

High abundance of larval rockfish over Cobb Seamount, an isolated seamount in the Northeast Pacific

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ABSTRACT

The larval fish community in the region of Cobb Seamount (500 km west of Oregon) is dominated by myctophid species commonly encountered in the subarctic North Pacific. However, during a survey in June 1992, the ichthyoplankton community within 30 km of the seamount summit was almost completely dominated by larvae of various rockfish (*Sebastes*) species. Given their very small size (and hence very young age) and the fact that they occurred only rarely in samples collected > 30 km from the seamount summit, we conclude that these *Sebastes* larvae were produced locally over Cobb Seamount. Previous studies have shown that the Cobb fish fauna is dominated by various *Sebastes* spp. and that, unlike other fish present on the seamount, the rockfish populations may be self-recruiting. We suggest that a persistent clockwise (i.e. downwelling) eddy, consistent with a stratified Taylor cone, plays a critical role in retaining larval rockfish over Cobb Seamount and may contribute to the process of self-recruitment. The key to the success of rockfish on Cobb and other shallow Northeast Pacific seamounts seems to be linked to their viviparous life history.

Key words: Larval fish, NE Pacific, rockfish, *Sebastes*, seamount, Taylor cone

INTRODUCTION

Since the late 1950s it has been known that rich fish stocks often occur at shallow seamounts (Uda and

Ishino, 1958; Hubbs, 1959). However, the mechanisms by which such stocks are established and maintained remain less clear. It is widely held that the high biological productivity of seamounts is intimately linked to various current–topography interactions including upwelling, enhanced turbulent mixing and the formation of closed recirculations (Boehlert and Genin, 1987). In addition to enhanced fish stocks, ‘seamount effects’ include locally enhanced standing stocks of phytoplankton and protozoans, enhanced benthic biomass, and unusually high abundances of seabirds and marine mammals (reviewed by Rogers, 1994). In contrast, the effect on ichthyoplankton and mesozooplankton is less clear. The biomass of these groups near seamounts has variously been shown to be higher than, equal to, or lower than that of the surrounding waters (Fedosova, 1974; Nellen, 1974; Voronina and Timonin, 1986; Boehlert and Mundy, 1993; Genin *et al.*, 1994; Dower and Mackas, 1996; Haurly *et al.*, 2000). Here we document relations between larval rockfish (*Sebastes* spp.) and a quasi-permanent Taylor cone over Cobb Seamount, a shallow Northeast (NE) Pacific seamount.

Cobb Seamount (46°46′N, 130°48′W) is located 500 km south-west of Vancouver Island (Fig. 1). Between 1989 and 1994, Cobb was the focus of a multidisciplinary oceanographic program that studied current–topography interactions at shallow seamounts. Cobb rises steeply from a depth of 2800 m and is capped by a broad plateau extending from 300 to 100 m below the surface (Budinger, 1967). A small pinnacle reaches to within 25 m of the surface. Background currents near the seamount move east/south-eastward at 10–12 cm s⁻¹ (Freeland, 1994). During each of four cruises between 1990 and 1992, a closed anticyclonic eddy, consistent with a stratified Taylor cone, was observed over the seamount (Dower, 1994; Freeland, 1994).

Seamount effects observed at Cobb Seamount include an enhanced standing stock of phytoplankton and microzooplankton (Dower *et al.*, 1992; Sime-Ngando *et al.*, 1993; Comeau *et al.*, 1995), plus a shift in mesozooplankton community composition detectable up to 30 km from the Cobb summit (Dower and Mackas, 1996). Large schools of rockfish (*Sebastes* hereafter) have been observed over the summit (V.J.

