A review of the evidence for density dependence or independence in the life history of Coho (*Oncorhynchus kisutch*) and other salmonids from the west coast of North America. References in **bold** refer specifically to Coho from Oregon or California.

DD = Density Dependence; CDD = Compensatory Density Dependence

Spawner-to-fry relationship

Spawner-to-fry relationship shows compensatory DD (evidence)	Hunter 1959 - BC pink and chum
Each spawner requires a certain amount of space (evidence), suggesting a spawner-to-fry carrying capacity	Van den Berghe and Gross 1989 - WA wild coho
Spawner-to-fry relationship shows compensatory DD or carrying capacity (opinion)	Bjorkstedt 2000 - General salmonid model Foerster 1968 - AK and BC sockeye Maunder 1997 - W. coast pink model **Reeves et al. 1989 - Key for WA and OR wild coho** Reiser and Bjornn 1979 - W. coast wild coho
Assumptions of carrying capacity & random spawning produce a spawner-to-fry curve intermediate between Ricker & B-H	Maunder 1997 - W. coast pink model

Summer survival

Summer survival stock-recruitment curve is non-linear	Hartman and Scrivener 1990 - BC wild coho
Summer survival stock-recruitment curve shows compensatory DD (evidence)	Holtby and Scrivener 1989 - BC wild coho
Summer survival stock-recruitment curve shows compensatory DD or carrying capacity (opinion)	Beechie et al. 1994 - WA wild coho **Chapman 1965 - OR wild coho** **House and Crispin 1990 - OR wild coho model** **Kruzic and Scarnecchia 2001 - OR hatchery coho** Mullan et al. 1992 - WA wild coho Murphy et al. 1984 - AK wild coho Nass et al. 1996 - BC wild coho assessment **Nickelson and Lawson 1998 - OR wild coho model** **Reeves et al. 1989 - Key for WA and OR wild coho** Tschaplinski 2000 - BC wild coho
Evidence for existence of summer carrying capacity: Consistent numbers by unit of area or habitat type	**Burns 1971 - CA wild coho** **Chapman 1962 - OR wild coho** **Chapman 1965 - OR wild coho** Dolloff 1987 - AK wild coho Hartman et al. 1982 - BC wild coho **Leidholt-Bruner et al. 1992 - OR wild coho** Murphy et al. 1984 - AK wild coho **Nickelson et al. 1992 - OR wild coho**
Evidence for existence of summer carrying capacity: An increase in available habitat results in higher fish abundance	**House 1996 - OR wild coho** **Roni and Quinn 2001 - WA and OR wild coho** **Solazzi et al. 2000 - OR wild coho**
Evidence for existence of summer carrying capacity: A decrease in available habitat results in lower fish abundance	Scrivener and Andersen 1982 - BC wild coho Tschaplinski 2000 - BC wild coho
Evidence for existence of summer carrying capacity: Excess fish are forced out	Bilby and Bisson 1987 - WA hatchery coho **Chapman 1962 - OR wild coho**
Finite summer habitat is limiting in some systems	Beechie et al. 1994 - WA wild coho Hartman et al. 1982 - BC wild coho Sharma and Hilborn 2001 - WA wild coho
Summer habitat is not limiting in some systems	Nass et al. 1996 - BC wild coho assessment

Summer survival DD mechanism

Habitat with a combination of food and cover from predators is crucial in summer (opinion)	Chapman 1966 - Salmonids in general **Kruzic and Scarnecchia 2001 - OR hatchery coho**
Territoriality sets the carrying capacity in summer	**Chapman 1962 - OR wild coho** **Mason and Chapman 1965 - OR captive coho** Mullan et al. 1992 - WA wild coho
During summer, territorial fish move less and suffer less mortality	Martel 1996 - BC wild coho Martel and Dill 1995 - BC hatchery coho

