

Volatile bromocarbons produced by *Falkenbergia* stages of *Asparagopsis* spp. (Rhodophyta)

Abstract—Volatile halocarbons released by 12 *Falkenbergia* phase isolates of *Asparagopsis taxiformis* and *Asparagopsis armata* collected from widely scattered geographical locations were identified using a purge and trap technique and gas chromatography/mass spectrometry. Production of the compounds under normal and high irradiance was quantified where possible. Bromoform (CHBr_3), dibromomethane (CH_2Br_2), 1,2-dibromoethylene ($\text{C}_2\text{H}_2\text{Br}_2$), dibromochloromethane (CHBr_2Cl), and tribromoethylene (C_2HBr_3) were identified as algal products. $\text{C}_2\text{H}_2\text{Br}_2$ and C_2HBr_3 have not previously been recorded as natural products. Considerable qualitative and quantitative differences existed between isolates in the halocarbons released. The rates of CHBr_3 and $\text{C}_2\text{H}_2\text{Br}_2$ production were negatively correlated. Increased irradiance invariably resulted in higher rates of release of halocarbons. Initial rates of production ranged between <8 and 866 ng g^{-1} fresh weight (FW) h^{-1} for CHBr_3 , <3 and 59 ng g^{-1} FW h^{-1} for CH_2Br_2 , and <0.4 and 17 ng g^{-1} FW h^{-1} for $\text{C}_2\text{H}_2\text{Br}_2$.

Volatile halocarbons are produced by many marine algae (Gschwend et al. 1985; Manley and Dastoor 1987; Manley et al. 1992; Gribble 1996; Goodwin et al. 1997b). The red alga *Asparagopsis taxiformis* (Delile) Trev., which is cosmopolitan in warm-temperate, subtropical, and tropical waters, is a particularly prolific source releasing over 100 such compounds, mainly brominated and iodinated methanes and acetones (Burrenson et al. 1976; McConnell and Fenical 1977). This alga is a dioecious gametophytic stage that alternates in its life cycle with a heteromorphic sporophyte known as *Falkenbergia hillebrandii* (Born.) Falkenb. (Dixon and Irvine 1977). Surprisingly, Burrenson et al. (1976) were unable to demonstrate production of any volatile halogenated compounds by the asexual form that they identified as *Falkenbergia rufolanosa* (Harvey) Schmitz. However, the latter attribution is open to question as *F. rufolanosa* is the tetrasporophyte form of the only other currently recognized *Asparagopsis* taxon, *A. armata*, a species endemic to cold-temperate waters. This confusion probably arises as the *Falkenbergia* stages of both *Asparagopsis* species are considered morphologically indistinguishable (Dixon 1964). Both form small dense fluffy balls of branched filaments in shallow sublittoral environments.

We have studied volatile halocarbon production by laboratory-grown cultures of 12 *Falkenbergia* stages of *Asparagopsis* spp. from a wide range of geographical locations including both warm- and cold-water environments and have demonstrated release of several bromocarbons, two previously unreported as natural products. Production of several of the bromocarbons has been quantified under both normal and high irradiance because increased irradiance can stimulate volatile halocarbon production by many marine algae (Mtolera et al. 1996).

Isolates and culture conditions—Isolates of *Falkenbergia* stages were obtained from the collection of Professor Michael Guiry of the Department of Botany, National University of Ireland, Galway, Ireland. The collection accession numbers of each isolate, together with the geographical locations where they were collected are indicated in Table 1. Isolates were maintained in seawater enriched with 20% von Stosch medium (von Stosch 1964). Initially algal cultures were established in petri dishes (50 mm diameter \times 20 mm) containing culture medium (15 ml) and incubated at 20°C illuminated from above with Thorn GroLux and Sylvana Lifeline fluorescent lights at an irradiance of $30 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (16:8 light:dark [LD] cycle). The algae were later subcultured into fresh medium (100 ml) in 250-ml conical flasks shaken at 100 rpm at 20°C under a similar light regimen.