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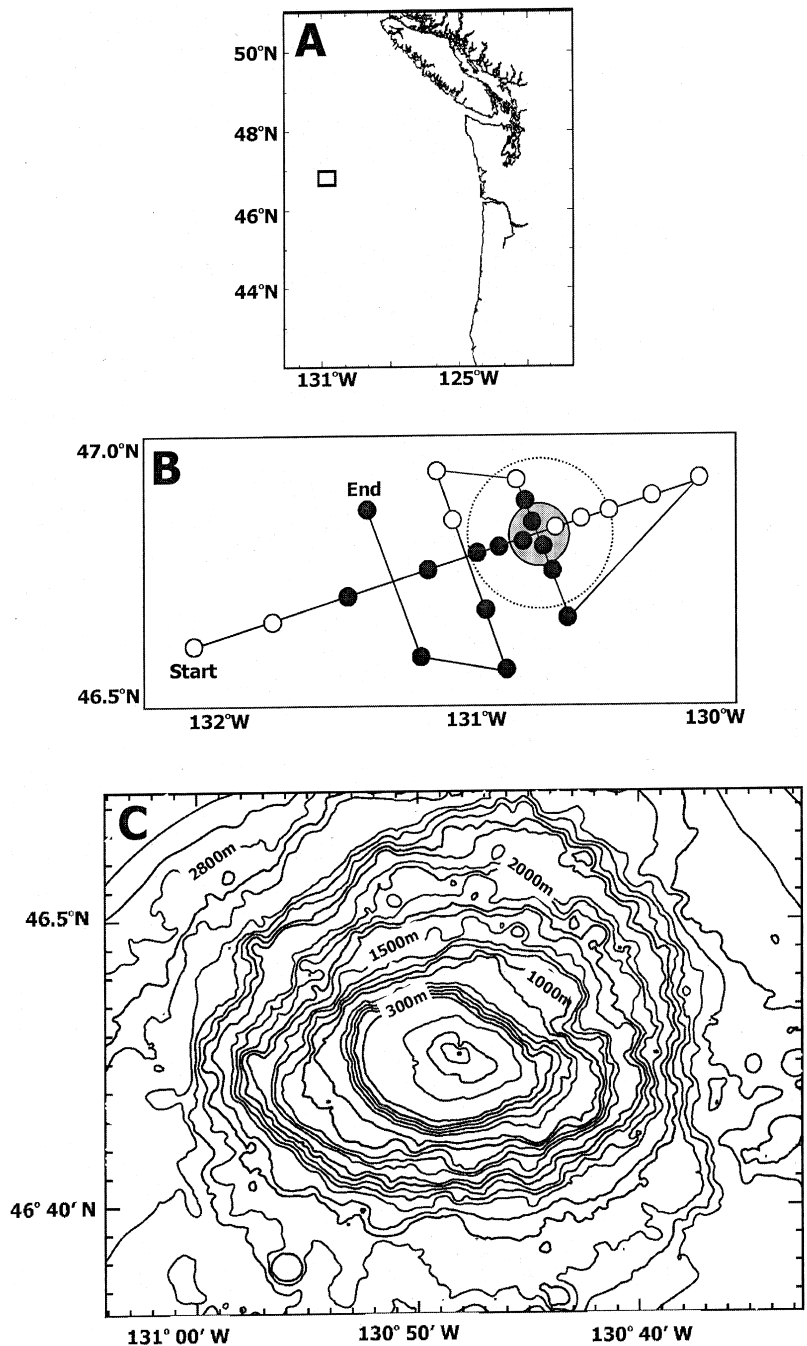


Figure 1. Map of the study area. (A) Location of Cobb Seamount in the Northeast Pacific. (B) Cruise track of the ship. Sampling proceeded from west to east and was completed in ~ 72 h. Small open circles denote daytime samples, filled circles denote night samples. The grey circle denotes the area of the seamount shallower than 1000 m, the large dotted circle marks the 30 km radius used to delimit on-seamount from off-seamount samples. (C) Detailed topography of Cobb Seamount (courtesy of Dr C. Eriksen, University of Washington).