Winter survival

Winter survival stock-recruitment curve shows compensatory DD or carrying capacity (opinion)	Beechie et al. 1994 - WA wild coho Bustard and Narver 1975 - BC wild coho Dolloff 1987 - AK wild coho **Nickelson and Lawson 1998 - OR wild coho model** **Reeves et al. 1989 - Key for WA and OR wild coho** Swales et al. 1986 - BC wild coho Swales et al. 1988 - BC wild coho
Evidence for existence of winter carrying capacity: Consistent numbers by unit of area or habitat type	Dolloff 1987 - AK wild coho **Nickelson et al. 1992 - OR wild coho**
Evidence for existence of winter carrying capacity: Higher survival or retention where there is more habitat	Quinn and Peterson 1996 - WA wild coho Tschaplinski and Hartman 1983 - BC wild coho
Evidence for existence of winter carrying capacity: An increase in available habitat results in higher fish abundance	Bryant 1988 - AK wild coho Cederholm et al. 1997 - WA wild coho **House and Boehne 1985 - OR wild coho** **Roni and Quinn 2001 - WA and OR wild coho** **Solazzi et al. 2000 - OR wild coho**
Finite winter habitat is limiting in some systems	Bustard and Narver 1975 - BC wild coho Cederholm et al. 1997 - WA wild coho Hartman et al. 1987 - BC wild coho **Nickelson et al. 1992 - OR wild coho** **Solazzi et al. 2000 - OR wild coho**
Dissenting opinion: No evidence for density-dependent survival in winter	Hartman and Scrivener 1990 - BC wild coho Murphy et al. 1984 - AK wild coho
Dissenting opinion: Winter survival assumed not to be density-dependent	**House and Crispin 1990 - OR wild coho model**

Winter survival DD mechanism

Habitat which provides protection from high-flow washout is crucial for winter survival (evidence)	**Bell et al. 2001 - CA wild coho** Tschaplinski and Hartman 1983 - BC wild coho
Habitat which provides protection from high-flow washout is crucial for winter survival (opinion)	Bustard and Narver 1975 - BC wild coho Chapman 1966 - Salmonids in general Sharma and Hilborn 2001 - WA wild coho
Habitat which provides cover (protection from predators) is crucial for winter survival (opinion)	Bustard and Narver 1975 - BC wild coho Tschaplinski and Hartman 1983 - BC wild coho

Smolt outmigration survival

Survival during outmigration shows depensatory DD due to predators taking a fixed number	Wood 1987 - BC mixed coho
Smolt-to-spawner survival of hatchery fish shows DD (could be B-H or Ricker) due to mortality shortly after release	**Anderson and Wilen 1985 - WA to CA hatchery coho**

Marine survival

Marine survival correlates strongly with climate and sea conditions	Beamish & Bouillon 1993 - N. Pacific pink, chum & sockeye Beamish et al. 1999 - BC mixed coho **Beamish et al. 2000 - BC to CA hatchery coho** **Clark and McCarl 1983 - OR hatchery coho** **Cole 2000 - WA to CA hatchery coho** **Coronado and Hilborn 1998a - AK to CA hatchery coho** **Coronado and Hilborn 1998b - AK to CA hatchery coho** **Emlen et al. 1990 - WA to CA mixed coho** **Lawson 1997 - OR wild coho** **Nickelson and Lichatowich 1984 - OR hatchery coho** **Scarnecchia 1981 - OR wild coho**
No evidence for DD at sea	**Nickelson 1986 - WA to CA wild and hatchery coho** **Nickelson and Lichatowich 1984 - OR hatchery coho** **Peterman 1981 - WA to CA mixed coho** Walters et al. 1978 - BC salmonid model
No DD at sea (opinion)	**House and Crispin 1990 - OR wild coho model** Lee and Hyman 1992 - General salmonid model **Nickelson and Lawson 1998 - OR wild coho model**
Evidence for DD at sea	**Clark and McCarl 1983 - OR hatchery coho** **Coronado and Hilborn 1998a - BC to CA hatchery coho** **Coronado and Hilborn 1998b - BC to CA hatchery coho** **Emlen et al. 1990 - WA to CA hatchery coho** **Lin and Williams 1988 - OR hatchery coho** **McCarl and Rettig 1983 - WA to CA mixed coho** McDonald and Hume 1984 – BC sockeye Peterman 1982 - N. Pacific sockeye
Evidence for DD at sea only in years of low upwelling	**McGie 1984 - WA to CA mixed coho** **Peterman and Routledge 1983 - OR mixed coho**
Marine recruitment has a carrying capacity (opinion), suggesting compensatory DD	Eggers et al. 1984 - AK sockeye model Pearcy 1997 - Pacific salmonids in general
We cannot say whether or not there is DD at sea (no statistical power)	**Pearcy 1992 - WA to CA mixed coho** **Peterman 1989 - OR wild and hatchery coho**
Any appearance of marine DD in the data results from the fact that wild and hatchery stocks have different survival	**Nickelson 1986 - WA to CA wild and hatchery coho**
Evidence for depensatory DD at sea	Peterman 1982 - N. Pacific sockeye

