Deep cold-water corals as nurseries for fish larvae

Sandrine Baillon[1], Jean-François Hamel[2], Vonda E Wareham[3], and Annie Mercier[1*]

As a consequence of the decline of numerous commercial fish populations, an ecosystem-based approach to fisheries management, which includes the protection of essential fish habitat (EFH), has emerged. Cold-water coral (CWC) sites are recognized as biodiversity hotspots, but numerous examples of CWC destruction and degradation as a result of anthropogenic activities are well documented. However, although functional connections between CWCs and fish stocks are suspected, based on correlative evidence, proof of any close or direct relationship identifying CWCs as EFH is still lacking. Here, we provide evidence of the utilization of CWCs by fish larvae, mainly those of redfish (*Sebastes* spp). In multiyear surveys, fish larvae were consistently found closely associated with five species of sea pen (Octocorallia: Pennatulacea) in April and May. Prevalence and/or yields of fish larvae varied with coral host species, depth, location, and colony size. Evidence of the role of CWCs in the early life history of some fish species provides the strongest argument yet for the categorization of CWCs as EFH in the design of management programs.

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In light of the global decline and poor recovery of many fish populations, including commercial stocks, as a result of historical and anthropogenic factors (Pauly *et al.* 2002; Devine *et al.* 2006), the need for a holistic ecosystem-based approach to fisheries management is increasingly being recognized. Greater emphasis is being placed on habitat health and productivity, notably through the designation of essential fish habitat (EFH), which can be defined as "those waters and substrates necessary to fish for spawning, breeding, feeding, or growth to maturity" (Rosenberg *et al.* 2000). Concomitantly, cold-water coral (CWC) ecosystems are emerging as systems of ecological and economic value, raising concern over their rapid destruction (Fosså *et al.* 2002; Foley *et al.* 2010a). CWCs form one of the most complex biological habitats on continental slopes, where they act as biogenic substrates by offering a variety of microhabitats presumed to serve as feeding and spawning sites for other species (Buhl-Mortensen *et al.* 2010; Watling *et al.* 2011). Studies of their associated fauna have shown that biodiversity in deep-sea CWCs is comparable to that of tropical coral reefs (Buhl-Mortensen *et al.* 2010; Watling *et al.* 2011). However, contrary to the association between shallow coral reefs and fish, the exact relationship between CWCs and fish is not clear (Auster 2005), and CWCs are mostly considered to be facultative habitat (important but non-essential for the survival of a species). Evidence of a functional role that would qualify CWCs as EFH in support of their protection (Foley *et al.* 2010a) is still lacking.

The putative ecological importance of CWCs is magnified by their widespread distribution on continental slopes, canyons, and seamounts worldwide, in water depths ranging from 39 m to more than 3000 m (Foley *et al.* 2010a). It has often been suggested that CWCs may be used as nursery grounds by fish (Etnoyer and Warrenchuk 2007; Buhl-Mortensen *et al.* 2010), based on the assumption that corals offer protection against predators (Auster 2005). It has been further suggested that CWCs fit the definition of essential habitat for redfish (*Sebastes* spp) in Norway, on the basis of habitat–fish models (Foley *et al.* 2010b). However, to date, no direct evidence of the presence of juvenile or larval fish in CWCs has been presented (Husebø *et al.* 2002; Foley *et al.* 2010a). Correlative studies and predictive models have shown increasing adult fish densities and sizes around deep-water corals compared with non-coral areas (Husebø *et al.* 2002; Auster 2005). Spring aggregations of swollen (presumably gravid) redfish females were detected around the scleractinian coral *Lophelia pertusa* in Norway (Fosså *et al.* 2002), and catshark (Family Scyliorhinidae) egg cases were found attached to the gorgonian coral *Callogorgia* sp in the Mississippi Canyon, Gulf of Mexico (Etnoyer and Warrenchuk 2007). Nevertheless, the potential importance of CWCs remains unclear because studies do not cover the period when fish might use this habitat (ie for spawning or as juveniles; Auster 2007).