Tunncliffe, University of Victoria, personal communication) and a rich benthic community has also been described (Parker and Tunncliffe, 1994).

METHODS

Biological sampling

Ichthyoplankton were collected as part of a zooplankton survey near Cobb Seamount between

June 24–27, 1992 (Fig. 1). Twenty-four samples were collected (during both day and night) using 0.50 m² bongo-nets with a 236- μ m mesh. Time constraints precluded stratified sampling. Nets were towed vertically at 1 m s⁻¹ from 250 m to the surface. There were no significant wire angle problems, and thus variations due to differences in volume filtered are not expected to be a significant source of error. Samples were preserved in Borax-buffered 5% formalin. Larval

fish were sorted (postcruise) under a dissecting microscope and identified to the lowest taxonomic level possible, following Matarese *et al.* (1989). Standard lengths (mm) of individual larvae were measured with an ocular micrometer. All abundances are expressed as number of individuals per 100 m³.

Statistical methods

Previous work (Dower and Mackas, 1996) has shown that a 'seamount effect' can be detected in mesozooplankton community composition up to 30 km from the Cobb summit. Thus, following Dower and Mackas (1996), we denote samples collected ≤ 30 km from the summit and > 30 km from the summit as 'on-seamount' and 'off-seamount', respectively. Prior to analysis, raw abundances were normalized using a 4th-root transformation (which is particularly suited to data containing many zeros). Two-way ANOVAS were used to test for interactions between day/night and on/off seamount effects on total larval abundance and for the species-specific abundances of the most abundant taxa. Individual standard lengths (mm) for the three most abundant taxa were also binned into 0.5 mm size classes and the resultant on/off seamount size-frequency distributions compared using chi-squared tests.

RESULTS

Ichthyoplankton community composition

We collected 954 larvae representing 10 taxa (Table 1). With the exception of various *Sebastes* larvae, the ichthyoplankton community consisted of larvae of common mesopelagic fish species from the north-east Pacific (Loeb, 1980; Matarese *et al.*, 1989). *Sebastes* larvae were by far the most abundant (48%), however, no attempt was made to distinguish between species since identifications of larval *Sebastes* are poorly known. Other relatively abundant species

included the myctophids *Diaphus theta* and *Stenobrachius leucopsarus*. Only these three taxa were abundant enough to permit detailed statistical analyses. Less abundant taxa included *Lampanyctus regalis*, *Protomyctophum thompsoni*, *P. crockeri*, *Tarletonbeania crenularis*, *Chauliodus macouni*, *Trachipterus altivelis*, *Lestidiops ringens*, plus unidentifiable myctophid larvae (collectively denoted as Myctophidae). The latter seven taxa were only used in tests of differences in total larval abundance.

Larval abundances

ANOVA results are reported in Table 2. There were statistically significant on/off seamount differences in total larval abundance ($P = 0.037$), with on-seamount samples containing, on average, about four times as many larvae (mean = 44 ± 36) as off-seamount samples (mean = 12 ± 6). There was also a significant day/night effect on total abundance ($P = 0.026$), with more larvae collected at night (mean = 36 ± 34) than by day (mean = 13 ± 13). There was no significant interaction between the on/off and day/night effects. Considering species-specific abundances, we detected two significant effects (Table 2). First, *Sebastes* larvae were significantly more abundant ($P = 0.005$) on-seamount (mean = 27 ± 30) than off-seamount (mean = 0.5 ± 0.8). Second, *Stenobrachius leucopsarus* larvae were significantly more abundant ($P = 0.001$) at night (mean = 6 ± 4) than by day (mean = 2 ± 1). *Diaphus theta* abundances were unaffected by either on/off seamount or day/night effects.