For monitoring of volatile halocarbon release, alga (1 g fresh weight [FW]) was suspended in culture medium (10 ml) under an atmosphere of air in each of a series of screw-capped vials (25 ml) fitted with polytetrafluoroethylene (PTFE) septa and incubated at 20°C at an irradiance of $50 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ under fluorescent lights or an irradiance of $330 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ from a quartz halogen lamp for periods from 6 to 48 h. Duplicate vials were removed from the incubation chamber after the appropriate time period, and medium (5 ml) was withdrawn from each for analysis as described below. The remaining medium was either discarded or stored at -20°C for future reference. Control experiments in which culture medium that had not been exposed to the alga was spiked with authentic samples of various halocarbons and incubated in the absence of algae were also conducted.

Halocarbon and other analyses—Halocarbons present in the algal incubation medium were identified and quantitatively determined using a DANI 37.50 purge and trap sampler linked to a Hewlett Packard 5890 gas chromatograph equipped with a mass selective detector (MSD). Incubation medium (5 ml) was placed in a vial (20 ml) and 1,2-dibromoethane (1 ml of a $10 \mu\text{g liter}^{-1}$ solution was employed as an internal standard), previous investigations in the laboratory having established that this compound was not released by any of the *Falkenbergia* isolates under the conditions of the experiments. Vials sealed with aluminum crimp caps fitted with PTFE-coated butyl rubber seals were equilibrated in the purge and trap sampler at 50°C before purging with helium at a flow rate of 30 ml min^{-1} for 30 s. For qualitative measurements the vials were purged for 5 min, but for quantitative determination a purge time of 30 s was used to ensure that analysis was conducted in the range where a linear relationship existed between concentration and response.

Volatiles were trapped on Tenax TA and thermally desorbed at 250°C for 1 min onto a Chrompak Poroplot Q cap-

Table 1. Rates of release of volatile brominated compounds by *Falkenbergia* stage isolates of *Asparagopsis* spp. from various geographical locations over a period of 6 h under low (30 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) or high (330 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) irradiance.

| Culture collection No. | Location of original collection | Mean release rate* (ng g ⁻¹ FW h ⁻¹) | | | Suggested species assignment of isolate (Ní Chualáin 1997) |
|------------------------|---------------------------------|---|---|---------------------------------|--|
| | | CHBr ₃ | C ₂ H ₂ Br ₂ | CH ₂ Br ₂ | |
| 1030 | Sicily | 435 (600) [†] | <0.4 (<0.4) [†] | <3 (<3) | <i>A. taxiformis</i> |
| 1076 | Italy | 409 (709) | <0.4 (<0.4) | <3 (<3) | <i>A. taxiformis</i> |
| 0510 | Ireland | 238 (686) | <0.4 (<0.4) | 4 (<3) | <i>A. armata</i> |
| 1077 | Italy | 205 [‡] (412) [‡] | <0.4 [†] (<0.4) [†] | <3 (17) | <i>A. taxiformis</i> |
| 0997 | Hawaii | 170 (347) | <0.4 (0.9) | 5 (15) | <i>A. taxiformis</i> |
| 0604 | Australia | 142 (154) | <0.4 (<0.4) | <3 (<3) | <i>A. armata</i> |
| 1026 | Spain | 68 (866) | 2.0 (2.5) | 23 (59) | <i>A. armata</i> |
| 0996 | California | 43 [‡] (57) [‡] | 1.0 (5.3) | 5 (18) | <i>A. armata</i> |
| 1033 | Japan | 41 (188) | <0.4 (1.3) | <3 (<3) | <i>A. taxiformis</i> |
| 1075 | Gran Canaria | 18 (54) [‡] | 2.5 (5.0) | <3 (7) | <i>Asparagopsis</i> (Carib. strain) |
| 0985 | Florida | 13 [‡] (32) [‡] | 3.3 (3.3) | 10 (29) | <i>Asparagopsis</i> (Carib. strain) |
| 0999 | Mexico | <8 <8 | 3.0 (17) | 4 (8) | <i>Asparagopsis</i> (Carib. strain) |

* Release rate under high irradiance given in parentheses. Relative standard deviation = 29% for CH₂Br₂, 37% for C₂H₂Br₂, and 35% for CHBr₃.

[†] Tribromoethylene present but not quantified.