Marine survival depends on size (evidence)	**Gowan and McNeil 1984 - OR hatchery coho** Hartman and Scrivener 1990 - BC wild coho Mathews and Buckley 1976 - WA hatchery coho **Mathews and Ishida 1989 - WA and OR hatchery coho** McGurk 1996 - W. coast salmonids Parker 1971 - BC pink and chum **Peterman 1981 - WA to CA mixed coho** Ricker 1962 - N. Pacific sockeye Ward and Slaney 1988 - BC steelhead
Marine survival depends on size, but only in years of low overall marine survival (evidence)	Holtby et al. 1990 - BC wild coho
Marine survival depends on size (opinion)	Bradford 1995 - W. coast salmonids Mortensen et al. 2000 - AK pink **Pearcy 1984 - WA and OR mixed coho** **Scarnecchia 1981 - OR wild coho** Thedinga and Koski 1984 - AK wild coho Walters et al. 1978 - BC salmonid model
Size dependence of marine survival results from size-selective predation (evidence)	Parker 1971 - BC pink and chum
Size dependence of marine survival results from size-selective predation (opinion)	**Gowan and McNeil 1984 - OR hatchery coho**
Most marine mortality happens shortly after ocean entry (evidence)	Mathews and Buckley 1976 - WA hatchery coho model Mortensen et al. 2000 - AK pink **Pearcy 1984 - WA and OR mixed coho** **Pearcy 1988 - WA and OR mixed coho** **Pearcy 1992 - WA and OR hatchery coho** Peterman 1982 - N. Pacific sockeye
Most marine mortality happens shortly after ocean entry (opinion)	Beamish et al. 1994 - BC mixed coho **Emlen et al. 1990 - WA to CA wild and hatchery coho** **Fisher and Pearcy 1988 - WA and OR mixed coho**
Dissenting opinions: Dependence of marine mortality on size is negative or non-significant	Bilton 1978 - BC hatchery coho Holtby and Healey 1986 - BC wild coho Tschaplinski 2000 - BC wild coho
Theory: Sea conditions determine growth rate, which determines duration of exposure to size-selective predation	**Cole 2000 - WA to CA hatchery coho** Holtby et al. 1990 - BC wild coho **Pearcy 1984 - WA and OR mixed coho** **Pearcy 1992 - WA to CA mixed coho** **Scarnecchia 1981 - OR wild coho**
Support for growth-predation theory of marine survival: No evidence that marine mortality results from starvation	**Fisher and Pearcy 1988 - WA and OR mixed coho** Walters et al. 1978 - BC salmonid model
Support for growth-predation theory of marine survival: Marine survival correlates strongly with early ocean growth rate	Holtby et al. 1990 - BC wild coho Mortensen et al. 2000 - AK pink
Growth at sea may also be determined by density (evidence)	Peterman 1984 - N. Pacific sockeye Rogers 1980 - AK sockeye
Growth at sea may also be determined by density (opinion)	Bjorkstedt 2000 - General salmonid model Childerhose and Trim 1979 - Mostly BC salmonids **Pearcy 1992 - WA to CA mixed coho**

Theory: Predators pursue alternative prey (offshore) in years of high upwelling, resulting in spatial mismatch with salmonids	**Fisher and Pearcy 1988 - WA and OR mixed coho** Holtby and Scrivener 1989 - BC wild coho **Pearcy 1988 - WA to CA mixed coho**
Support for alternative prey theory: First part of ocean residence is spent near shore	**Pearcy 1984 - WA and OR mixed coho**
Support for alternative prey theory: Murres that decimate hatchery fish during nearshore release are scarce in high-upwelling years	**Pearcy 1988 - OR hatchery coho**

Data spanning multiple life history transitions: Spawner-to-smolt or fry-to-smolt relationship