Larval lengths

Of the three most abundant taxa (*Sebastes* spp., *D. theta*, and *S. leucopsarus*) *Sebastes* larvae were the smallest ($\bar{x} = 3.8 \pm 0.37$ mm), and had the narrowest range of lengths (Fig. 2). Mean standard lengths of *D. theta* and *S. leucopsarus* were $4.5 (\pm 1.6)$ mm and

Taxon	Mean	Standard error	Maximum	Minimum
<i>Sebastes</i> spp.	12.67	5.00	93	0
<i>Diaphus theta</i>	8.42	1.32	23	1
<i>Stenobrachius leucopsarus</i>	4.13	0.73	14	0
<i>Tarletonbeania crenularis</i>	0.46	0.10	1	0
<i>Lampanyctus regalis</i>	0.33	0.10	1	0
<i>Protomyctophum</i> spp.	0.29	0.09	1	0
Myctophidae	0.21	0.10	2	0
<i>Chauliodus macouni</i>	0.21	0.10	2	0
<i>Trachipterus altivelis</i>	0.21	0.08	1	0
<i>Lestidiops ringens</i>	0.08	0.06	1	0

Table 1. Mean abundances (per 100 m³), standard errors, maximum and minimum abundances for the 10 taxa used in subsequent analyses. Numbers based on $n = 24$ samples.

Table 2. Results of two-way ANOVAs for total larval abundances, plus species-specific abundances of larval *Sebastes* spp., *D. theta* and *S. leucopsarus*. Asterisks indicate statistically significant differences. Values of statistically different means are reported in the text.

Taxa	Source	DF	MS	F	P
Total larval abundance	On/off	1	1.039	4.975	0.037*
	Day/night	1	1.21	5.794	0.026*
	On/off × day/night	1	0.63	3.018	0.98
	Residual	20	0.209		
	Total	23	0.356		
<i>Sebastes</i> spp.	On/off	1	8.921	9.856	0.005*
	Day/night	1	0.837	0.925	0.348
	On/off × day/night	1	0.937	1.035	0.321
	Residual	20	0.905		
	Total	23	1.431		
<i>Diaphus theta</i>	On/off	1	0.0034	0.0303	0.864
	Day/night	1	0.336	3.026	0.097
	On/off × day/night	1	0.288	2.599	0.123
	Residual	20	0.111		
	Total	23	0.121		
<i>Stenobrachius leucopsarus</i>	On/off	1	0.0007	0.0039	0.951
	Day/night	1	2.437	14.402	0.001*
	On/off × day/night	1	0.353	2.089	0.164
	Residual	20	0.169		
	Total	23	0.269		

5.6 (± 1.8 mm), respectively. On average, *Sebastes* were significantly smaller on-seamount than off-seamount (*t*-test, $P < 0.001$). A chi-squared test revealed that the size-frequency distributions of *Sebastes* (binned into 0.5 mm size classes) were significantly different ($\chi^2 = 28.6$, d.f. = 4, $P < 0.001$). Whereas 46% of the on-seamount *Sebastes* larvae were < 4.0 mm, only 25% of the off-seamount *Sebastes* larvae were < 4.0 mm (Fig. 2). In contrast, *D. theta* larvae were significantly larger on-seamount than off-seamount (*t*-test, $P < 0.001$). A Chi-square test revealed that the size-frequency distributions of *D. theta* (binned into 1.0 mm size classes) were significantly different ($\chi^2 = 16.3$, d.f. = 5, $P < 0.006$), with 53% of on-seamount *D. theta* larvae being > 4 mm in length, but only 31% of the off-seamount *D. theta* larvae > 4 mm in length (Fig. 2). *S. leucopsarus* larvae showed no significant on/off seamount differences in size.