To date, most of the limited studies on the distribution and biology of CWCs have focused on the Subclass Hexacorallia, Order Scleractinia (stony corals), and to a lesser degree on some species of the Subclass Octocorallia, particularly gorgonians (sea fans) and other members of the Order Alcyonacea (soft corals) (Buhl-

[1]*Ocean Sciences Centre, Memorial University, St John's, Newfoundland and Labrador, Canada* [*](amercier@mun.ca); [2]*Society for the Exploration & Valuing of the Environment, St Philips, Newfoundland and Labrador, Canada;* [3]*Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St John's, Newfoundland and Labrador, Canada*

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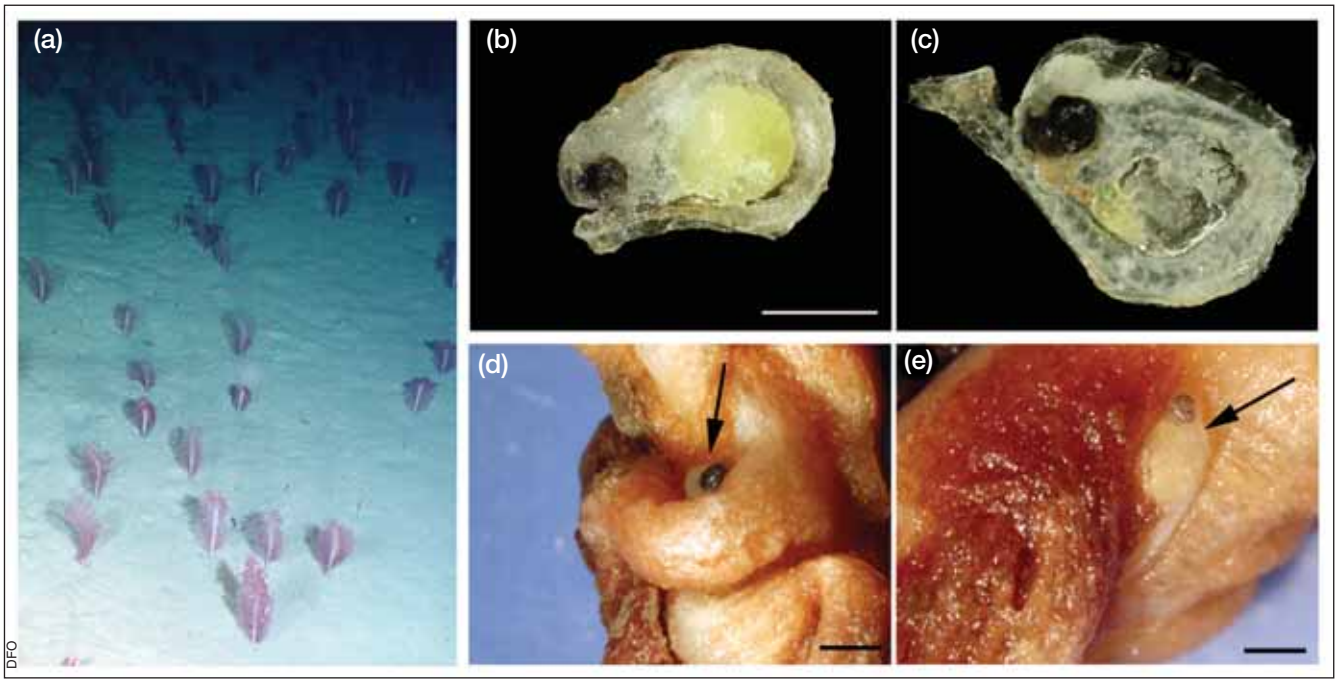

Figure 1. *(a) Field of sea pens. Larvae of redfish* (Sebastes *spp) were found with yolk sac either (b) present or (c) nearly resorbed. Scale bar in (b) also applies to (c). (d and e) Fish larvae (arrows) tucked among polyps of* Anthoptilum grandiflorum. *In panels (b), (d), and (e), scale bars = 1 mm.*

Mortensen *et al.* 2010). Members of the Order Pennatulacea (sea pens) are comparatively overlooked despite being common throughout the world's oceans and are considered as habitat-forming vulnerable species in both shallow and deep environments (Langton *et al.* 1990; Murillo *et al.* 2011; Williams 2011). Distributional data have hinted at the possible importance of soft corals, small gorgonians, and sea pens as potential fish habitat (Edinger *et al.* 2007). Here, we provide new evidence of the use of CWCs by larvae of commercial fish species, which were found in deep-water sea pens (Figure 1a) collected as bycatch from epibenthic surveys conducted from 2005 to 2010 off the east coast of Canada.