[‡] Dibromochloromethane present but not quantified.

illary column (10 m × 0.32 mm inner diameter with 10 μm divinylbenzene/styrene polymer as the bonded phase). The injector port temperature and MSD transfer line were maintained at a temperature of 250°C, and the gas chromatograph oven was held at 40°C for 1 min, then programmed at 10°C min⁻¹ to 230°C and maintained at this temperature for 5 min. For identification of halocarbons the MSD was operated in the full-scanning mode, but, where quantitative determination was required, the instrument was employed in the selected ion-monitoring mode. Ions monitored for the various compounds were as follows: bromoform m/z 250, 252, 254, and 256; dibromomethane m/z 172, 174, and 176; 1,2-dibromoethylene m/z 184, 186, and 188; and 1,2-dibromoethane (internal standard) m/z 107 and 109. The limits of detection for bromoform, dibromomethane, and 1,2-dibromoethylene were 5 $\mu\text{g liter}^{-1}$, 2 $\mu\text{g liter}^{-1}$, and 0.25 $\mu\text{g liter}^{-1}$, respectively. Henry's law constants (concentration of compound in gaseous phase/concentration of compound in aqueous phase) were determined by gas chromatography of samples of gaseous and aqueous phases from vials containing standard solutions of the compounds equilibrated at 20°C. The Henry's Law con-

stants at 20°C for all compounds monitored were comparatively small, i.e., 0.019, 0.051, and 0.024 for bromoform, dibromomethane, and dibromoethylene, respectively. Accordingly, in determination of the rates of production of halocarbons by algal cultures the halocarbons present in the incubation vials were considered to be located entirely in the aqueous phase. The resulting error in measurements was relatively small with an underestimation of 2.8%, 7.6%, and 3.6% in the calculated rates of production of bromoform, dibromomethane, and dibromoethylene, respectively. This difference must be considered in the context of the overall relative standard deviations in the determination of bromoform, dibromomethane, and dibromoethylene by this method of 35%, 29%, and 37%, respectively (Table 1).

Cis and *trans* isomers of 1,2-dibromoethylene were distinguished by gas chromatography under the conditions outlined above using a Hewlett Packard 5965B infrared detector. Oxygen concentrations above cultures were measured by injecting headspace (25 μl) into a Shimadzu GC-9A gas chromatograph equipped with a stainless steel Alltech CTRI combined column (0.9 m × 2 mm) and fitted with a thermal conductivity detector. The oven was programmed from 60°C to 250°C at 20°C min⁻¹. Oxygen concentrations were determined from a single injection using a three-point external calibration with an authentic gas standard.

Halocarbon production—Preliminary investigations in which *Falkenbergia* isolate 0985 was incubated for 24 h under low (30 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) irradiance showed that several volatile halocarbons were released in significant quantities by the alga. These compounds were identified by comparison of their retention times and mass spectra with those of authentic standards of dibromomethane, bromoform, and the *cis* and *trans* isomers of 1,2-dibromoethylene (Fig. 1). Infrared spectra of the gas chromatographic peaks of the latter compound from the algal culture indicated it was present mainly as the *trans* isomer. While both dibromomethane and bromoform are known to be produced wide-

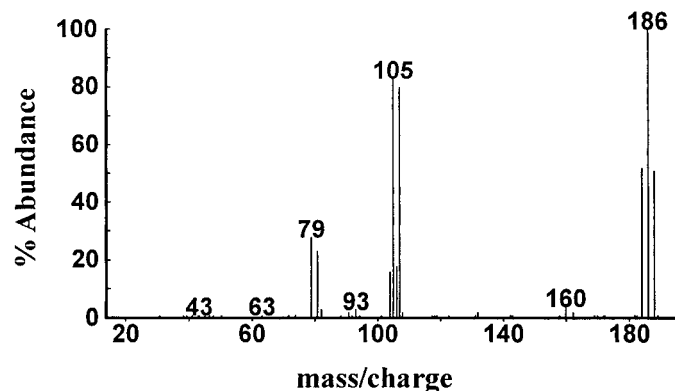


Fig. 1. Mass spectrum of gas chromatographic peak identified as dibromoethylene released by *Falkenbergia* isolate 0985.