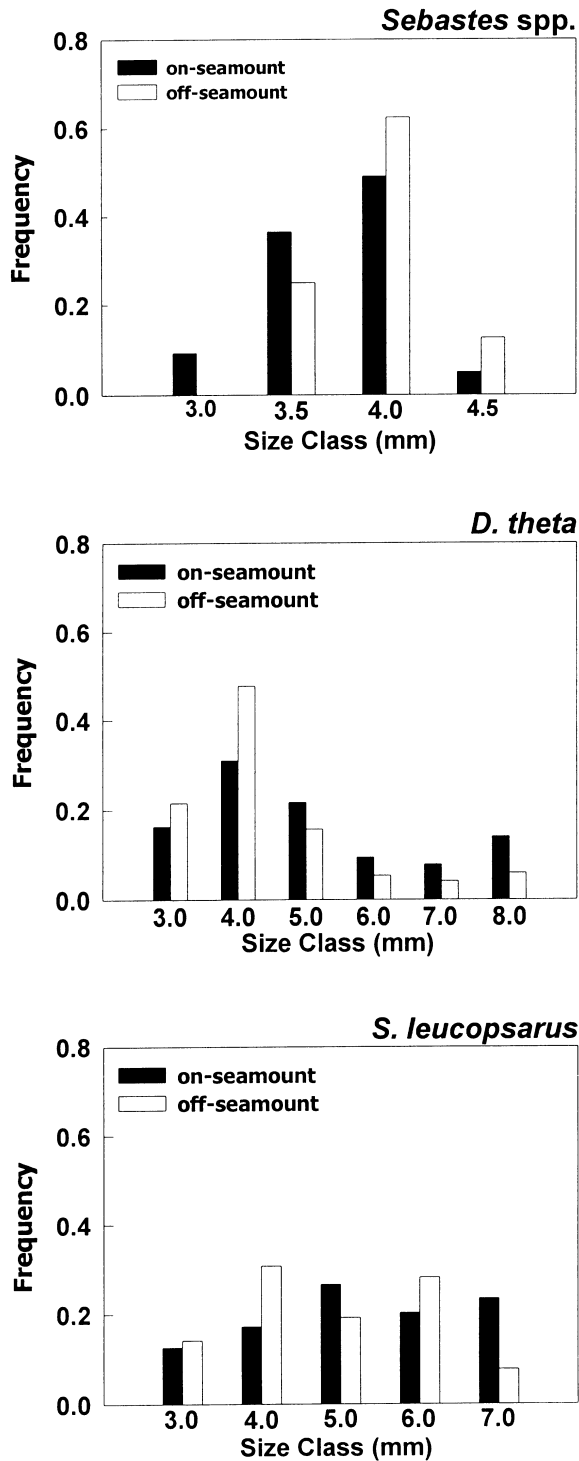
DISCUSSION

Cobb Seamount supports numerous fish, including sablefish (*Anoplopoma fimbria*), Pacific halibut (*Hippoglossus stenolepis*) and at least seven *Sebastes* spp. species (Sasaki, 1986; Pearson *et al.*, 1993; Parker and

Tunncliffe, 1994). Although genetic studies have not been undertaken, morphometric analyses suggest that some of the Cobb rockfish populations may be self-sustaining (Pearson *et al.*, 1993), especially given the distance to the nearest coastline (500 km) and the fact that pelagic juvenile rockfish are not usually found more than 200 km offshore.

Our analyses provide further support for this claim. First, given that the nearest topography shallow enough to support adult rockfish is over 500 km away, it seems unlikely that these *Sebastes* larvae were produced elsewhere and advected over Cobb. Second, only 48 of the 447 *Sebastes* larvae came from off-seamount samples. Furthermore, the off-seamount *Sebastes* larvae were significantly larger than the on-seamount larvae (Fig. 2), as would be expected if the seamount is a point source for the production of *Sebastes* larvae. Third, *Sebastes* spp. are viviparous and extrude live young: the size-at-extrusion for the *Sebastes* spp. known to occur at Cobb ranges from 3 to 6 mm (Matarese *et al.*, 1989). Thus, even allowing for postpreservation shrinkage of 10–20% in length (Pepin *et al.*, 1998), the small size and the low variability in size of the rockfish larvae (3.8 ± 0.37 mm) suggests that they had been very recently extruded over Cobb Seamount.

