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Marine fish life history strategies: applications to fishery management

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Abstract The life history traits of 42 marine fish species were grouped according to the theoretical classifications of life history strategies. This provides a conceptual framework of management options, because life history strategies are the underlying determinants for population responses to climate and ocean changes, they can be used to classify typical population responses. When faced with providing management advice for species for which there is no information on absolute or relative biomass, such as newly exploited species, life history traits can be used to classify the species into a strategist grouping and the appropriate management options can be selected from the conceptual framework.

KEYWORDS: fisheries management, life history traits, population dynamics, regimes.

Introduction

Fishery scientists and managers are facing difficulties in assessing and managing marine resources in the 21st century. Growing concern over issues such as bycatch species and impacts of gear on habitat, coupled with the realization that climate can have major impacts on the natural regulation of populations, has led agencies to develop more holistic approaches to the assessment and management of resources. The objective has been to move away from single species stock assessment to ecosystem management (ESA 1998; FRCC 1998; NMFS 1999). While there has been much general discussion, there has yet to be any effective implementation of such an approach. At best, single species stock assessments have incorporated ecosystem considerations when estimating the status of a stock. In addition, there has been much discussion and research on the precautionary approach and objective-based management frameworks (Caddy 1998; Gislason, Sinclair, Sainsbury & O'Boyle 2000). Again, these have yet to be implemented on a wide scale in fisheries management.

As ecosystem assessment requires information on the whole, or at least major, components of an ecosystem, including abiotic and biotic factors, one of the obstacles to its implementation will be the lack of abundance information for most biotic components. Without costly surveys, these gaps in data will not probably be filled. Additionally, basic life history information, such as age at maturity, which are essential for stock assessments are often lacking for newly exploited species. One way of addressing these information gaps is to characterize groupings of commercially exploited species based on known life history traits and use these groupings to characterize the nature of species abundance trends over various time-scales. Conceptual management scenarios based on life history traits could be used for the management of newly exploited species.

Much research has been done on life history traits and population regulation in marine fishes. Kawasaki (1980, 1983) suggested that the grouping of life history traits of marine fishes differed from the traditional *r* and *K* strategists developed for terrestrial animals (MacArthur & Wilson 1967; Pianka 1970). Typically, *r*-strategists are characterized as short-lived, small in size, with early maturation. *K*-strategists are long-lived, large in size and have a delayed maturation. Kawasaki (1983) suggested a third intermediate grouping for fishes characterized as long-lived, large in size but with early maturation. However, these groupings were based on a small range of taxonomic groups, mainly clupeoid fishes, and were used to identify differences among populations, not species.

Winemiller & Rose (1992) used a quantitative approach to develop groupings of life history strategies by examining 16 life history traits in a large sample (216 species from 57 families) of North American

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freshwater and marine species. Based on a final selection of five life history traits for 82 freshwater species and 65 marine species, they suggested a trilateral continuum model with three endpoint strategies: (1) small, rapidly maturing, short-lived fishes (*opportunistic strategists*); (2) larger, highly fecund fishes with longer life spans (*periodic strategists*); and (3) fishes of intermediate size that often exhibit parental investment and produce fewer, larger offspring (*equilibrium strategists*). McCann & Shuter (1997) extended the work of Winemiller & Rose (1992) to focus on differentiating allometric relationships for fecundity and age at maturity across the endpoint strategies. Their empirical evidence identified a fourth, *salmonic strategist* grouping.

Life history traits are the underlying determinants for population responses to environmental forcing. Consideration of life history strategies should be fundamental to fisheries management. In this study, biological traits are used for several commercially exploited marine fish to characterize them into life history groupings. In addition to the existing classifications of periodic, opportunistic, equilibrium and salmonic strategists, a fifth group is proposed (*intermediate strategist*). These life history strategies are linked to population dynamics and responses to environmental forcing. Conceptual management frameworks are suggested for each life history strategy, irrespective of current management practices for specific species. As an example of the applicability of this research to newly exploited species, a species is selected for which there is very little information to provide traditional stock assessment advice and it is classified into a life history strategy to develop a management scenario.

Materials and methods

It was recognized that a range of species, representing many life history adaptations should be compared to assess applicability of results for fisheries management as a whole. Species were selected that are currently caught in the west coast Canadian commercial fishery, including salmonids, pelagic and benthic fish, and others which have the potential to support fisheries.

Life history traits

An extensive literature search was conducted for published life history parameters. If published estimates were not available, grey literature was used where possible to provide estimates. In many instances a range of parameter values for life history traits were published and for these the mid-point of any range was selected. If separate estimates were available for males and females, the estimate for females was used. When available, estimates from studies conducted in the north-east Pacific were selected.

Estimates were obtained for the following life history parameters:

1 size at maturity – fork length (mm) at 50% maturity;
2 maximum size – maximum fork length (mm) reported;
3 growth rate – von Bertalanffy growth coefficient (k) determined from a size-at-age curve (if the value of k was not published in the literature, it was calculated from available data);
4 fecundity – mid-point of the reported range of number of eggs per individual;
5 maximum age in years;
6 egg size – mean diameter (mm) of mature oocytes;
7 parental investment – using the approach outlined by Winemiller (1989), which quantifies three components of parental investment: (i) placement of zygotes or larvae, (ii) parental protection of zygotes or larvae and (iii) nutritive contribution to larvae was used. The parental investment value is calculated as Σx_i for $i = 1$ to 3 for the above three components (Table 1). Parental investment values ranged from 0, e.g. Pacific herring, *Clupea harengus pallasi* (Val.), to 12 for spiny dogfish, *Squalus acanthias* (L.), with an extended gestation period.

Ecological parameters

Habitat and trophic levels were classified for each species. The adult habitat of each species was classified by the following criteria: 1, for surface pelagic (0–50 m); 2, for midwater pelagic (50–200 m); 3, for deep water pelagic (> 200 m); 4, for near shore benthic (including continental shelf species) and 5, for deep water benthic (occurring in deep gullies and the continental slope). The classification of trophic levels outlined by Legendre, Galzin & Harmelin Vivien (1997) to quantify adult diet was modified: 1, detritivores and herbivores; 2, species consuming only zooplankton; 3, carnivores consuming small crustaceans; 4, carnivores consuming larger crustaceans, cephalopods and fish; 5, piscivores. Species that consume zooplankton and small crustaceans, e.g. Pacific sardine, *Sardinops sagax* (Jenyns), were ranked at 2.5.

Data analysis

Principal components analyses (PCA) was used to investigate the associations between life history variables as well as the ordination of species. PCA based on

Table 1. Values assigned to attribute of each component of parental investment

Component	Attribute	Value
Placement of zygotes or larvae (x_1)	No placement	0
	Zygotes placed in a special habitat	1
	Zygotes and larvae are maintained in a nest	2
Parental protection of zygotes or larvae (x_2)	No parental protection	0
	Brief protection (< 1 month) by one parent	1
	Lengthy protection (> 1 month) by one parent or brief protection by both parents	2
	Lengthy protection by both parents	4
Nutritive contribution to larvae (x_3)	No contribution (excluding yolk sac)	0
	Brief period of nutritive contribution (e.g. < 1 month gestation period)	2
	1–2 month gestation period	4
	> 2 month gestation period	8

correlation matrices were performed with Statistica version 5.5 software (StatSoft 1999). All variables were tested for normality and transformed ($\log_{10}$ or square root transformation) prior to multivariate analyses. Parental investment was excluded from all PCA analyses as it was an ordinal variable that did not approximate a normal distribution. Initially, a PCA was performed on a matrix with $n = 28$ species for which information on all life history parameters was available. Mean values of similar species were used to estimate unknown life history parameters. For example, the mean egg size of shortspine thornyheads, *Sebastolobus alascanus* (Bean), was used for the unknown egg size of longspine thornyheads *Sebastolobus altivelis* (Gilbert). A PCA was performed on a matrix with $n = 42$ species when some life history parameters were estimated with means.

In all PCA, significant components were determined using the broken stick method (Legendre & Legendre 1983). Eigenvectors were used to assess associations between life history traits. Individual species scores were plotted for the first and second components to ordinate species into life history groups. The ordination of species was overlaid with the codes for parental investment, adult habitat and adult diet to elucidate general ecological characteristics to the different life history groupings. The influence of using mean life history values on the final ordination into life history groups was tested by Procrustes analysis (10 000 iterations) and the PROTEST computer program (Jackson 1995). Procrustes analysis uses a rotational-fit algorithm that minimizes the sum-of-the-squared residuals (m^2 statistic) between two matrices and allows for the direct comparison between a pair of data matrices. If the addition of species and mean values did influence the PCA and resulting ordination, PROTEST would produce a non-significant m^2 statistic as the two ordinations would not overlap significantly.