Materials and methods

Sampling

This study took advantage of routine multispecies research surveys conducted by Fisheries and Oceans Canada (DFO) from 2005 to 2010 in the Laurentian Channel and southern Grand Banks, located off the coast of the Atlantic Provinces of eastern Canada (WebFigure 1). Surveys followed a stratified random sampling design with a Campellen 1800 trawl towed for 15 minutes on ~1.4 km of seafloor (gear opened and closed at depth). Bycatch was examined for corals by trained technicians. Different species of sea pens were sampled at 58 stations between 98 m and 719 m depth (WebTable 1); samples were immediately frozen at –20°C. An analysis of the sea pen *Anthoptilum grandiflorum* was first conducted on all samples collected in 2006 and 2007 (spanning a 7–8-month period each year) in a comprehensive study of their biology and species that are associated with them. This investigation revealed the presence of fish larvae in April and May. Consequently, available samples of all sea pen species collected in April and May between 2005 and 2010 were examined for the present study. A total of 288 sea pen colonies (each individual is a colony of polyps) belonging to five species – *A grandiflorum*, *Halipteris finmarchica*, *Funiculina quadrangularis*, *Pennatula aculeata*, and *Pennatula grandis* – were studied (Table 1). A complementary analysis of other soft corals in the Order Alcyonacea (*Duva florida*, *Drifa glomerata*, and *Gersemia fruticosa*) was conducted for the 23 sites where fish larvae were present on sea pens.

Sample analysis

For *A grandiflorum* and *P aculeata*, ascertaining the number of colonies to be examined was based on (1) the quantity of samples available for a given site and (2) the presence or absence of fish larvae. A minimum of three haphazardly chosen colonies per site were initially inspected (however, if there were fewer than three colonies at a given site, all colonies were inspected). When fish larvae were found on at least one of the three colonies examined at a site with more than three colonies, the number of subsamples examined was increased to account for 20% of the samples available. For *H finmarchica*, *F quadrangularis*, and *P grandis*, all colonies were inspected, except for *F quadrangularis* at three sites where fish larvae were absent in the first three samples. There were also several sites where only one colony had apparently been preserved by DFO,

although the presence of additional colonies was indicated in survey records. Incomplete or damaged colonies of sea pens were excluded from the analysis.

The frozen colonies were thawed in filtered seawater before examination. We measured the size (from base to tip) and damp weight of each colony, and determined the presence, quantity, and size of fish larvae under a stereomicroscope (Nikon SMZ1500). Polyps were carefully manipulated to expose and uncover fish larvae. A separate study of polyp digestive tract did not find any evidence of fish larvae, ruling out a prey–predator relationship. Fish tissues (whole or half larvae) preserved in 100% ethanol were shipped to the Canadian Centre for DNA Barcoding (University of Guelph, Canada) for genetic analysis. A subsample of 196 specimens was analyzed through standard polymerase chain reaction and DNA sequencing protocols (Ivanova *et al.* 2006; DeWaard *et al.* 2008). Partial sequences of the cytochrome *c* oxidase subunit I gene with all metadata are registered in the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007), project FLSB, and deposited in GenBank (accession numbers JX008540–JX008735). Identifications were made by running the sequences against the BOLD and Basic Local Alignment Search Tool (BLAST) databases (99.5–100% certainty).

The mean yield (MY) was defined as the mean number of fish larvae per colony (fish larvae colony^{-1}) considering all sea pens examined, and the mean exact yield (MEY) was defined as the mean number of fish larvae colony^{-1} considering only sea pens with fish larvae. The MY for a site (site mean yield [SMY] or site mean exact yield [SMEY]) was defined as the number of fish larvae found in that site divided by the number of sea pen colonies inspected for that site (as fish larvae colony^{-1}). The number of fish larvae at a site was extrapolated from the total number of colonies sampled there, multiplied by MY. Concentrations were recorded as the number of fish larvae per 100 grams of coral (100-g^{-1}).