Figure 2. Length–frequency plots for the three most abundant taxa. *Sebastes* standard lengths were binned into 0.5 mm size classes (given the narrow size range), while *D. theta* and *S. leucopsarus* were binned into 1.0 mm size classes.



In contrast, neither *D. theta* nor *S. leucopsarus* show significant on/off seamount trends in abundance (Table 2). Both species hatch at < 5 mm length (Matarese *et al.*, 1989). Thus, the presence of post-flexion individuals of both species > 8 mm in length suggests that these larvae had been in the water for a considerable time (likely weeks) before capture. This, in addition to the fact that neither species spawns over shallow topographies, leads us to conclude that the *D. theta* and *S. leucopsarus* larvae in our collections were probably advected over Cobb. However, given that the *D. theta* larvae collected over the seamount were significantly larger (and thus older) than off-seamount individuals (Fig. 2) it seems likely that some of these larvae are at least temporarily entrained as they are advected over the seamount.

Freeland (1994) reports that Cobb is capped by a closed anticyclonic current (consistent with a stratified Taylor cone) that persists for at least a month. Subsequent measurements have led to the suggestion that this Taylor cone is a quasi-permanent feature (Dower, 1994; Dower and Mackas, 1996). The clockwise rotation results in downwelling with a characteristic 'flushing time' of about 17 days and a radial outflow of about 4 cm s^{-1} in the bottom Ekman Layer, implying a downward velocity of about 0.3 mm s^{-1} (Freeland, 1994). Recent modelling studies of shallow seamounts suggest that Taylor cones, coupled with bottom-intensified tidal currents, can have a dramatic effect on the retention of particles released near the bottom (Goldner and Chapman, 1997). Specifically, Goldner and Chapman (1997) report that neutrally buoyant particles released within 50 m of the bottom can be 'retained by this combined circulation – apparently forever!' Coincidentally, the model seamount used by Goldner and Chapman (basal diameter of 25 km, fractional seamount height = 0.9 of the water column, inflow current speed of 0.09 m s^{-1}) is quite similar to the actual conditions at Cobb (basal diameter = 30 km, fractional height ~ 0.95 , inflow current = 0.10 m s^{-1}). Moreover, Codiga and Eriksen (1997) document a similar amplification of tidal currents at Cobb.

How might such a flow affect particles in the water over Cobb Seamount? Parker and Tunnicliffe (1994) reported that the Cobb benthos was dominated by species with larvae that spend little (i.e. < 2 weeks) or no time in the plankton. Their explanation for this effect was that larval forms spending more than 17 days in the plankton may be flushed out of the Cobb ecosystem before they can settle. Why, then, were larval *Sebastes* so abundant over Cobb Seamount? Were they retained by the Taylor cone? Although the

weak downward velocity might be enough to eventually wash the eggs of oviparous fish and many benthic organisms out of the ecosystem (at a rate of $\sim 26 \text{ m day}^{-1}$), it seems likely that newly extruded *Sebastes* larvae, which are active, positively phototactic swimmers (Moser, 1967), could easily overcome the downwelling and remain over the seamount. Indeed, dense schools of juvenile rockfish have been observed from a submersible on Cobb (V.J. Tunnicliffe, University of Victoria, personal communication).