Results

Information on 42 species (Appendix 1) ranging from planktivores such as northern lampfish, *Stenobrachus leucopsarus* (Eigenmann & Eigenmann), to piscivores such as the sixgill shark, *Hexanchus griseus* (Bonnaterre), was obtained. The species selected included 10 surface pelagic species, three mid-water pelagic species, three deep-water pelagic species, 18 near-shore benthic species and nine offshore benthic species. Parameter estimates for all life history traits were found for 28 species. For the remaining 14 species, no estimates for either fecundity or egg size and sometimes both were found. For some rockfish, no estimates for the growth coefficient (k) were available.

The first three components from the PCA on the 28 species data set were significant and accounted for a total of 89.6% of the total variance (Table 2). The PCA on the 42 species data set resulted in two significant components that accounted for 78.4% of the total variance (Table 2). The Procrustes analysis produced $m^2 = 0.0098$ ($P < 0.001$) which indicated that the addition of species with mean values did not significantly alter the ordination of species with known values. Therefore, the results of the PCA on the 42 species data set were ordinated to elucidate life history groupings (Fig. 1). Principal component (PC) 1 was most influenced by maximum size, size at maturity and egg size, with positive scores representing species that are large, mature at later ages and have large eggs (Table 2). PC 2 was most influenced by maximum age, growth coefficient (k) and fecundity, with positive scores representing long-lived, slow growing and highly fecund species (Table 2).

The bivariate plot of the standardized scores has a definite three endpoint pattern (Fig. 1). At one end are clupeids (e.g. Pacific sardine, herring), smelts [e.g. eulachons, *Thaleichthys pacificus* (Richardson)] and other forage fishes such as northern lampfish and Pacific sandlance, *Ammodytes hexapterus* (Pallus). These fishes are short-lived with a small body size and size at maturation, low fecundity, high growth

Table 2. Eigenvalues, percent variation and eigenvectors (variable loadings) for significant principal components (PC) from principal components analyses for the 28 and 42 species datasets based on six life history parameters

	Twenty-eight species			Forty-two species	
	PC 1	PC 2	PC 3	PC 1	PC 2
Eigenvalue	2.65	1.76	0.97	2.64	2.06
Percent variation	44.12	29.29	16.14	44.05	34.31
Eigenvector					
Size at maturity (50%)	0.94	–0.10	0.18	0.94	–0.15
Maximum size	0.95	–0.03	0.23	0.95	–0.13
Growth (k)	–0.23	–0.77	0.46	–0.34	–0.76
Fecundity	–0.08	0.59	0.77	0.06	0.76
Maximum age	0.16	0.88	–0.13	0.34	0.84
Egg size	0.87	–0.18	–0.23	0.79	–0.41

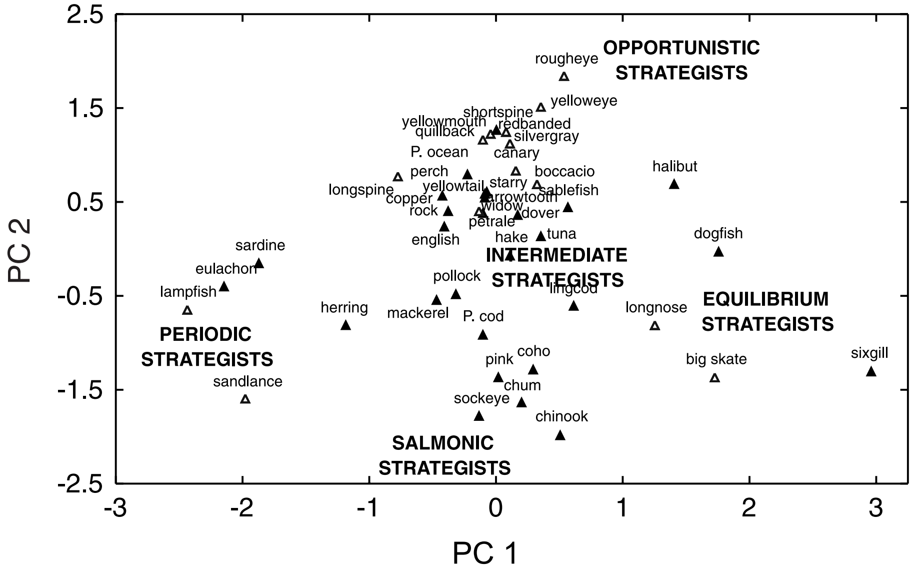

Figure 1. Bivariate plot of standardized scores from the significant components of principal components analysis on six life history traits of 42 marine species. The positive scores on PC 1 represent species that are large in size, mature at later ages and have large eggs. Positive scores on PC 2 represent long-lived, slow growing and highly fecund species. Open circles denote the 14 species for which a life history parameter (fecundity or egg size) was estimated from a related species.

rates and small eggs. They are also surface and mid-water pelagic species that exhibit little if any parental investment and are planktivores or lower-order carnivores (Fig. 2). This grouping most closely resembles the opportunistic strategists (Winemiller & Rose 1992). Another group was dominated by rockfish and flatfish (Fig. 1). These fishes are long-lived, slow growing with a high fecundity, but are medium in size, have a mid-range for size at maturity and have medium sized-eggs. These fishes are higher order carnivores that inhabit shelf or slope benthic habitat and exhibit some parental investment (Fig. 2). This grouping is similar to the periodic strategist (Winemiller & Rose 1992). A third group was dominated by elasmobranchs (skates and sharks), which are slow-growing, have a low fecundity, are large in size, and have large eggs (Fig. 1). These species exhibit some or a great degree of parental investment, are higher order carnivores and piscivores, and inhabit a range of habitats (Fig. 2).

Elasmobranchs were not included in the Winemiller & Rose (1992) analyses and they noted that the equilibrium strategy in fishes is consistent with the K-strategy suite of life history characteristics (Pianka 1970). Generally, the K- strategy describes large-sized individuals that have a very low fecundity and a very high degree of parental investment. These traits characterize

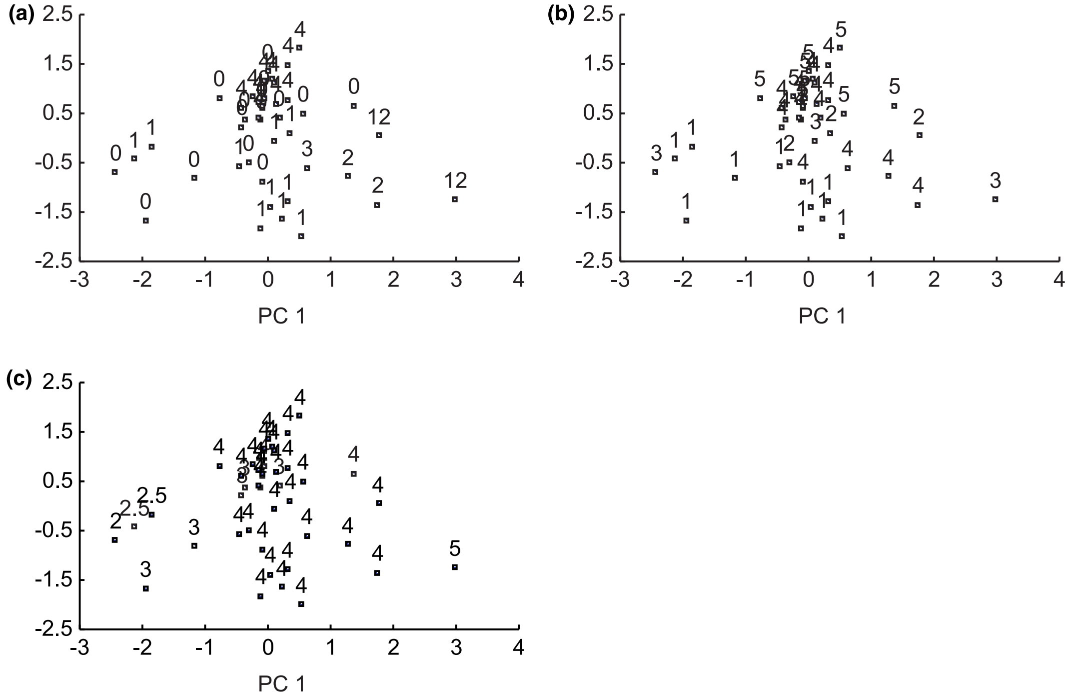

Figure 2. The ordination of species from Figure 1 labelled with codes for parental investment (a), adult habitat (b) and adult diet (c). The three endpoints are typically represented by species that (i) exhibit no or little parental investment, inhabit surface waters and are planktivores; (ii) exhibit some degree of parental investment, inhabit bottom waters and are carnivores feeding on large crustaceans, cephalopods and fish; (iii) exhibit a great degree of parental investment, inhabit bottom and deepwater waters, are piscivores. See text for code definitions.

the elasmobranch species, so this life history grouping is best described by the equilibrium strategy.