Data analysis

Parametric tests were conducted when assumptions of normality and equal variance were met; otherwise non-parametric counterparts were used. Kruskall-Wallis tests were conducted to assess differences in fish larvae yields at various locations and depths, followed by Dunn's post-hoc tests. A Mann-Whitney test was used to compare yields in day and night samplings. Two-way analyses of variance (no interactions) on the abundance of *A grandiflorum* colonies per site showed a significant influence of year ($F_{4,42}$ = 3.57, P = 0.014) but not month (April or May, P = 0.137). Similarly, colony size was significantly affected by year ($F_{4,102}$ = 2.76, P = 0.032) but not by month (P = 0.379). Months were therefore pooled for the analysis of annual trends. Regression analyses and correlations (Pearson or Spearman) were used to examine relationships between variables. All data are expressed as mean ± standard error (SE).

Principal component analyses (PCAs) were used to explore which of the biotic (various sea pen species, adult redfish at different maturity stages) or abiotic (depth, latitude, month, temperature, day/night) factors best explained the presence of fish larvae. Normalization for the abiotic data and log(x + 1) transformation for the biotic data were applied before all PCAs. The log(x + 1) transformation allows for the consideration of both the most abundant and more rare species. A correlation matrix for the abiotic data and a variance–covariance matrix for the biotic data (Quinn and Keough 2002) were used.

Results and discussion

DNA analysis confirmed that most of the fish larvae detected in sea pens belonged to two redfish species (*Sebastes fasciatus* and *Sebastes mentella*), both of which are commercially exploited and listed as endangered or threatened in Canada (COSEWIC 2010). The two species cannot accurately be distinguished through DNA analysis and are suspected to hybridize; we therefore grouped them together as *Sebastes* spp in this study. Eggs or larvae of the lantern fish (*Benthosema glaciale*) and the eelpout (*Lycodes esmarkii*) were also found. The MEY for redfish was 5.4 ± 0.8 larvae colony^{-1}. No evidence of a predatory relationship was found.

Occurrences of redfish larvae were consistently concentrated between April and May in the Laurentian

Table 1. Distribution of fish larvae in the various sea pen species

	Sea pen species				
	Anthoptilum grandiflorum	*Pennatula aculeata*	*Funiculina quadrangularis*	*Halipteris finmarchica*	*Pennatula grandis*
Number of colonies	109	96	43	35	5
Prevalence of association (% colonies with larvae)	35.8	11.5	27.9	17.1	100
Total number of fish larvae	148	58	98	69	20
Mean yield (fish larvae colony^{-1})	1.4	0.6	2.3	1.9	4
Mean exact yield (fish larvae colony^{-1})	3.8	5.3	8.2	11.5	4
Maximum yield (fish larvae colony^{-1})	36	16	22	26	4
Mean concentration (fish larvae 100-g^{-1})	12.5	106	405	19.1	6.3
Maximum concentration (fish larvae 100-g^{-1})	91.6	222.2	540.7	35.33	14.1

