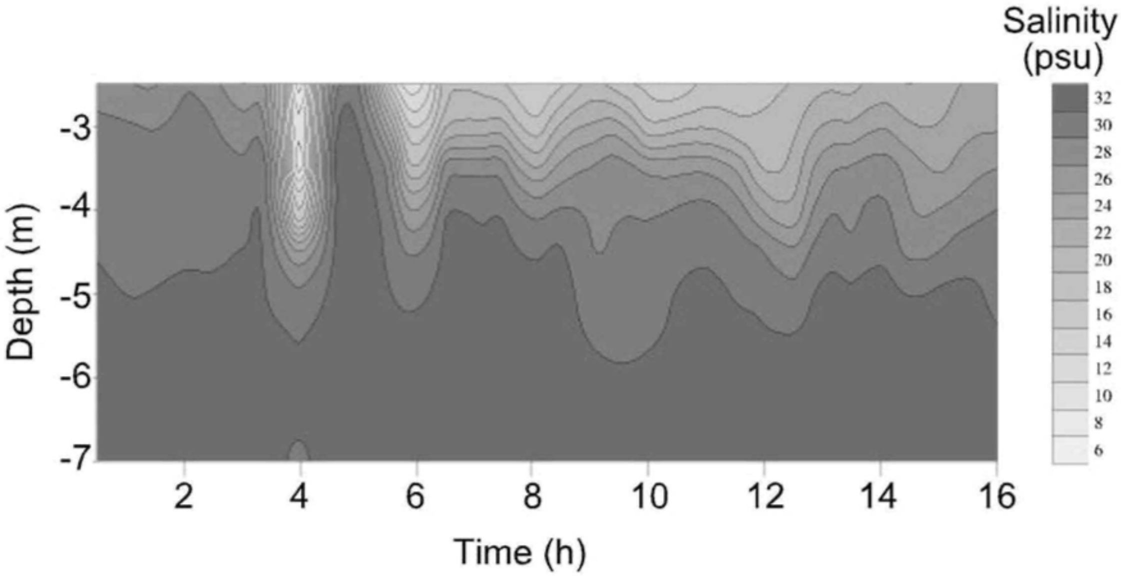


Fig. 5 Contour plot of salinity profiles recorded to 7 m during the salinity tolerance experiment of the black coral *Antipathes fiordensis* colonies over a 16 h period, at the Underwater Observatory, Milford Sound, New Zealand, October 2000.

Table 3 Photon flux density (PFD) (μmol photons m^{-2} s^{-1}) at four discrete depths at the Underwater Observatory, Milford Sound, Fiordland, New Zealand on 29 August and 3 October 2000.

	PFD (μmol photons m^{-2} s^{-1})	
Depth (m)	29 August 2000	3 October 2000
3	203.8	4.5
5	125.6	1.6
7	82.5	0.9
10	46.2	0.5

1100 h), the LSL was almost non-existent. Light levels on the day of the experiment were low with PFD ranging between 4.45 μmol photons m^{-2} s^{-1} at 3 m depth and 0.5 μmol photons m^{-2} s^{-1} at 10 m (Table 3). Furthermore, the PFD at 7 m measured before the experiment on a sunny day were considerably less than those observed in Doubtful Sound at the same depth (82.51 compared with 425.7 μmol photons m^{-2} s^{-1}, respectively; Tables 2 and 3).

DISCUSSION

The observed upper depth limit of the black coral *A. fiordensis* at sites near the head of the fiord was deeper by c. 5 m than at sites near the fiord entrance, suggesting that salinity plays a major role in determining the upper depth distribution of black coral. The mean salinities at the upper depth limit of *A. fiordensis* were almost identical at both sites, providing strong evidence that salinity controls the upper depth distribution of black coral in Doubtful Sound. Despite very large differences in the underwater light field between the sides of Doubtful Sound, there was no significant difference in the upper depth limit of *A. fiordensis* colonies between the north and south face walls of the fiord.