In addition to these obvious groupings (endpoints), there were two other distinct groups in Figure 1. The salmonids grouped together at the base of the trilateral continuum. *Oncorhynchus* spp. are relatively short-lived, but fast growing and large sized. Compared with other marine species, they are not extremely fecund, but have large eggs. The life history traits of the *Oncorhynchus* spp. are very similar to the opportunistic strategists, however, in agreement with McCann & Shuter (1997), a separate grouping for salmonids was considered appropriate as they differ from the opportunistic strategists with their semelparous nature and the higher degree of parental investment (Fig. 2).

Several species, including codfishes and scombrids, were located within the middle of the trilateral continuum (Fig. 1). These were a distinct grouping which are termed intermediate strategists. These species have life history traits that are mid-range compared with the suite of marine fishes. Codfishes are usually considered to be typical groundfish species (i.e. benthic or bathypelagic), but it is important to note that they are different from the other groundfish species (e.g. rockfish, flatfish and sablefish) that grouped at the periodic strategists endpoint. For example, codfish are not as long-lived and scombrids are highly migratory surface pelagics, but differ from the other surface pelagics at the opportunistic strategists endpoint because of their larger size and longevity. In terms of life history traits, these intermediate strategists should be considered separately from other species they might typically be associated with.

Another species that is located in the middle of the trilateral continuum was the lingcod, *Ophidion elongatus* (Girard). Lingcod is a large, fast growing, highly fecund species with early maturation and large eggs. As with the codfishes, lingcod (with a maximum age of 20 years), is not as long-lived as many groundfish species at the periodic endpoint (e.g. sablefish with a maximum age of 113). It also differs in its life history because of the high degree of parental investment as eggs masses are laid in rocky crevices and the males actively guard the egg masses from predators.

Discussion

Multivariate analyses of life history parameters for 42 marine fish indicated five distinct groupings of species. Three of these grouping agreed with the opportunistic, periodic and equilibrium strategists of Winemiller & Rose (1992). Salmonids were also distinct strategists (McCann & Shuter 1997) and a fifth group (intermediate strategists) is proposed. Overall these groupings provide a foundation for developing conceptual management scenarios based on generalized population dynamics and responses to environmental conditions. It would be preferable to examine a range of successful management policies and attempt to apply a quantitative measure of management success and association with life history traits. However, a diverse range of implemented management policies are difficult to identify, as is quantifying management success. Below a conceptual framework of management scenarios for fishes of various life history strategies is discussed.

Opportunistic strategists

Opportunistic strategists have a shorter generation time which helps to maximize their intrinsic rate of population growth despite their relatively low individual fecundity. These pelagic species occupy habitats not only with a high degree of variability, but also, potentially, with large resources of energy. As such, their population responses tend to be large in amplitude and species grouped according to this life history strategy have been classified as having either cyclical, irregular or spasmodic population patterns (Caddy & Gulland 1983; Kawasaki 1983; Spencer & Collie 1997). In the North Pacific, climate and environmental conditions have been observed to be relatively stable on decadal scales, during periods called regimes, but they can abruptly shift from one state to another during regime shifts (Ebbesmeyer, Cayan, McLain, Nichols, Peterson & Redmond 1991; Beamish, McFarlane & King 2000a; Hare & Mantua 2000; McFarlane, King & Beamish 2000). Abundance and distribution of opportunistic strategists (e.g. Pacific sardine and Pacific herring) are known to fluctuate concurrently with climate–ocean regimes (Beamish *et al.* 2000a; McFarlane *et al.* 2000; McFarlane & Beamish 2001). For example, Pacific sardine increased in abundance prior to the regime shift in 1947, decreased in abundance through to the 1977 regime shift, increased again until 1989 and with the 1989 regime shift decreased in overall abundance (Fig. 3). Within a regime period, their abundance is dynamic, i.e. increasing or decreasing over time, and across regime periods the populations experience high amplitude of variability. The magnitude of variability in survival makes the opportunistic strategists susceptible to rapid depletion augmented by fishing pressure.

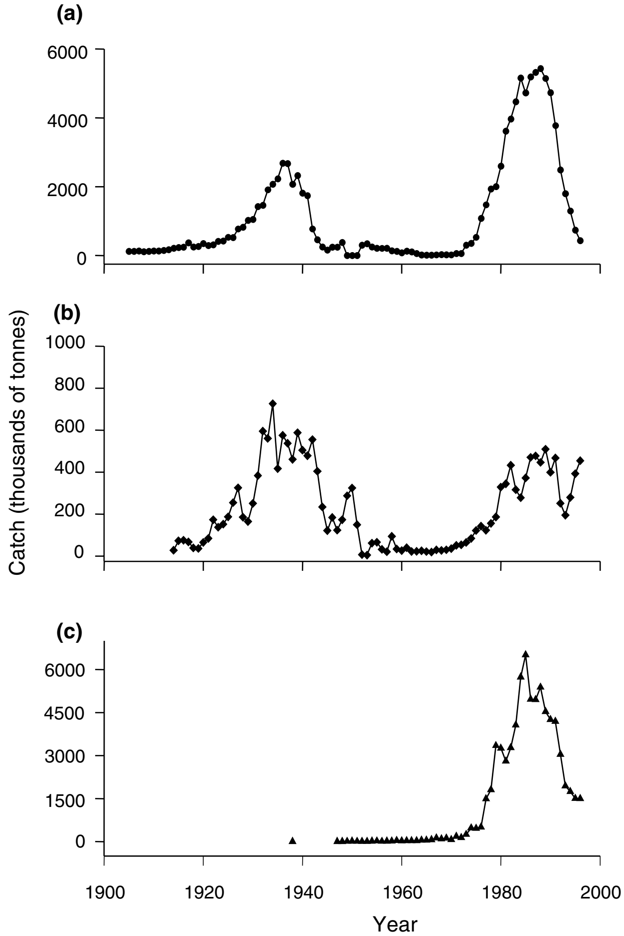

Figure 3. Catch ($t \times 1000$) from the three major stocks (Japan, California, Chile) of Pacific sardine illustrating biomass fluctuations (updated from Kawasaki & Omori 1986). Pacific sardines represent opportunistic strategists with a short life span, small size and early maturation. Periodic strategists exhibit a high degree of variability in their population dynamics with irregular cycles concomitant with regime shifts.

These strategists should be managed to maintain a critical minimum spawning biomass. This implies that as a population approaches a minimum spawning biomass, that fishing removals should cease (i.e. that there are periods when the populations cannot be exploited). The historical low abundance experienced by the populations during regimes of low recruitment might be assumed to be the critical minimum spawning biomass. These abundance levels at least represent levels from which the population can increase when environmental conditions favour high recruitment. These strategists might represent higher maintenance stocks that require careful monitoring to ensure a critical minimum spawning biomass is maintained. The most effective management decisions will be those that compensate quickly for changes in survival. While inter-annual variability might require adaptive management, or in-season adjustment, it is also important to recognize the points of inflection in long-term abundance trend. As such, the management time frame must be shorter than the period of the natural system. As opportunistic strategists mature, and recruit to the fisheries, at an early age, these species are more likely to require annual or biannual assessments.

Periodic strategists

Slow-growing, long-lived demersal species have a lower degree of variability in abundance and have been classified as having a steady-state population pattern (Caddy & Gulland 1983; Kawasaki 1983; Spencer & Collie 1997). While these species might have a relatively low amplitude of variability, recruitment is still not constant. Longevity (i.e. lifespan greater than 20 years) benefits a species by ensuring a relatively long reproductive cycle, which minimizes the risk that periods of unfavourable environmental conditions will result in the loss of a stock (Leaman & Beamish 1984). The period between strong year classes can be relatively long (up to several decades), and these species can exhibit decadal scale patterns in recruitment coincident with climate–ocean regimes (McFarlane *et al.* 2000; Hollowed, Hare & Wooster 2001). Periodic strategists such as yellowtail, Pacific ocean perch, rock sole and dover sole experienced average or above average year classes during the 1980s, following a regime shift in 1977 (McFarlane *et al.* 2000). However, after the 1989 regime shift, these species experienced below average year classes. An extensive (1960–1997) year class index for sablefish revealed similar patterns (Fig. 4), with below average year classes prior to 1977, above average year classes from 1977 to 1990, and average or below average year classes after 1989 (King, McFarlane & Beamish 2000).