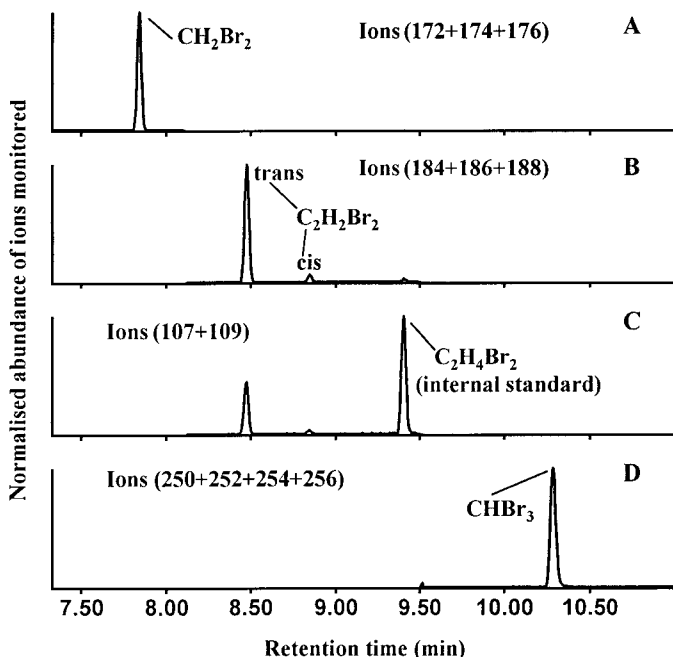


Fig. 2. Selected ion chromatograms for various bromocompounds released by *Falkenbergia* isolate 0985.

ly by marine algae (Gschwend et al. 1985), 1,2-dibromoethylene has not previously been identified as an algal product or indeed a natural product of any organism.

The concentration of each compound was determined by gas chromatography/mass spectrometry by monitoring selected fragment ions characteristic of each compound. A typical chromatogram obtained from an algal culture is shown in Fig. 2. Production of the three halocarbons over a 48-h period by isolate 0985 under low and high irradiance is displayed in Fig. 3. The concentrations of both dibromomethane and bromoform attained a maximum after 12 h but subsequently decreased so markedly that dibromomethane could not be detected after 48 h under either light regimen (Fig. 3). Control experiments using culture medium spiked with bromoform and dibromomethane in the absence of algae indicated that both compounds were stable under the light regimens employed. In contrast to production of bromoform and dibromomethane, release of dibromoethylene continued throughout the duration of the experiment, although the rate declined after 24 h. Stressing the alga by subjecting it to high irradiances appeared to increase the initial rate of production of all the halocarbons without affecting the general pattern of release. The reason for the losses of halocarbons after the longer periods of incubation is not immediately apparent. The compounds might undergo physical absorption or chemical/biochemical conversion within the algal biomass, but there is no evidence of such effects occurring in similar experiments by Klick (1993) with the brown alga *Fucus vesiculosus*. In this latter investigation the release of several volatile halocarbons by *F. vesiculosus* was examined during incubation under a light/dark cycle in closed containers in the laboratory over 2 d. Both dibromomethane and bromoform release was initially observed, but the rate of production declined after 10 h and ceased entirely after 30