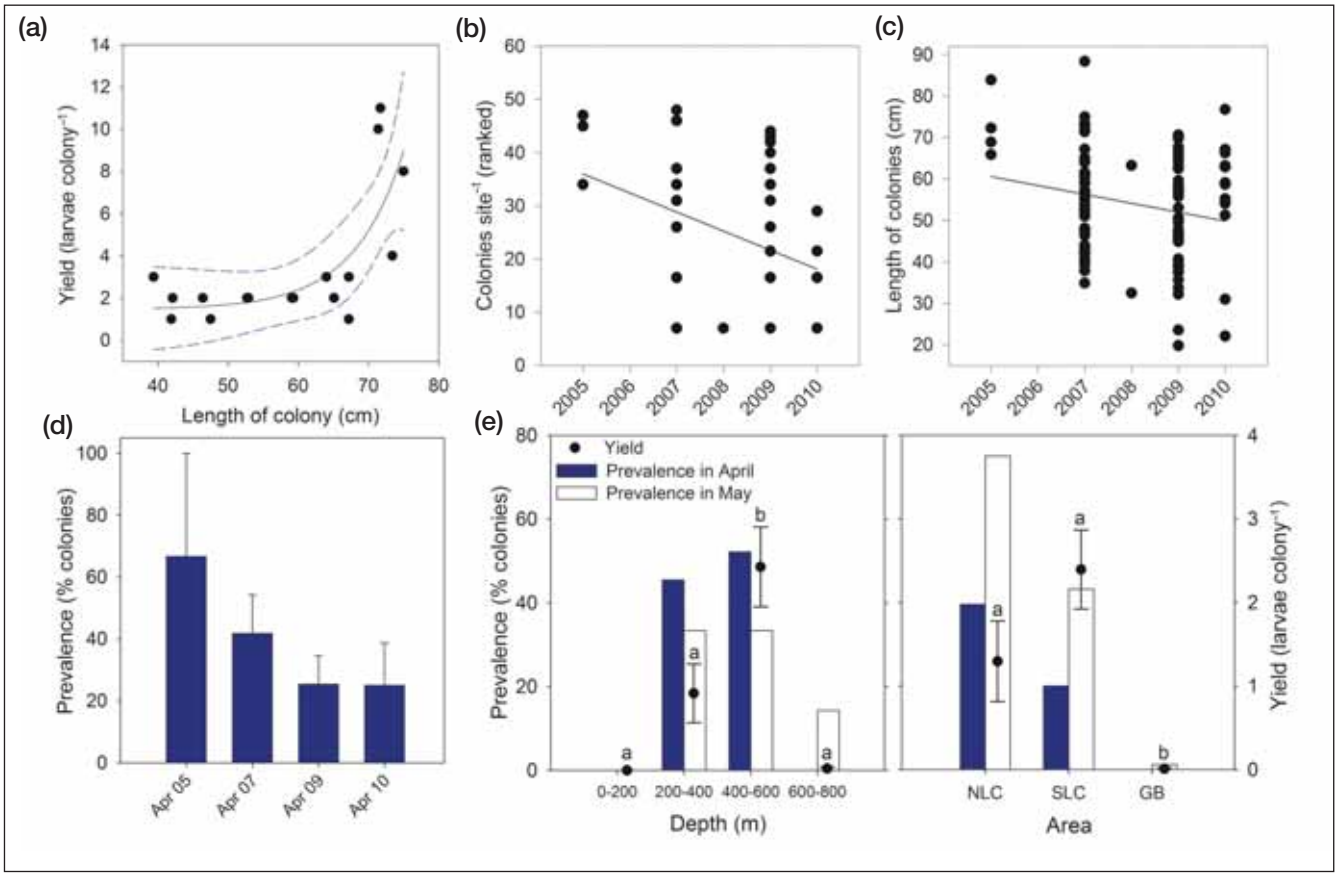

Figure 2. *(a) Relationship between colony length and yield in* A grandiflorum *collected in April 2007 (regression,* $y = y_0 + ab^x$; $F_{2,14} = 9.06$, $P = 0.003$, $r = 0.751$*); dashed lines, 95% confidence interval. Downward trends in (b) number of colonies per site* ($P = 0.015$, $r_s = 0.349$*) and (c) colony size* ($P = 0.027$, $r = 0.213$*) in* A grandiflorum *from 2005 to 2010. (d) Prevalence of the association (% colonies with fish larvae + standard error) in* A grandiflorum *collected in April of 2005, 2007, 2009, and 2010. (e) Prevalence of colonies with fish larvae (bars) according to depth (left panel) and area (right panel), with corresponding mean yields (closed circles; ± standard error). Different letters indicate significant differences* ($P < 0.001$)*. NLC = North Laurentian Channel; SLC = South Laurentian Channel; GB = southern Grand Banks.*

Channel, which features one of the highest known densities of sea pens (Kenchington *et al.* 2010), perhaps because the high primary and secondary production at the surface generates planktonic material that sinks to the seafloor, providing food for suspension-feeding azooxanthellate corals (Sherwood *et al.* 2008). The small size of the fish larvae (< 8 mm with/without yolk sac; Figure 1, b and c) and the closeness of the association (Figure 1, d and e) suggest that the viviparous redfish release their progeny near corals, where they remain during early ontogeny. The calcified parts (sclerites) of and/or toxic chemicals produced by soft corals deter potential predators (Changyun *et al.* 2008). Therefore, fish may release larvae deliberately among corals to provide them with shelter and protection. The rapid retraction of sea pen polyps and branches upon disturbance (observed during capture) probably trapped the fish larvae within the colonies. Whether sea pens and other CWCs provide nourishment to larval fish in the form of mucus and/or associated particles remains to be determined.