For periodic strategists, annual recruitment is only a fraction of the spawning stock biomass, and maintaining an appropriate age-structure in the spawning stock biomass should be a paramount management goal for long-lived, late maturing species. An effective management tool would be spatial refuges directed at the adult portion of the population to retain older fishes in the age-structure of the spawning stock biomass. These spatial refuges could be static, such as the no-take reserves suggested for rockfish conservation (Parker, Berkeley, Golden, Gunderson, Heifetz, Hixon, Larson, Leaman, Love, Musick, O'Connell, Ralston, Weeks & Yoklavich 2000; Murray, Ambrose, Bohnsack, Botsford, Carr, Davis, Dayton, Gotshall, Gunderson,

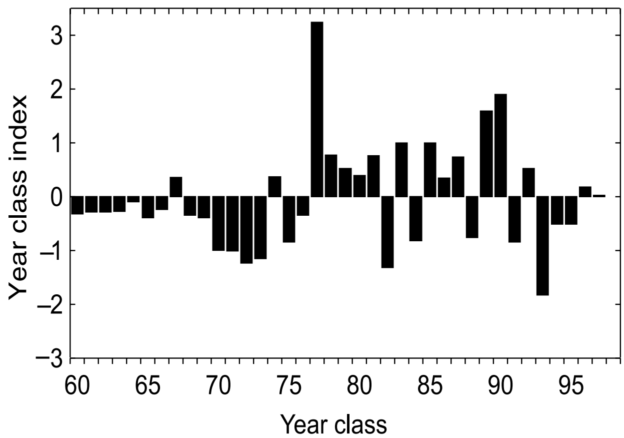

Figure 4. The index of relative year class success for sablefish, 1960–1997 (from King *et al.* 2000). Sablefish represent periodic strategists with relatively stable population dynamics within climate regime periods. Longevity and high fecundity allow these strategists to maintain a spawning biomass through low productivity regimes and to take advantage of shifts in the environment that are favourable to year class success.

Hixon, Lubchenco, Mangel, MacCall & McArdle 1999), or dynamic, such as the curtailing of deep water fishing (i.e. the habitat occupied by mature fish) during the less productive regimes suggested for sablefish (King, McFarlane & Beamish 2001). Dynamic spatial refugia may be effective for flatfishes and other groundfish that exhibit traits of periodic strategists, namely longevity, late maturity, slow growth, and large size. An alternate to spatial refuges could be maximum size limit, conditional on high release survival and would be applicable to non-destructive gear, such as traps.

Equilibrium strategists

The equilibrium strategists are dominated by species that have a very low intrinsic rate of increase (Smith, Au & Show 1998). As such, equilibrium strategists should exhibit steady population dynamics overtime. Unfortunately, biomass estimates are not available for species in the equilibrium strategist grouping. These species are able to withstand only modest harvest rates, otherwise population depletion and stock collapse results (Hoff & Musick 1990; Musick 1999). Equilibrium strategists have a low fecundity and late maturation, and are therefore not able to recover as quickly as other fishes after population reduction by fisheries (Hoenig & Gruber 1990; Sminkey & Musick 1995). If equilibrium strategists are caught as bycatch from mixed species fisheries, they are at a greater risk of collapse as the fisheries target the more productive fishes and will continue to occur even when the low productive fishes are driven to stock collapse (Musick, Burgess, Calliet, Camhi & Fordham 2000). Management options in mixed fisheries should account for the vulnerability of the less productive species and precautionary quotas and bycatch limits should be established (Musick *et al.* 2000). Traditional stock assessment models may not apply to equilibrium strategists as their population dynamics have very low variability. Age-based demographic matrix models or Bayesian stock production techniques are probably the most appropriate (Musick *et al.* 2000). Equilibrium strategists should be harvested at low or moderate rates.

Salmonic strategists

The population trends of Pacific salmon are similar to other surface pelagics, such as those in the opportunistic strategist grouping. There have been numerous examples of the coincidence of changes in salmon productivity with decadal-scale changes in climate and ocean conditions (Beamish & Bouillon 1993; Hare & Francis 1995; Beamish, Neville & Cass 1997; Mantua, Hare, Zhang, Wallace & Francis 1997). Typically, salmon production exhibits dramatic increases or decreases during decadal-scale regime periods (Fig. 5). A recent study has suggested that the marine component of salmonid population dynamics is determined by first ocean summer conditions (Beamish & Mahnken 2001). Management advice could be improved by recognizing change in ocean survival of salmonids, perhaps with ocean surveys during the first marine summer (Beamish, McCaughran, King, Sweeting & McFarlane 2000b). Management advice could be formulated using information on freshwater density-dependent relationships (i.e. egg-smolt production) and on marine survival rate (smolt-adult production) (Bradford, Myers & Irvine 2000). These production relationships and rates may vary across decadal-scales with regime shifts. Additionally, management of hatchery programmes must be able to adapt smolt production to changing marine survival. If marine survival is density dependent, then during regimes with low marine carrying capacity, high levels of smolt production by hatcheries will negatively impact wild salmon marine survival (Levin, Zabel & Williams 2001). As with the opportunistic strategists, the most difficult period for assessment and management will be at a regime shift when production changes.

Intermediate strategists

The intermediate strategists tend to exhibit the same population dynamics as opportunistic strategists, i.e. rapid and high amplitude changes in biomass (Fig. 6). Their life history characteristics are mid-range to the opportunistic and the periodic strategists. They have a longer life span than the opportunistic strategists, with maximum ages typically 10–20 years. However, these maximum ages are below the typical periodic strategists that, in the case of rockfish, can be in excess of 100 years. Hence, their populations can withstand periods of unfavourable environmental conditions for recruitment better than the opportunistic strategists, but they do not exhibit the more stable populations within regimes found in periodic strategists. Their shorter generation time makes them more vulnerable to fluctuations in biomass through fluctuations in recruitment. Some intermediate strategists (tuna,

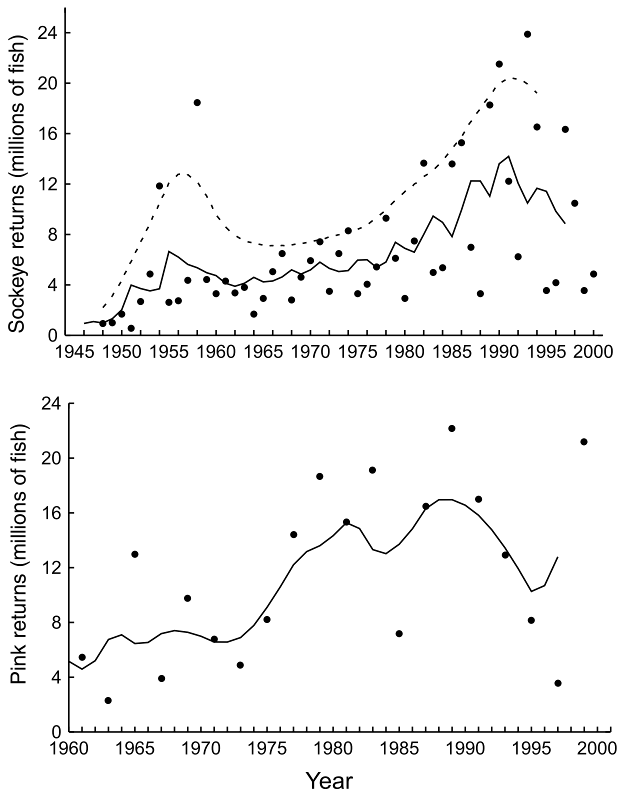

Figure 5. Fraser River sockeye, *Oncorhynchus nerka* (Walbaum), and pink salmon, *Oncorhynchus keta* (Walbaum), total returns (escapement and catch) in millions of fish. Sockeye salmon return to spawn after an ocean residency of 4 years. Effects of regime shifts (1977 and 1989 ocean entry years) are delayed and evident in returns approximately 4 years later. Fraser River sockeye have distinct dominant year cycles (typically quadrennial) that underlay the overall trends in abundance. The dotted line is a loess smoothing filter for the dominant year returns and the solid line is a loess smooth for all returns. Pink salmon return to spawn after an ocean residency of 1 year and effects of regime shifts on returns are delayed by 1 year. Pink salmon exhibit a 2-year cycle dominance, with odd years dominating the Fraser River returns. The solid line represents a loess smoothing filter through these odd year returns.

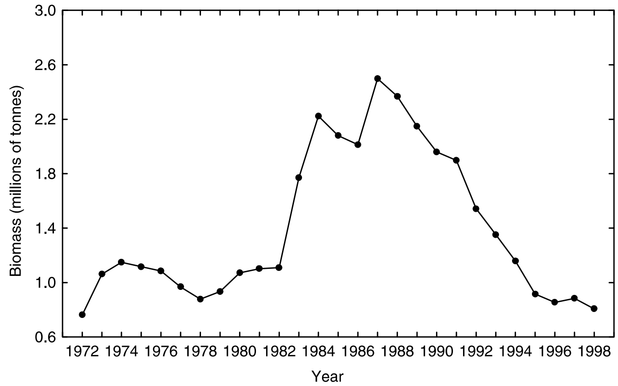

Figure 6. Female spawning biomass of Pacific hake for the offshore US and Canada population (from Dorn, Saunders, Wilson, Guttormsen, Cooke, Kieser & Wilkins 1998). Hake represent intermediate strategists with a larger size than opportunistic strategists. The population responses are typically increasing or decreasing trends within a regime, with abrupt changes concomitant with regime shifts.

mackerel and hake) are large-sized, highly migratory pelagic species (Fig. 2) that are able to move from areas of poor conditions to areas of better conditions as reflected in large distributional changes (Polovina 1996; McFarlane *et al.* 2000). The groundfish in the intermediate strategists will require short-scale quota periods and assessment time frames than the periodic strategist's endpoint. During periods of poor recruitment, fishing plans need to be conservative. These strategists should be managed similar to the opportunistic strategists, with the maintenance of a critical spawning biomass.