The question, of course, is whether the *Sebastes* larvae occur at the right depth to be retained. The closed recirculation over Cobb is apparently confined to depths below about 110 m, and anticyclonic current deflections are not detected shallower than 80 m (Freeland, 1994). Given that our collections were based on vertically integrated tows, we cannot establish the precise depth over which the *Sebastes* larvae were distributed. Larval *Sebastes* generally occur at depths of about 30–100 m (Ahlstrom, 1959). However, most of the adult rockfish that inhabit Cobb are found at depths well below 100 m. Although little is known about the behaviour of female rockfish during extrusion, it is believed that bottom-dwelling *Sebastes* spp. also release their larvae near the bottom (Moser, 1967; Yoklavich *et al.*, 1996). Thus, although we do not suggest that *Sebastes* larvae are passive, neutrally buoyant particles, we do contend that by virtue of their being released near the bottom, the particular suite of physical conditions that characterize Cobb make it almost certain that these larvae were being retained over the seamount at the time of sampling. Of course, the ultimate fate of larvae spawned over the seamount (and whether this represents a common occurrence) remains uncertain. However, in at least one other instance an anomalously high concentration of *Sebastes* larvae was recorded near Cobb Seamount (Waldron, 1972).

The question still remains as to how rockfish colonize isolated seamounts in the first place. It would appear that episodic offshore transport must occasionally transport larval or pelagic juvenile rockfish from the adjacent continental shelf. Given their preference for shallow topographies, it seems unlikely that adults migrate from the continental shelf (Pearson *et al.*, 1993). Interestingly, *Sebastes* spp. are also abundant on other NE Pacific seamounts (Herlinveaux, 1971; Raymore, 1982; Genin *et al.*, 1994). We propose that, in addition to the benefits of a viviparous life history, the fact that many *Sebastes* spp. are very slow-growing and live up to 50–100 years (Leaman, 1991) further enhances their ability to establish and maintain populations on isolated seamounts such as Cobb. This could be particularly important on sea-

mounts where recirculating flows occur only rarely (i.e. rather than the quasi-permanent recirculation that seems to occur at Cobb), and where recruitment may be highly episodic.

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REFERENCES

- Ahlstrom, E.H. (1959) Vertical distribution of pelagic fish eggs and larvae off California and Baja California. *U.S. Fish. Wildl. Serv. Fish. Bull.* **60**:107–146.
- Boehlert, G.W. and Genin, A. (1987) A review of the effects of seamounts on biological processes. In: *Seamounts, Islands and Atolls*. B.H. Keating, P. Fryer, R. Batiza and G.W. Boehlert, eds. *Geophysical Monographs* **43**:319–334.
- Boehlert, G.W. and Mundy, B.C. (1993) Ichthyoplankton assemblages at seamounts and oceanic islands. *Bull. Mar. Sci.* **53**:336–361.
- Budinger, T.F. (1967) Cobb Seamount. *Deep-Sea Res.* **14**:191–201.
- Codiga, D.L. and Eriksen, C.C. (1997) Observations of low-frequency circulation and amplified subinertial tidal currents at Cobb Seamount. *J. Geophys. Res. Oceans* **102** (C10):22993–22307.
- Comeau, L.A., Vézina, A.F., Bourgeois, M. and Juniper, S.K. (1995) Relationship between phytoplankton production and the physical structure of the water column near Cobb Seamount, northeast Pacific. *Deep-Sea Res.* **42**:993–1005.
- Dower, J.F. (1994) Biological consequences of current-topography interactions at Cobb Seamount. PhD Dissertation, University of Victoria.
- Dower, J.F. and Mackas, D.L. (1996) 'Seamount effects' in the zooplankton community near Cobb Seamount. *Deep-Sea Res.* **43**:837–858.
- Dower, J.H., Freeland, H. and Juniper, K. (1992) A strong biological response to oceanic flow past Cobb Seamount. *Deep-Sea Res.* **39**:1139–1145.
- Fedosova, R.A. (1974) Distribution of some copepod species in the vicinity of the underwater Hawaiian Ridge. *Oceanology* **14**:724–727.
- Freeland, H.J. (1994) Ocean circulation at and near Cobb Seamount. *Deep-Sea Res.* **41**:1715–1732.
- Genin, A., Greene, C., Haury, L., Wiebe, P., Gal, G., Kaartvedt, S., Mier, E., Fey, C. and Dawson, J. (1994) Zooplankton patch dynamics: Daily gap formation over abrupt topography. *Deep-Sea Res.* **41**:941–951.