Prevalence of the association between sea pens and redfish larvae varied between 11.5% and 100% among five host species (Table 1). *A grandiflorum* had the second highest fish larvae prevalence (35.8%), had the highest maximum yield (36 fish larvae colony^{-1}), and was the most abundant sea pen species (present at 79% of all sites). Fifty-three percent of the 23 sites where fish larvae occurred were monospecific for sea pens; of those monospecific sites, 84% featured only *A grandiflorum*. Fish larvae were absent at the remaining monospecific sites. Of the multispecific sites excluding *A grandiflorum*, only 20% were associated with fish larvae, suggesting the importance of this sea pen species, which has a worldwide distribution (Williams 2011). Sea pen colony size and the number of fish larvae they harbored were positively correlated (Figure 2a), a finding that raises some concern, given (1) the longevity and slow growth of sea pens and other CWCs (Andrews *et al.* 2002; Wilson *et al.* 2002) and (2) the apparent decline in both number and size of *A grandiflorum* colonies (Figure 2, b and c). Prevalence of fish larvae in *A grandiflorum* colonies collected in April also decreased between 2005 and 2010 (Figure 2d). Other soft corals in the Order Alcyonacea (*D florida*, *D glomerata*, and *G fruticosa*) exhibited a MEY of 2.6 ± 0.7 fish larvae

colony^{-1} (n = 11) at sites where sea pens hosted fish larvae (excluding 244 larvae found in one *D florida* colony).

PCAs on abiotic factors revealed that month and latitude were the main contributors to the first principal component (PC1; 39.5%), temperature was the main contributor to the second principal component (PC2; 26.2%), and depth had a moderate influence in both components (Figure 3a). Most sites (92%) where fish larvae occurred on sea pens were characterized by bottom temperatures of 4–6°C and had greater yields at 400–600 m than at other depths (Kruskal-Wallis H-test; H = 34.33, degrees of freedom [df] = 3, P < 0.001; Figure 2e). Nearly all sites where sea pens harbored larvae were in the Laurentian Channel (WebFigure 1) where greater yields occurred (Kruskal-Wallis H-test; H = 37.73, df = 2, P < 0.001; Figure 2e). Day or night sampling did not influence yields (Mann-Whitney U-test; U = 146.5, P = 0.197).

The PCA integrating abundance of coral species and female redfish (immature, maturing [with some ripe eggs], mature [presence of larvae], and spent [having spawned]) in research surveys did not clearly explain the occurrence of fish larvae (Figure 3b), suggesting an ontogenetic shift in habitat use. Eigenvectors indicated that 42.8% of the site variations could be accounted for by PC1, with both immature and spent females as positive contributors. In PC2 (accounting for 21.4% of site variations), mature females made the most significant contribution. Unlike fish larvae, adult redfish were found at 57 of the 58 sites; mature and spent females were present at 78% and 66% of sites, respectively; and there was no link between the number of sea pens and the number of adult (P = 0.983) or female (P = 0.162) redfish at the sites. The number of adult redfish did not correlate with the yield of fish larvae colony^{-1} or the abundance of larvae extrapolated for each site (P = 0.210 and P = 0.432, respectively). The extrapolated abundance of larvae followed that of mature (r_s = 0.303, P = 0.023) but not spent (P = 0.115) females. Finally, the largest research-based catches of redfish in April and May occurred in the Grand Banks region, where few fish larvae were found (WebFigure 2a). A similar trend was observed in concurrent commercial catches (WebFigure 2b).