Applying life history strategies and management scenarios to developing fisheries

One of the challenges for fisheries scientists is the provision of management advice for developing fisheries for which there is no catch history, no biomass information and limited biological data. Test fisheries can be used to augment published life history parameters by collecting information on maximum length, egg size, fecundity and size at maturity data. For example, an experimental fishery for Pacific hagfish, *Eptatretus stoutii* (Lockington), has been conducted off the south-west coast of Vancouver Island (1988–1992; 1999–2000). After reviewing data collected from the experimental fishery and other published data (Benson, Neville & McFarlane 2001), the following biological parameters were estimated: size at 50% maturity = 35.4 cm; maximum size = 63.1 cm; mid-range fecundity = 15; maximum age = 17 (unvalidated estimate); oocyte size = 5 mm, von Bertalanffy growth parameter (k) = 0.07. Pacific hagfish is a species with a relatively large size at maturation, relatively large eggs, low fecundity, is not very long-lived and appears to be slow-growing. As a conservative approach to managing this species, managers might consider Pacific hagfish to be close to the equilibrium strategist. An initial management framework should include moderate to low harvest rates. However, harvest rates could not be estimated without biomass estimates. Therefore, the fishing plan could be experimental with different removal levels in different areas. This would provide information on the effects of various exploitation rates on abundance trends and biological attributes of the population.

Ecosystem assessment and management

A major impediment in developing ecosystem assessments and management is the need to consider many species, most of which will not have been assessed or monitored. Knowledge of life history parameters will provide a starting point for management frameworks. Placing species into life history groupings can help to establish an understanding of the probable nature of that species population dynamics, in relation to both environment and fisheries impacts. Stock assessments and management implementations are typically conducted on an annual basis, even for long-lived species such as sablefish. Assessing and managing resources according to life history strategies is a possible first step in developing ecosystem approaches. Fisheries managers presently manage inter-annual noise in fish populations, although population dynamics have been characterized on decadal-scales in relation to climate regimes. Ecosystem management suggests that managers also need to focus on long-term decadal-scale processes. This requires monitoring climatic processes and the response of lower trophic level (e.g. zooplankton, benthos) dynamics to develop a more holistic assessment framework, such as the report card approach suggested by King *et al.* (2001). The report card presents an aggregation of parameters (climate, oceanographic, lower trophic levels and recruitment) that, on average, gives an impression of productivity during a specific regime. The conceptual framework presented here can establish an understanding of the probable nature of that species population dynamics, particularly within climate regimes.

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References

Beamish R.J. & Bouillon D.R. (1993) Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 1002–1016.

Beamish R.J. & Mahnken C. (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* **49,** 423–437.

Beamish R.J., Neville C.M. & Cass A.J. (1997) Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 543–554.

Beamish R.J., McFarlane G.A. & King J.R. (2000a) Fisheries climatology: understanding the decadal scale processes that regulate British Columbia fish populations. In: P. Harrison & T. Parsons (eds) *Fisheries Oceanography: An Integrative Approach to Fisheries Ecology and Management*. Oxford: Blackwell Scientific Publications, pp. 94–139.

Beamish R.J., McCaughran D., King J.R., Sweeting R.M. & McFarlane F.A. (2000b) Estimating the abundance of juvenile coho salmon in the Strait of Georgia by means of surface trawls. *North American Journal of Fisheries Management* **20,** 369–375.

Benson A.J., Neville C.M. & McFarlane G.A. (2001) An update for the British Columbia experimental fishery for Pacific hagfish (*Eptatretus stoutii*). *Canadian Science Advisory Secretariat Research Document* No. 2001/149, 26 pp.

Bradford M.J., Myers R.A. & Irvine J.R. (2000) Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production. *Canadian Journal of Fisheries and Aquatic Sciences* **57,** 677–686.

Caddy J.F. (1998) A short review of precautionary reference points and some proposals for their use in data-poor situations. *FAO Fisheries Techical Paper* No. 379, 30 pp.

Caddy J.F. & Gulland J.A. (1983) Historical patterns of fish stocks. *Marine Policy* **7,** 267–278.

Dorn M.W., Saunders M.W., Wilson C.D, Guttormsen M.A., Cooke K., Kieser R. & Wilkins M.E. (1998) Status of the coastal Pacific hake/whiting stock in U.S. and Canada in 1998. *Canadian Science Advisory Secretariat Research Document* No. 99/90, 104 pp.

Ebbesmeyer, C.C., Cayan D.R., McLain D.R., Nichols F.H., Peterson D.H. & Redmond K.T. (1991) 1976 Step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1984. In: J.L. Betancourt & V.L. Tharp (eds) *Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop, April 1990*. California: California Department of Water Resources, *Interagency Ecological Studies Technical Report* No. 26, pp. 115–130.

Ecological Society of America (ESA) (1998) Ecosystem management for sustainable marine fisheries. *Ecological Applications* 8 (Suppl. 1) 174 pp.

Fisheries Resource Conservation Council (FRCC) (1998) Towards an ecosystem approach to fisheries management, Report of the Environment and Ecology Workshop held at the University of Moncton, 15–16 December, 1997. *Resource Conservation Council Report 98-2*, 29 pp.

Gislason H., Sinclair M.M., Sainsbury K. & O'Boyle R. (2000) Symposium overview: incorporating ecosystem objectives within fisheries management. *Journal of Marine Sciences* **57,** 468–475.

Hare S.R. & Francis R.C. (1995) Climate change and salmon production in the northeast Pacific. In: R.J. Beamish (ed.) *Climate Change and Northern Fish Populations. Canadian Special Publications of Fisheries and Aquatic Sciences* 121, 357–372.

Hare S.R. & Mantua N.J. (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* **47,** 103–145.

Hoenig J.M. & Gruber S.H. (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. In: H.L. Pratt, S.H. Gruber & T. Taniuchi (eds) *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of Fisheries. NOAA Technical Report NMFS* No. 90, pp. 1–16.

Hoff T.B. & Musick J. (1990) Western North Atlantic shark-fishery management problems and information requirements. In: H.L. Pratt, S.H. Gruber & T. Taniuchi (eds) *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of Fisheries. NOAA Technical Report NMFS* No. 90, pp. 455–472.

Hollowed A.B., Hare S.R. & Wooster W.S. (2001) Pacific basin climate variability and patterns of northeastern Pacific marine fish production. *Progress in Oceanography* **49,** 257–282.

Jackson D.A. (1995) PROTEST: PROcrustean randomization TEST of community environment concordance. *Ecoscience* **2,** 297–303.

Kawasaki T. (1980) Fundamental relations among the selections of life history in marine teleosts. *Bulletin of the Japanese Society of Science and Fisheries* **46,** 289–293.

Kawasaki T. (1983) Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology. *FAO Fisheries Report* **291,** 1065–1080.

Kawasaki T. & Omori M. (1986) Fluctuations in three major sardine stocks in the Pacific and the global temperature. In: T. Wyatt & G. Larranenta (eds) *Long Term Changes in*

Marine Fish Populations. A symposium held in Vigo, Spain, 18–21 November 1986. Bayona, Spain: Imprenta REAL, pp. 37–53.

King J.R., McFarlane G.A. & Beamish R.J. (2000) Decadal scale patterns in the relative year class success of sablefish (*Anoplopoma fimbria*). *Fisheries Oceanography* **9,** 62–70.

King J.R., McFarlane G.A. & Beamish R.J. (2001) Incorporating the dynamics of marine systems into the stock assessment and management of sablefish. *Progress in Oceanography* **49,** 619–639.

Leaman B.M. & Beamish R.J. (1984) Ecological and management implications of longevity in some northeast Pacific groundfishes. In: *Symposium on Determining Effective Effort and Calculating Yield in Groundfish Fisheries, and on Pacific Cod Biology and Population Dynamics, Vancouver, BC, 28–30 October, 1981. International North Pacific Fisheries Commissiion Bulletin* No. 42, pp. 85–97.

Legendre P., Galzin R. & HarmelinVivien M.L. (1997) Relating behaviour to habitat: solutions to the fourth-corner problem. *Ecology* **78,** 547–562.

Legendre L. & Legendre P. (1983) *Numerical Ecology*. Amsterdam: Elsevier Publishing, 853 pp.

Levin P.S., Zabel R.W. & Williams J.G. (2001) The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **268,** 1153–1158.

MacArthur R.H. & Wilson E.O. (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press, 203 pp.

Mantua N.J., Hare S.R., Zhang Y., Wallace J.M. & Francis R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* **78,** 1069–1079.

McCann K. & Shuter B.J. (1997) Bioenergetics of life history strategies and the comparative allometry of reproduction. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 1289–1298.