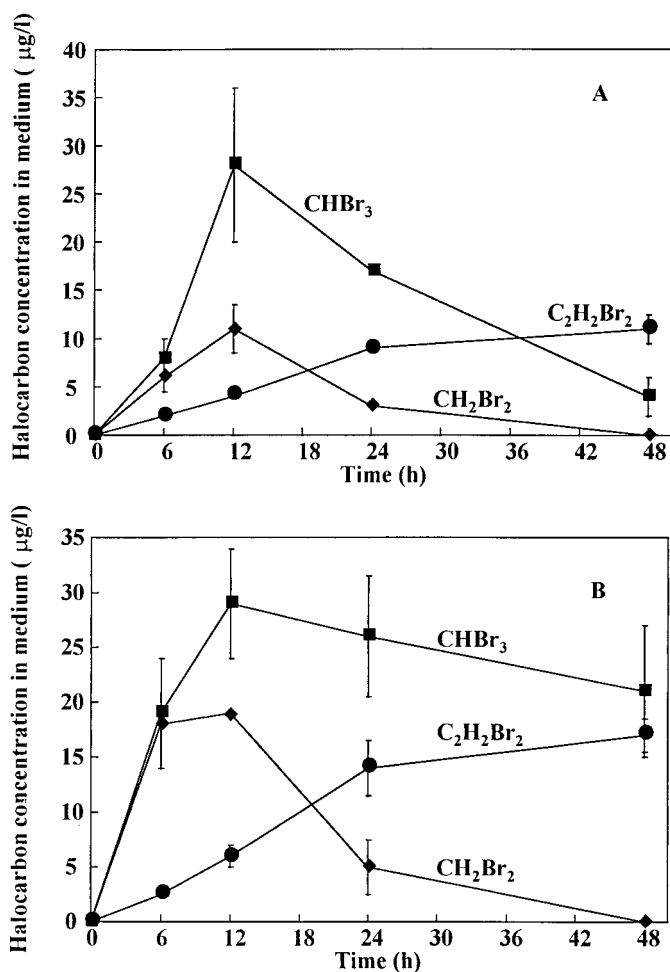


Fig. 3. Production of bromoform, dibromomethane, and dibromoethylene by *Falkenbergia* isolate 0985 incubated under irradiances of (A) $30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and (B) $330 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Error bars indicate ± 1 standard deviation.

h. Nevertheless, no significant fall in the concentration of either compound in the medium was detected even after 50 h. Although Moore et al. (1996) in studies of halocarbon production by the diatom *Porosira glacialis* observed a sharp decrease in bromoform concentrations in the culture medium in the later part of the growth cycle, this only became apparent after about 10 d incubation. Alternatively, halocarbon losses may be attributable to bacterial degradation. Goodwin et al. (1997a) reported degradation of dibromomethane in seawater incubated with this bromocarbon but only after a lag period of 5 d and no significant losses of bromoform were observed a month after supplementation of seawater with the compound.

In order to explore further the possible mechanism of such losses in cultures of *Asparagopsis*, isolate 0985 was incubated for 48 h under the conditions of Fig. 3A. Cultures were then spiked with dibromomethane or bromoform at $20 \mu\text{g liter}^{-1}$, and the concentration of the halocarbons monitored over the ensuing 48 h. The experiment was performed both with the alga still in situ and with the alga removed from the incubation vessel.

Dibromomethane was undetectable after 24 h in cultures spiked with the compound regardless of whether the alga remained in situ or was removed, suggesting that microbial degradation had occurred. As losses were not observed on spiking normal seawater with dibromomethane, the microorganisms responsible for degradation are presumably epiphytic on the alga but released into the medium on prolonged incubation. By contrast, bromoform displayed only 10% loss after 48 h incubation in culture medium from which the alga had been removed. However, when the alga remained in situ, 75% of the compound was lost within 48 h, implying that probably the alga itself was largely responsible for bromoform disappearance either by physical absorption or biochemical conversion within the algal biomass.

Halocarbon production by each of the 12 isolates of *Asparagopsis* spp. was monitored over a period of 6 h under low and high irradiances. The results are presented in Table 1 in which the isolates are ranked according to the rate of bromoform production under low irradiance. There were substantial differences among the isolates in the production of all three brominated compounds. Release of dibromomethane and dibromoethylene could not be detected in some of the isolates, but the production rates of bromoform and dibromomethane by several isolates exceeded the maximum release rates (100–250 ng g⁻¹ FW h⁻¹ for bromoform; 5–20 ng g⁻¹ FW h⁻¹ for dibromomethane) that have been reported for brown, green, and red macroalgae from temperate waters (Gschwend et al. 1985; Nightingale et al. 1995) or from the Antarctic (Laternus et al. 1996). Moreover, greatest rates of release recorded in previous studies for both of these bromocarbons were observed in brown algae, whereas green and red algae showed considerably lower rates of production.

The production of bromoform and dibromoethylene appeared to be negatively related because release of dibromoethylene under low irradiance was detected only in isolates that released <100 ng g⁻¹ FW h⁻¹ of bromoform. Isolate 0999 that released the greatest quantities of dibromoethylene under high irradiance displayed no detectable bromoform production. By contrast there was a significant positive correlation ($r = 0.694$) between the release rates of dibromoethylene and dibromomethane in low light (Table 1). The production of each of the bromocarbons was increased (often severalfold) by exposure to high irradiance in all isolates that released substantial amounts of the compound. This observation suggests that, as in the giant kelp *Macrocystis pyrifera* (Goodwin et al. 1997b), the production of bromocarbons is dependent on photosynthesis. The lowest production of bromoform and the highest rate of dibromoethylene release under low irradiance was observed in the three isolates (1075, 985, 999) of *Asparagopsis* that have been tentatively assigned to a separate species (provisionally described as the Caribbean strain) on the basis of studies of DNA restriction fragment length polymorphism (Ní Chualáin 1997). However, there were no significant differences in the production of any of the bromocarbons between the isolates assigned by Ní Chualáin (1997) to *A. taxiformis* and *A. armata* or between isolates that had been maintained at different temperatures in the culture collection.