This is the first study to examine the salinity tolerance of corals *in situ*. Results showed that when *A. fiordensis* colonies were subjected to salinities below 20 psu, mortality occured within 5 h. Furthermore, *A. fiordensis* can tolerate salinity values between 20 and 30 psu for up to 6 h as long as low salinities were interrupted by higher less detrimental values above 32 psu. Sensitivity of corals to reduced salinity has also been observed in laboratory studies. For example, mortality of the coral *Stylophora pistillata* owing to osmotic stress also occurred within 2 and 12 h of exposure to salinities of 10 and 15 psu, respectively (Kerswell & Jones 2003). A laboratory study conducted on a reef-building coral with algal symbionts showed that corals were able to survive at low (12 psu) and high (55 psu) salinities for several hours, but only when the salinity changes occurred gradually. These results highlight the sensitivity of corals to the cumulative effect of mean salinity changes, and to the rate of change in salinity.

In this study it was not clear if mortality of *A. fiordensis* was the result of rapid changes in salinity or a cumulative effect of low mean salinities owing to the physical disturbances of the LSL that occurred early in the salinity tolerance experiment. These initial perturbations in the LSL were likely to have been associated with internal waves propagating along the fiord as the LSL developed during the day, and were presumably associated with a strong wind and rain event (Gibbs et al. 2000). It is possible that a gradual decline in salinity allows *A. fiordensis* to initiate physiological and physical tolerance mechanisms that reduce the effect of low salinity. Reduction of surface area to volume by contracting the tentacles was observed by *A. fiordensis* when exposed to low salinities (<25 psu). Similar responses to low salinities have been observed for other marine invertebrates such as annelids, molluscs, and hydroids (Kinne 1967).

Within Doubtful Sound, annual monitoring of the salinity structure of the water column demonstrated that there were a number of periods when the salinity at the upper depth range of black corals at both the low salinity sites (9 m) and the high salinity sites (4 m) was 25 psu or less (Table 1). For example, events when the salinity was 25 psu or less for a period of 6 h occurred 179 times (12%) at the high salinity sites and 207 times (14%) at the low salinity sites over the year, and the corals survived these events. However salinity data were collected hourly, and it is possible that short period perturbations in the LSL, not captured in the data, allowed higher salinity water to immerse the corals (Gibbs et al. 2000). Further investigation is needed on the effect of salinity on *A. fiordensis* to determine whether the rate of change in salinity or the cumulative effect of lower mean salinities causes mortality. Further data are also needed to determine how much time is required to initiate mechanisms, such as mucus production, that may help *A. fiordensis* combat sub-optimal salinities.

The light data obtained in March and July 2000 showed that the south face of Doubtful Sound received more irradiance than the north face on days with broken cloud to full sun, even though corals were growing to the same upper depth limit at both sides of the fiord (Fig. 2). Although these data were collected from only two sampling sites within Doubtful Sound, it can be assumed that the whole of Doubtful Sound has a similar light regime. Grange et al. (1981) obtained similar results to the present study on the north face (maximum annual mean values of 3.5–15.6 μmol photons m^{-2} s^{-1}) at Tricky Cove, Doubtful Sound. If light was limiting the upper depth limit of *A. fiordensis* between sides of the fiord, it would be expected that corals would grow at different depths. However corals were growing at similar depths on the north and south face of the fiord.

The qualitative agreement between the salinity fields at the upper distribution limit at the low and high salinity sites, and the agreement between these values and the tolerances predicted by the salinity tolerance experiment, all lead to the conclusion that although the reduced light probably allows the deep-water emergence of black corals (Grange & Singleton 1988), it is ultimately the salinity in the LSL that determines the upper depth limit of *A. fiordensis*. This conclusion has implications for the management of Doubtful Sound in that changes to the surface salinity field, either through natural or anthropogenic processes, may lead to the loss of the unique shallow water black coral colonies.

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