McFarlane G.A. & Beamish R.J. (2001) The re-occurrence of sardine off British Columbia characterises the dynamic nature of regimes. *Progress in Oceanography* **49,** 151–165.

McFarlane G.A., King J.R. & Beamish R.J. (2000) Have there been recent changes in climate? Ask the fish. *Progress in Oceanography* **47,** 147–169.

Murray S.N, Ambrose R.F., Bohnsack J.A., Botsford L.W., Carr M.H., Davis G.E., Dayton P.K., Gotshall D., Gunderson D.R., Hixon M.A., Lubchenco J., Mangel M., MacCall A. & McArdle D.A. (1999) No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries* **24,** 11–25.

Musick J.A. (1999) Ecology and conservation of long-live marine animals. *American Fisheries Society Symposium* **23,** 1–10.

Musick J.A., Burgess G., Calliet G., Camhi M. & Fordham S. (2000) Management of sharks and their relatives (Elasmobranchii). *Fisheries* **25,** 9–13.

National Marine Fisheries Service (NMFS) (1999) *Ecosystem-Based Fishery Management. A Report to Congress by the Ecosystem Principles Advisory Committee*. United States Department of Commerce, National Oceanic and Atmospheric Administration, NMFS, Silver Springs, Maryland, 54 pp.

Parker S.J., Berkeley S.A., Golden J.T., Gunderson D.R., Heifetz J., Hixon M.A., Larson R., Leaman B.M., Love M.S., Musick J.A., O'Connell V.M., Ralston S., Weeks H.J. & Yoklavich M.M. (2000) Management of Pacific rockfish. *Fisheries* **25,** 22–30.

Pianka E.R. (1970) On *r*- and *K*-selection. *American Naturalist* **104,** 592–597.

Polovina J.J. (1996) Decadal variation in the trans-Pacific migration of northern bluefin tuna (*Thunnus thynnus*) coherent with climate-induced change in prey abundance. *Fisheries Oceanography* **5,** 114–119.

Sminkey T.R. & Musick J.A. (1995) Age and growth of the sandbar shark, *Carcharhinus plumbeus,* before and after population depletion. *Copeia* **1995,** 871–883.

Smith S.E., Au D.W. & Show C. (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **41,** 663–678.

Spencer P.D. & Collie J.S. (1997) Patterns of population variability in marine fish stocks. *Fisheries Oceanography* **6,** 188–204.

StatSoft (1999) STATISTICA for Windows. Tulsa, OK: StatSoft, Inc.

Winemiller K.O. (1989) Patterns of variation in life history among south American fishes in seasonal environments. *Oecologia* **81,** 225–241.

Winemiller K.O. & Rose K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 2196–2218.

Appendix 1. Life history parameters for species used in analyses. Letter and number code beneath parameter value matches value to citations provided in Appendix 2. Values without a letter and number code denote a biological parameter for which there was no available data and a mean value was used. Values for parental investment, adult habitat and trophic level were determined from information provided by Hart (1973)

Species name	Common name	Size at 50% maturity (mm)	Maximum size (mm)	Growth coefficient (k)	Fecundity	Maximum age	Egg size (mm)	Parental investment	Adult habitat	Trophic level
Ammodytes hexapterus (Pallas)	Pacific sandlance	128 F7	260 F7	0.89 T2	12 650 T2	5 T2	0.60	0	1	3
Anoplopoma fimbria (Pallas)	Sablefish	587 M2	1140 M2	0.297 H1	679 500 H1	113 F9	2.08 H3	0	5	4
Atheresthes stomias (Jordan and Gilbert)	Arrowtooth flounder	355 F4	840 H3	0.12 F4	1 295 000 Z2	15 E1	0.94 R3	0	5	4
Clupea harengus pallasi (Valenciennes)	Herring	177 H3	330 H3	0.45 W1	10 500 H3	15 H8	1.35 H3	0	1	3
Eopsetta jordani (Lockington)	Petrale sole	443 H3	599 H3	0.167 K3	800 000 H3	25 H3	1.3 H3	0	4	4
Gadus macrocephalus (Tilesius)	Pacific cod	515 W2	1000 F8	0.46 W2	148 250 W2	11 W2	1.02 H3	0	4	4
Hexanchus griseus (Bonnaterre)	Sixgill shark	4000 B2	4820 C1	0.12 K4	65 H3	17 K4	65 H3	12	3	5
Hippoglossus stenolepis (Schmidt)	Halibut	960 I1	2670 H3	0.21 S9	2 250 000 I1	55 I1	3.25 H3	0	5	4
Lepidopsetta bilineata (Ayres)	Rock sole	324 F5	600 H3	0.20 F3	950 000 F6	22 F5	0.92 H3	0	4	3
Merluccius productus (Ayres)	Hake	370 M1	800 M1	0.345 M1	1 147 000 M3	23 M1	4.95 M3	1	3	4
Microstomus pacificus (Lockington)	Dover sole	395 F1	710 H3	0.09 F5	1 514 000 H3	49 F3	2.31 H3	0	4	3
Oncorhynchus gorbuscha (Walbaum)	Chum salmon	394 F15	840 S4	0.50 I2	3000 S1	4 P1	5.92 P1	1	1	4
O. keta (Walbaum)	Pink salmon	560 B1	1020 H3	0.51 I2	1550 H7	7 H3	5.5 S4	1	1	4
O. kisutch (Walbaum)	Coho salmon	550 H3	980 H3	0.2 I2	3500 S2	4 S4	5.25 S4	1	1	4
O. nerka (Walbaum)	Sockeye salmon	432 S4	760 H3	0.2 I2	3500 B4	3 S4	6 S4	1	1	4
O. tshawytscha (Walbaum)	Chinook salmon	755 S4	1470 S4	0.62 I2	9500 H6	5 S4	6.5 S4	1	1	4
Ophidion elongatus (Girard)	Lingcod	680 K5	1520 H3	0.360 S8	300 000 H3	20 K5	2.8 S5	3	4	4
Parophrys vetulus (Girard)	English sole	351 F1	570 H3	0.275 F3	913 800 H3	23 F5	0.91 H3	0	4	3
Platichthys stellatus (Pallas)	Starry flounder	350 H3	910 H3	0.19 O1	1 516 000 T1	24 C4	0.91 H3	0	5	4
Raja binoculata (Girard)	Big skate	1300 Z1	2400 H3	0.37 Z1	5 H3	30 Z1	35	2	4	4

R. rhina	Longnose	700	1400	0.160	1	30	35	2	4	4
(Jordan and Gilbert)	skate	Z1	H3	Z1	H3	Z1				
Sardinops sagax	Sardine	210	394	0.45	115 000	13	0.02	1	1	2.5
(Jenyns)		H3	H3	W1	H3	H3	H3			
Sebastes aleutianus (Jordan	Rougheye	445	970	0.015	1 279 813	166	0.97	4	5	4
and Evermann)	rockfish	F12	Y1	S7		Y1				
S. alutus	Pacific ocean	350	510	0.105	168 000	100	0.77	4	5	4
(Gilbert)	perch	F10	L3	A2	H3	F10	L2			
S. babcocki	Redbanded	420	650	0.11	1 279 813	93	0.97	4	4	4
(Thompson)	rockfish	H3	Y1			Y1				
S. brevispinis	Silvergray	400	910	0.085	900 000	81	0.97	4	4	4
(Bean)	rockfish	Y1	S30	H2	S30	S30				
S. caurinus	Copper	250	550	0.12	310 000	45	0.95	4	4	4
(Richardson)	rockfish	H3	H3	S32	H3	F13	S32			
S. entomelas	Widow	380	590	0.11	72 500	58	0.97	4	4	4
(Jordan and Gilbert)	rockfish	W4	L4		H3	L4				
S. flavidus	Yellowtail	435	660	0.157	341 500	64	0.67	4	4	4
(Ayres)	rockfish	W4	F11	A2	H3	L4	H3			
S. maliger	Quillback	280	610	0.11	1 279 813	76	1.5	4	4	4
(Jordan and Gilbert)	rockfish	Y1	H3			Y1	H3			
S. paucispinis	Boccacio	620	910	0.120	1 160 000	30	0.97	4	4	4
(Ayres)		W4	Y1	W3	H3	Y1				
S. pinniger	Canary	480	760	0.152	820 000	75	0.97	4	4	4
(Gill)	rockfish	W4	H3	A2	H3	L4				
S. reedi	Yellowmouth	380	100	0.123	1 279 813	100	0.97	4	5	4
(Westrheim and Tsuyuki)	rockfish	W4	F14	A1		F14				
S. ruberrimus	Yelloweye	460	910	0.11	2 000 000	117	0.97	4	4	4
(Cramer)	rockfish	Y1	Y1		H3	Y1				
Sebastolobus alascanus	Shortspine	230	700	0.009	235 000	100	1.3	4	5	0
(Bean)	thornyhead	F11	F11	K6	F11	K6	H3			
Sebastolobus altivelis	Longspine	160	350	0.072	235 000	50	1.1	4	5	0
(Gilbert)	thornyhead	F11	F11	S31	F11	K6				
Scomber japonicus	Mackerel	350	630	0.32	250 000	10	1.1	1	1	4
(Houttuyn)		H3	H3	C2	C2	H3	H3			
Squalus acanthias (L.)	Dogfish	925	1600	0.044	9	100	35	12	2	4
		S3	K3	S3	K3	C3	K2			
Stenobrachus leucopsarus	Northern	65	130	0.34	12 650	6	0.60	0	3	2
(Eigenmann and Eigenmann)	lampfish	B3	B3	B3		B3	B3			
Thaleichthys pacificus (Richardson)	Eulachon	125	229	0.28	42 195	5	0.09	1	1	2.5
		H3	H3	H4	H5	H5	H3			
Theragra chalcogramma	Pollock	414	670	0.414	597 800	12	1.40	0	2	4
(Pallas)		S6	S6	S6	S6	S6	H3			
Thunnus alalunga	Albacore tuna	900	1250	0.25	1 700 000	10	0.57	1	2	4
(Bonnaterre)		C2	L1	L1	M4	C2	R1			

Appendix 2.