Some isolates examined in the current study also released small quantities of other halocarbons that were identified by

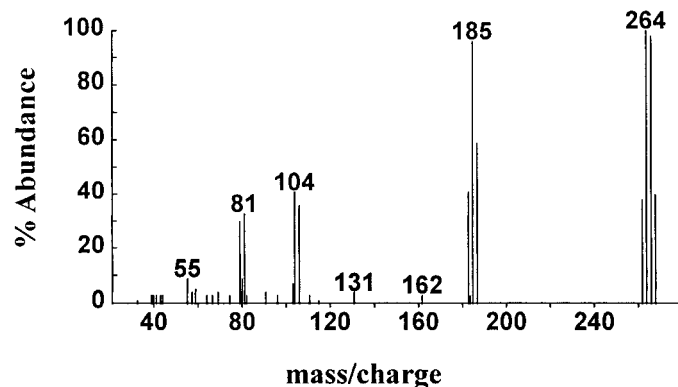


Fig. 4. Mass spectrum of gas chromatographic peak identified as tribromoethylene released by *Falkenbergia* isolate 1077.

comparison of their mass spectra with the MBS Library of mass spectra (Hewlett Packard Chemstation software) as dibromochloromethane and tribromoethylene (Fig. 4). Their release was not quantified because authentic standards of the compounds were not available. Tribromoethylene, like dibromoethylene, has not previously been reported as a natural product.

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References

- BURRESON, B. J., R. E. MOORE, AND P. M. ROLLER. 1976. Volatile halogen compounds in the alga *Asparagopsis taxiformis* (Rhodophyta). *J. Agric. Food Chem.* **24**: 856–861.
- DIXON, P. S. 1964. Taxonomic and nomenclatural notes on the Florideae IV. *Bot. Not.* **117**: 56–78.
- , AND L. M. IRVINE. 1977. Seaweeds of the British Isles. V. 2—Rhodophyta. British Museum.
- GOODWIN, K. D., M. E. LIDSTROM, AND R. S. OREMLAND. 1997a. Marine bacterial degradation of brominated methanes. *Environ. Sci. Technol.* **31**: 3188–3192.

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- , W. J. NORTH, AND M. E. LIDSTROM. 1997b. Production of bromoform and dibromomethane by giant kelp: Factors affecting release and comparison to anthropogenic bromine sources. *Limnol. Oceanogr.* **42**: 1725–1734.
- GRIBBLE, G. W. 1996. Naturally occurring organohalogen compounds—A comprehensive survey. In W. Herz, G. W. Kirby, R. E. Moore, W. Steglich, and C. Tamm [eds.], *Progress in the Chemistry of Organic Natural Products*. V. 68. Springer.
- GSCHWEND, P. M., J. K. MACFARLANE, AND K. A. NEWMAN. 1985. Volatile halogenated organic compounds released to seawater from temperate marine macroalgae. *Science* **227**: 1033–1035.
- KLICK, S. 1993. The release of volatile halocarbons to seawater by untreated and heavy metal exposed samples of the brown seaweed *Fucus vesiculosus*. *Mar. Chem.* **42**: 211–221.
- LATURNUS, F., C. WIENCKE, AND H. KLÖSER. 1996. Antarctic macroalgae—Sources of volatile halogenated organic compounds. *Mar. Environ. Res.* **41**: 169–181.
- MANLEY, S. L., AND M. N. DASTOOR. 1987. Methyl halide (CH₃X) production from the giant kelp, *Macrocystis*, and estimates of global CH₃X production by kelp. *Limnol. Oceanogr.* **32**: 709–715.
- , K. GOODWIN, AND W. J. NORTH. 1992. Laboratory production of bromoform, methylene bromide and methyl iodide by macroalgae and distribution in nearshore southern Californian waters. *Limnol. Oceanogr.* **37**: 1652–1659.
- MCCONNELL, O., AND W. FENICAL. 1977. Halogen chemistry of the red alga *Asparagopsis*. *Phytochemistry* **16**: 367–374.
- MOORE, R. M., M. WEBB, R. TOKARCZYK, AND R. WEVER. 1996. Bromoperoxidase and iodoperoxidase enzymes and production of halogenated methanes in marine diatom cultures. *J. Geophys. Res.* **101**: 20,899–20,908.
- MTOLERA, M. S. P., J. COLLÉN, M. PEDERSÉN, A. EKDAHL, K. ABRAHAMSSON, AND A. K. SEMESI. 1996. Stress-induced production of volatile halogenated organic compounds in *Eucheuma denticulatum* (Rhodophyta) caused by elevated pH and high light intensities. *Eur. J. Phycol.* **31**: 89–95.
- NÍ CHUALÁIN, F. 1997. The genus *Asparagopsis* (Bonnemaisoniaceae, Rhodophyta): Comparative morphological, physiological and molecular studies. Ph.D. thesis, University College, Galway, Ireland.
- NIGHTINGALE, P. D., G. MALIN, AND P. S. LISS. 1995. Production of chloroform and other low molecular-weight halocarbons by some species of macroalgae. *Limnol. Oceanogr.* **40**: 680–689.
- VON STOSCH, H. A. 1964. Wirkungen von Jod und Arsenit auf Meeresalgen in Kultur, p. 142–151. In A. D. Davyde Virville and J. Feldmann [eds.], *Proceedings of the International Seaweed Symposium*. V. 4. Pergamon.