- Goldner, D.R. and Chapman, D.C. (1997) Flow and particle motion induced above a tall seamount by steady and tidal background currents. *Deep-Sea Res.* **44**:719–744.
- Haury, L., Fey, C., Newland, C. and Genin, A. (2000) Zooplankton distribution around four eastern North Pacific seamounts. *Prog. Oceanogr.* **45**:69–105.
- Herlinveaux, R.H. (1971) Oceanographic features of and biological observations at Bowie Seamount 14–15, August, 1969. *Fish. Res. Bd. Can.* Technical Report no. 273.
- Hubbs, C.L. (1959) Initial discoveries of fish faunas on seamounts and offshore banks in the eastern Pacific. *Pac. Sci.* **13**:311–316.
- Leaman, B.M. (1991) Reproductive styles and life-history variables relative to exploitation and management of Sebastes stocks. *Environ. Biol. Fish.* **30**:253–271.
- Loeb, V.J. (1980) Vertical distribution and development of larval fishes in the north Pacific central gyre during summer. *Fish. Bull.* **77**:777–793.
- Matarese, A.C., Kendall, A.W., Blood, D.M. and Vinter, B.M. (1989) Laboratory guide to early life stages of Northeast Pacific fishes. NOAA Technical Report NMFS 80.
- Moser, H.G. (1967) Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off Southern California. *Copeia* **1976**:773–797.
- Nellen, W. (1974) Investigations on the distribution of fish larvae and plankton near and above the Great Meteor Seamount. In: *The Early Life History of Fish*. J.H. Blaxter, ed. New York: Springer-Verlag, pp. 213–214.
- Parker, T. and Tunnicliffe, V.J. (1994) Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. *Biol. Bull.* **187**:336–345.
- Pearson, D.E., Douglas, D.A. and Barss, B. (1993) Biological observations from the Cobb Seamount rockfish fishery. *Fish. Bull.* **91**:573–576.
- Pepin, P., Dower, J.F. and Leggett, W.C. (1998) Changes in the probability density function of larval fish body length following preservation. *Fish. Bull.* **96**:633–640.
- Raymore, P.A. (1982) Photographic investigations on three seamounts in the Gulf of Alaska. *Pac. Sci.* **36**:14–34.
- Rogers, A.D. (1994) The biology of seamounts. *Adv. Mar. Biol.* **30**:305–350.
- Sasaki, T. (1986) Development and present status of Japanese trawl fisheries in the vicinity of seamounts. In: *The Environment and Resources of Seamounts in the North Pacific*. R.N. Uchida, S. Hayasi and G.W. Boehlert, eds. NOAA Technical Report NMFS **43**:21–30.
- Sime-Ngando, T., Juniper, K. and Vézina, A. (1993) Ciliated protozoan communities over Cobb Seamount: increase in biomass and spatial patchiness. *Mar. Ecol. Prog. Ser.* **89**:37–51.
- Uda, M. and Ishino, M. (1958) Enrichment patterns resulting from eddy systems in relation to fishing grounds. *J. Tokyo Uni. Fish.* **44**:105–119.
- Voronina, N.M. and Timonin, A.G. (1986) Zooplankton of the region of seamounts in the western Indian Ocean. *Oceanology* **26**:745–748.
- Waldron, K.D. (1972) Fish larvae, collected from the north-eastern Pacific Ocean and Paget Sound during April and May 1967. NOAA Tech. Rep. NMFS Spec. Sea. Rep. Fish. **663**. 16 pp.
- Yoklavich, M.M., Loeb, V.J., Nishimoto, M. and Daly, B. (1996) Nearshore assemblages of larval rockfishes and their physical environment off central California during an extended El Niño event. 1991–93. *Fish. Bull.* **94**:766–782.