A1 Allen M.J. & Smith G.B. (1988) Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. *National Oceanic and Atmospheric Administration Technical Report of the National Marine Fisheries Service* No. 66, 151 pp.

A2 Archibald C.P., Shaw W. & Leaman B.M. (1981) Growth and mortality estimates of rockfishes (Scorpaenidae) from B. C. coastal waters, 1977–1979. *Canadian Technical Report Fisheries Aquatic Sciences* No. 1048, 57 pp.

B1 Bakkala R.G. (1970) Synopsis of biologcial data on the chum salmon, *Oncorhynchus keta* (Walbaum) 1792. *Fisheries and Agriculture Organisation Fisheries Synopsis* No. 41. 89 pp.

B2 Bass A.J., Heemstra P.C. & Compagno L.J.V. (1986) Carcharhinidae. In: M.M. Smith & P.C. Heemstra (eds) *Smith*'s Sea Fishes. Berlin: Springer-Verlag, pp. 88–95.

B3 Beamish R.J., Leask K.D., Ivanov O.A., Balanov A.A., Orlov A.M. & Sinclair B. (1999) The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. *Progress in Oceanography* 43, 399–442.

B4 Burgner R.L. (1991) Life history of sockeye salmon (*Oncorhynchus nerka*). In: C. Groot & L. Margolis (eds) *Pacific Salmon Life Histories*. Vancouver: University of British Columbia Press, pp. 1–117.

C1 Castro J.I. (1983) *The Sharks of North American Waters*. College Station, TX: Texas A & M University Press, 180 pp.

C2 Collette B.B. & Nauen C.E. (1983) FAO Species Catalogue: Vol. 2 Scombrids of the world: an annotated and illustrated catalogue of tunas, mackerels, bonitos, and related species known to date. *Fisheries and Agriculture Organisation Fisheries Synopsis* No. 125(2), 137 pp.

C3 Compagno L.J.V. (1984) FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1: Hexanthiformes to Lamniformes. *Fisheries and Agriculture Organisation Fisheries Synopsis* No. 125(4), 249 pp.

C4 Cooper J.A. & Chapleau F. (1998) Monophyly and intrarelationship of the family pleuronectidae (pleuronectiformes) with a revised classification. *Fisheries Bulletin* 96, 686–726.

E1 Eschmeyer W.N., Herald E.S. & Hammann H. (1983) *A Field Guide to the Pacific Fishes of North America*. Boston: Houghton Mifflin Co., 336 pp.

F1 Fargo J. (1999) Flatfish stock assessments for the west coast of Canada for 1999 and recommended yield options for 2000. *Canadian Stock Assessment Secretariat Research Document* No. 99/199, 30 pp.

F2 Fargo J. (1998). Flatfish stock assessments for the west coast of Canada for 1998 and recommended yield options for 1999. *Canadian Stock Assessment Secretariat Research Document* No. 98/17, 51 pp.

F3 Fargo J. (1995) Flatfish. In: M. Stocker & J. Fargo (eds) Groundfish stock assessments for the west coast of Canada in 1994 and recommended yield options for 1995. *Canadian Technical Report Fisheries Aquatic Sciences* No. 2069, pp. 160–222.

F4 Fargo J. (1988) Flatfish. In: J. Fargo, M.W. Saunders & A.V. Tyler (eds) Groundfish Stock Assessments for the West Coast of Canada in 1987 and Recommended Yield Options for 1988. *Canadian Technical Report Fisheries Aquatic Sciences* No. 1617, pp. 75–106.

F5 Fargo J. & Kronlund, A.R. (1997) Flatfish stock assessments for the west coast of Canada for 1996 and recommended yield options for 1997. *Canadian Technical Report Fisheries Aquatic Sciences* No. 2149, 124 pp.

F6 Fargo J., Kronlund, A.R., Schnute, J.T. & Haigh, R. (2000) Stock assessment of rock sole and English sole in Hecate Strait for 2000/2001. *Canadian Stock Assessment Secretariat Research Document* No. 2000/166, 83 pp.

F7 Field L. J. (1988) Pacific sand lance, *Ammodytes hexapterus,* with notes on related *Ammodytes* species. In: N.J. Wilimovsky, L.S. Incze & S.J. Westrheim (eds) *Species Synopses: Life Histories of Selected Fish and Shellfish of the Northeast Pacific and Bering Sea*. Seattle, WA: Washington Sea Grant Program Publication, pp. 15–30.

F8 Fisheries and Oceans Canada (1999) Pacific cod in Hecate Strait. *Fisheries and Oceans Canada Science Stock Status Report* No. A6-01. 3 pp.

F9 Fisheries and Oceans Canada (1999) Sablefish. *Fisheries and Oceans Canada Science Stock Status Report* No. A6-02. 4 pp.

F10 Fisheries and Oceans Canada (1999) Pacific Ocean Perch, British Columbia coast. *Fisheries and Oceans Canada Science Stock Status Report* No. A6-11. 5 pp.

F11 Fisheries and Oceans Canada (1999) Thornyheads (Shortspine and Longspine), British Columbia coast. *Fisheries and Oceans Canada Science Stock Status Report* No. A6-12, 4 pp.

F12 Fisheries and Oceans Canada (1999) Rougheye Rockfish. *Fisheries and Oceans Canada Science Stock Status Report* No. A6-15, 6 pp.

F13 Fisheries and Oceans Canada (1999) Inshore Rockfish. *Fisheries and Oceans Canada Science Stock Status Report* No. A6-16, 3 pp.

F14 Fisheries and Oceans Canada (1999) Yellowmouth Rockfish, British Columbia coast. *Fisheries and Oceans Canada Science Stock Status Report* No. A6-17, 3 pp.

F15 Foerster R.E. (1968) The sockeye salmon (*Oncorhynchus nerka*). *Fisheries Research Board of Canada Bulletin* No. 162, 422 pp.

H1 Haist V., Saunders M.W., Hillborn R. & Maunder, M. (1997) Sablefish stock assessment for 1997 and recommended yield options for 1998. *Canadian Stock Assessment Secretariat Research Document* No. 97/146, 85 pp.

H2 Haldorson L. & Love M. (1991) Maturity and fecundity in the rockfishes, *Sebastes* spp., a review. *Marine Fisheries Review* **53,** 25–31.

Appendix 2. Continued

H3 Hart J.L. (1973) Pacific Fishes of Canada. *Bulletin of the Fisheries Research Board of Canada* No. 180, 740 pp.

H4 Hay D.E. (unpublished data). *Fisheries and Oceans Canada*. Pacific Biological Station, Nanaimo, BC, V9R 5K6.

H5 Hay D.E. & McCarter P.B. (2000) Status of the Eulachon, *Thaleichthys pacificus* in Canada. *Canadian Stock Assessment Secretariat Research Document* No. 20o0/145, 95 pp.

H6 Healey M.C. (1991) Life history of chinook salmon (*Oncorhynchus tshawytscha*). In: C. Groot & L. Margolis (eds), *Pacific Salmon Life Histories*. Vancouver: University of British Columbia Press, pp. 313–393.

H7 Heard W.R. (1991) Life history of pink salmon (*Oncorhynchus gorbuscha*). In: C. Groot & L. Margolis (eds) *Pacific Salmon Life Histories*. Vancouver: University of British Columbia Press, pp. 119–230.

H8 Hourston A.S. & Haegele C.W. (1980) Herring on Canada's Pacific Coast. *Canadian Special Publication of Fisheries and Aquatic Sciences* No. 48. 23 pp.

I1 International Pacific Halibut Commission. (1998) The Pacific halibut: biology, fishery and management. *International Pacific Halibut Commission Technical Report* No. 40, 64 pp.

I2 Ishida Y., Ito S., Ueno Y. & Sakai J. (1998) Seasoanl growth patterns of Pacific salmon (*Oncorhynchus* spp.) in offshore waters of the North Pacific Ocean. *North Pacific Anadromous Fisheries Commission Bulletin* No. 1, 66–80.