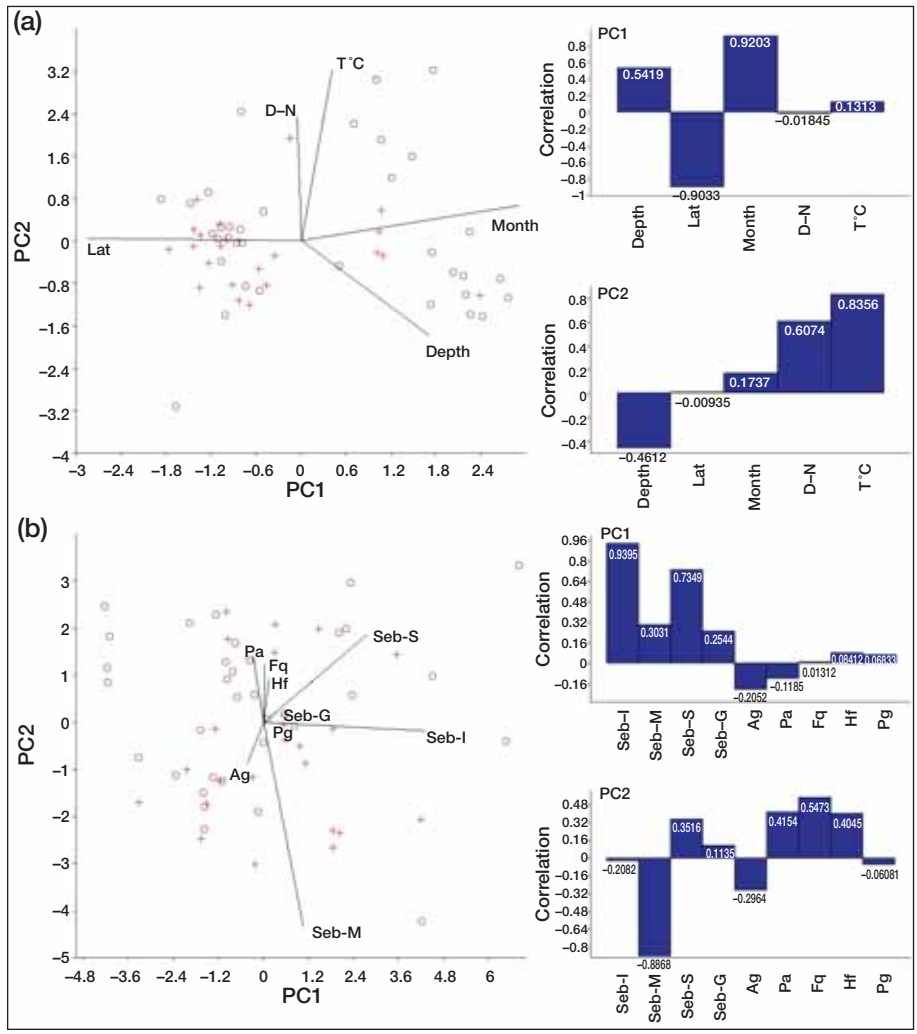

Figure 3. *Principal component analysis biplots and corresponding loadings for (a) abiotic and (b) biotic parameters at sites with the presence (+) or absence (o) of fish larvae on sea pens. Lat = latitude; D–N = day–night; T°C = temperature in degrees Celsius; Seb-I* = Sebastes *immature; Seb-M* = Sebastes *mature; Seb-S* = Sebastes *spent; Seb-G* = Sebastes *maturing; Ag* = A grandiflorum; *Pa* = P aculeata; *Fq* = F quadrangularis; *Hf* = H finmarchica; *Pg* = P grandis.

Conclusions

Evidence for fish–CWC associations has, to date, largely been limited to habitat–fishery or distributional studies (Stone 2006; Edinger *et al.* 2007; Foley *et al.* 2010b) that suggest co-occurrences but provide no direct functional links (Auster 2007). Now, with evidence that fish larvae shelter around soft corals, we believe there is a strong argument for classifying those CWCs as EFH and as vulnerable marine ecosystems. Annual occurrences restricted to specific months confirm that key associations may be transient and easily overlooked, as suggested previously (Auster 2007). Furthermore, barring natural spatial variation, bycatch data for 2005–2010 reveal decreasing numbers and sizes of sea pens, and a decline in the prevalence of colonies hosting fish larvae. Loss of

CWCs has previously been documented and a diversity of current and future threats identified (Roberts *et al.* 2006; Watling *et al.* 2011). When combined with this knowledge, we believe that the findings reported here underscore the need for fisheries managers to assess available data on sea pens and other soft corals and the urgent need to define marine protected areas and limit trawl fisheries where sea pens are present.

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