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Fish or jellies—a question of visibility?

Abstract—Light is an important limiting factor for the visual foraging process in fishes, and the light regime may potentially affect the competition between visual and tactile predators. We investigated two equal-sized fjords of quite different pelagic food web structure. Earlier studies have revealed that the jellyfish *Periphylla periphylla* dominates Lurefjorden, while fish predators dominate in the other fjord, Masfjorden. Furthermore, the mesozooplankton stock of Lurefjorden is larger in both total biomass and size of the individuals. Hence, earlier hypotheses linking the competitive advantage of tactile gelatinous plankton predators to smaller-sized mesozooplankton communities are unable to explain the present phenomenon. To see if the difference in the pelagic biota of the two fjords could be associated with characteristics of the light regime, we measured the light absorbance in the basin water of the two fjords. We found that, due to a slightly stronger influence of coastal water in the basin water of Lurefjorden, the exponential light absorbance coefficient below 100 m is two to three times higher there than in other fjords. This results in a reduction in light flux of several orders of magnitude, effectively reducing the possibility of visual foraging. The tactile mode of predation in jellyfish, however, is not influenced, and we hypothesize that the visibility regime has a decisive role in structuring the pelagic food webs of the two fjords.

The question why some pelagic ecosystems support large stocks of fish while others are dominated by jellyfish has received much attention in marine ecology. Mills (1995) points out that as world fisheries begin to experience serious

declines, it is relevant to recognize that the carnivorous jellyfishes are ubiquitous and are thus opportunistically positioned to utilize secondary production that is ordinarily consumed by fish. It has been hypothesized that while fish forage most efficiently on large forms of zooplankton (Brooks and Dodson 1965), they may be out-competed by jellyfish if the prey stock is dominated by small size classes (Greve and Parsons 1977), and that fish recruitment can fail, due to prey depletion by large standing stocks of jellyfish (Möller 1980). Here we show that neither of these hypotheses are likely to account for pelagic food web differences observed among fjords. Instead we argue for an alternative hypothesis recently worked out in theory (Eiane et al. 1997): that poor visibility in the water column may prevent the visually foraging planktivorous fishes from obtaining the foraging rates required for population maintenance while tactile planktivores, such as jellyfish, are not affected.

Light limitation in visual foraging—The present work and the study of Eiane et al. (1997) emerged as a result of theoretical and experimental work on how predation by fish is affected by light and optical properties of prey and environment (Aksnes and Giske 1993; Giske et al. 1994; Aksnes and Utne 1997; Utne 1997). Furthermore, field studies on the mesopelagic fish *Maurollicus muelleri*, an important zooplanktivore in Norwegian fjords, have revealed that both the feeding and the vertical behavior are highly sensitive to the prevailing light conditions of the water column (Giske and