K1 Ketchen K.S. (1975) Age and growth of dogfish, *Squalus acanthias* in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 32, 43–59.

K2 Ketchen K.S. (1988) The Spiny Dogfish (*Squalus acanthias*) in the Northeast Pacific and a History of its Utilization. *Canadian Special Publication of Fisheries and Aquatic Sciences* No. 88, 78 pp.

K3 Ketchen K.S. & Forrester C. (1966) Population dynamics of the petrale sole, *Eopsetta jordani,* in waters off Western Canada. *Bulletin of the Fisheries Research Board of Canada* No. 115, 195 pp.

K4 King J.R. (unpublished data). *Fisheries and Oceans Canada*. Pacific Biological Station, Nanaimo, BC, V9R 5K6.

K5 King J.R. & Surry, A.M. (2000) Lingcod stock assessment and recommended yield options for 2001. *Canadian Stock Assessment Secretariat Research Document* No. 2000/164, 50 pp.

K6 Kline D. (1996) *Radiometric Age Verification for Two Deep-sea Rockfish* (*Sebastolobus altivelis* and *Sebastolobus alacanus*). MSc Thesis. San Jose: San Jose State University, 124 pp.

L1 Laurs R.M. & Wetherall J.A. (1981) Growth rates of North Pacific albacore, *Thunnus alalunga,* based on tag returns. *Fisheries Bulletin* **79,** 293–302.

L2 Leaman B.M. (1988) *Reproductive and Population Biology of Pacific Ocean Perch* (*Sebastes alutus* (Gilbert)). PhD Thesis. Vancouver: University of British Columbia, 200 pp.

L3 Leaman B.M., Cornthwaite A.M., & Stanley R.D. (1996) Cruise details and biological information from the Pacific Ocean Perch survey, R/V W. E. Ricker, June 19–30, 1993. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* No. 2388, 71 pp.

L4 Love M.S., Yoklavich M., Thorsteinson L. & Butler J. (2002) *The Rockfishes of the Northeast Pacific*. Berkley: University of California Press, 404 pp.

M1 McFarlane G.A. & Beamish R.J. (1985). Biology and fishery of Pacific whiting, *Merluccius productus,* in the Strait of Georgia. *Marine Fisheries Review* **47**, 23–34.

M2 McFarlane G.A. & Beamish R.J. (1983) Biology of adult sablefish, (*Anoplopoma fimbria*) in waters off western Canada. In: B. Melteff (ed.) *Proceedings of the International Sablefish Symposium.* Lowell Wakefield Series. *Alaska Sea Grant Report* No. 83-8, pp. 59–93.

M3 McFarlane G.A. & Saunders M.W. (1997) Fecundity of Pacific hake (*Merluccius productus*) for three stocks off the west coast of North America. *California Current Oceanography and Fisheries Investigations* No. 38, 112–119.

M4 Mooney-Seus M.L. & Stone G.S. 1996. *The Forgotten Giants: Giant Ocean Fishes of the Atlantic and Pacific*. Washington: Ocean Wildlife Campaign, 64 pp.

O1 Orcutt H.G. (1950) The life history of the starry flounder *Platichthys stellatus* (Pallas). *California Department of Fish and Game Fish Bulletin* No. 78, 64 pp.

P1 Pauly G.B., Risher R. & Thomas G.L. (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): Sockeye salmon. *United States Department of Fish and Wildlife Service Biological Report* No. 82(11.116), 22 pp.

R1 Ramon D. & Bailey K. (1996) Spawning seasonality of albacore, *Thunnus alalunga,* in the South Pacific Ocean. *Fisheries Bulletin* 94, 724–733.

R2 Rexstad E.A. & Pikitch E.K. (1986) Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus*. *Fisheries Bulletin* 84, 947–956.

R3 Rickey M.H. (1995) Maturity, spawning, and seasonal movement of arrowtooth flounder, *Atheresthes stomias,* off Washington. *Fisheries Bulletin* 93, 127–138.

S1 Salo E.O. (1991) Life history of chum salmon (*Oncorhynchus keta*). In: C. Groot & L. Margolis (eds) *Pacific Salmon Life Histories*. Vancouver: University of British Columbia Press, pp. 231–309.

S2 Sandercock F.K. (1991) Life history of coho salmon (*Oncorhychus kisutch*). In: C. Groot & L. Margolis (eds) *Pacific Salmon Life Histories*. Vancouver: University of British Columbia Press, pp. 395–445.

Appendix 2. Continued

S3	Saunders M.W. & McFarlane G.A. (1993) Age and length at maturity of the female spiny dogfish, *Squalus acanthias,* in the Strait of Georgia, British Columbia, Canada. *Environmental Biology of Fishes* 38, 49–57.
S4	Scott W.B. & Crossman E.J. (1998) *Freshwater Fishes of Canada.* Oakville: Galt House Publications Ltd., 966 pp.
S5	Shaw W.N. (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest) – Lingcod. *United States Fish and Wildlife Service, Fish and Wildlife Species Profiles* No. 82(11.119), 10 pp.
S6	Shaw W. & McFarlane G.A. (1983) Biology, distribution and abundance of walleye pollock (*Theragra chalcogramma*) off the west coast of Canada. *International North Pacific Fisheries Commission Bulletin* No. 45, pp. 262–283.
S7	Schnute J., Olsen N. & Haigh R. (1999) Slope rockfish assessment for the west coast of Canada in 1999. *Canadian Stock Assessment Secretariat Research Document* No. 99/184, 110 pp.
S8	Smith B. & McFarlane G. (1990) Growth analysis of Strait of Georgia lingcod by use of length–frequency and length–increment data in combination. *Transactions of the American Fisheries Society* **119,** 802–812.
S9	Southward G. & Chapman D. (1965) Utilization of Pacific halibut stocks: study of Bertalanffy's growth equation. *Report of the International Pacific Halibut Commission* No. 39, 33 pp.
S30	Stanley R. & Kronlund A.R. (2000) Silvergray rockfish (*Sebastes brevispinis*) assessment for 2000 and recommended yield options for 2001/2002. *Canadian Stock Assessment Secretariat Research Document* 2000/173. 114 pp.
S31	Starr, P.J. & Haigh R. 2000. Assessment of the Canadian longspine thornyhead (*Sebastolobus altivelis*) for 2000. *Canadian Stock Assessment Secretariat Research Document,* 2000/154, 66 pp.
S32	Steni D. & Hassler T.J. (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific southwest): brown rockfish, copper rockfish, and black rockfish. *United States Department of Fish and Wildlife Service Biological Report* No. 82(11.113), 15 pp.
T1	Tikhonov V.I. (1983) Fecundity of flounder on the West Kamchatka shelf. *Soviet Journal of Marine Biology* 8, 136–140.
T2	Trumble R.J. (1973) *Distribution, Relative Abundance, and General Biology of Selected Underutilized Fishery Resources of the Eastern North Pacific Ocean.* MSc Thesis, Seattle, WA: University of Washington, 178 pp
W1	Ware D.M. & McFarlane G.A. (1989) Fisheries production domains in the northeast Pacific ocean. In: R.J. Beamish & G.A. McFarlane (eds) *Effects of Ocean Variability on Recruitment and An Evaluation of Parameters Used in Stock Assessment Models. Canadian Special Publication of Fisheries and Aquatic Sciences* No. 108, pp. 359–379.
W2	Westrheim S.J. (1996) On the Pacific cod (*Gadus macrocephalus*) in BC and a comparison with Pacific cod elsewhere and Atlantic cod (*G. morhua*). *Canadian Technical Report of Fisheries and Aquatic Sciences* No. 2092. 390 pp.
W3	Wilkins M.E. (1980) Size composition, age composition, and growth of chilepepper (*Sebastes goodei*) and bocaccio (*Sebastes paucispinus*) from the 1977 rockfish survey. *Marine Fisheries Reviews,* 48–53.
W4	Wyllie-Echeverria T. (1987) Thirty-four species of California rockfishes: maturity and seasonality of reproduction. *Fisheries Bulletin* 85, 229–249.
Y1	Yamanaka, L. (unpublished data). *Fisheries and Oceans Canada.* Pacific Biological Station, Nanaimo, British Columbia, Canada, V9R 5K6.
Z1	Zeiner S.J. & Wolf P. (1993) Growth characteristics and estimates of age at maturity of two species of skates (*Raja binoculata* and *Raja rhina*) from Monterey Bay, California. In: S. Branstetter (ed.) *Conservation Biology of Elasmobranchs. National Oceanic and Atmospheric Administration Technical Report of the National Marine Fisheries Service* No. 115, pp. 87–99.
Z2	Zimmerman M. (1997) Maturity and fecundity of arrowtooth flounder, *Atheresthes stomias,* from the Gulf of Alaska. *Fisheries Bulletin* **95,** 598–611.