Spawner-to-smolt relationship is significantly nonlinear, supporting DD	**Bradford 1997 - BC to OR wild coho**
Spawner-to-smolt relationship fits the hockey stick model	**Barrowman and Myers 2000 - BC and OR wild coho** **Bradford et al. 2000 - BC to OR wild coho** Silliman 1970 - AK sockeye in lakes
Smolt production correlates w/local factors like stream length & flow, suggesting carrying capacity & CDD (evidence)	**Bradford 1999 - AK to OR wild coho** **Bradford et al. 1997 - AK to CA wild coho** Fraser 1969 - BC wild coho Nickelson and Lichatowich 1984 - WA wild coho **Scarnecchia 1981 - OR wild coho** Sharma and Hilborn 2001 - WA wild coho
Fry-to-smolt relationship shows depensatory DD due to predators taking consistent numbers (evidence)	Hunter 1959 - BC pink and chum
Spawner-to-smolt relationship shows DD (opinion)	Lee and Hyman 1992 - General salmonid model
Spawner-to-smolt recruitment correlates with stream flow, suggesting compensatory DD or carrying capacities (opinion)	**Anderson and Wilen 1985 - WA to CA wild coho** Reiser and Bjornn 1979 - W. coast salmonids
Spawner-to-smolt survival is limiting in many systems, and stream habitat loss has caused population declines (opinion)	**Brown et al. 1994 - CA wild coho** **Lichatowich 1989 - OR wild coho** **Nehlsen et al. 1991 - WA to CA mixed coho** **Weitkamp et al. 2000 - CA wild coho**

Data spanning multiple life history transitions: Spawner-to-spawner relationship

Spawner-to-spawner survival shows DD (could be B-H or Ricker)	**Anderson and Wilen 1985 - WA to CA wild coho**
Spawner-to-spawner recruitment curve may be intermediate between B-H and Ricker (evidence)	Holtby and Scrivener 1989 - BC wild coho model
Spawner-to-spawner carrying capacity is set in streams: Stream enhancement increases returning spawner numbers	**Crispin et al. 1993 - OR wild coho**
Conflicting evidence? Spawner-to-spawner recruitment correlates negatively with degree (not rate) of land use change	Bradford and Irvine 2000 - BC wild coho

Potential for delayed density dependence

Spawner size affects fecundity: Bigger females have more eggs	Fleming and Gross 1994 - BC mixed coho Foerster 1968 - AK and BC sockeye
Spawner size affects egg size: Bigger females have bigger eggs	Van den Berghe and Gross 1989 - WA wild coho
Spawner size affects egg-to-fry survival: Nests of bigger females are more likely to survive	Van den Berghe and Gross 1989 - WA wild coho
Egg size affects emerging fry size: Bigger eggs produce bigger emerging fry	Beacham et al. 1985 - BC wild coho
Spawner density affects summer growth & survival: Adding salmon carcasses increases density & size of summer fries	Bilby et al. 1998 - WA wild coho
Summer density affects summer growth and fall size: Evidence for DD growth	Hartman and Scrivener 1990 - BC wild coho Hartman et al. 1987 - BC wild coho Holtby and Scrivener 1989 - BC wild coho **Roni and Quinn 2001 - WA and OR wild coho** Scrivener and Andersen 1982 - BC wild coho
Size at emergence affects summer growth and fall size: Big fry win territories, grow fast, and become big winter juveniles	**Chapman 1962 - OR wild coho** **Mason and Chapman 1965 - OR captive coho** Nielson 1992 - WA wild coho Reinhardt 1999 - BC captive wild coho
Dissenting opinion: During summer, big fish actually grow more slowly than small ones	Rhodes and Quinn 1999 - WA planted coho
Summer size affects survival or retention: Big fish displace small fish	**Nickelson et al. 1986 - OR mixed coho**
Dissenting opinion: No evidence for size-dependent summer survival	Rhodes and Quinn 1999 - WA planted coho
Summer density negatively affects summer growth and fall size	Fraser 1969 - BC wild coho Nielson 1992 - WA wild coho Tschaplinski 2000 - BC wild coho
Fall size affects winter survival: Survival correlates with size	Hartman and Scrivener 1990 - BC wild coho Holtby 1988 - BC wild coho Holtby and Scrivener 1989 - BC wild coho Quinn and Peterson 1996 - WA wild coho Tschaplinski 2000 - BC wild coho
Fall size affects smolt size: Positive correlation	Hartman and Scrivener 1990 - BC age 1+ wild coho
Smolt size affects survival at sea: Positive correlation (evidence)	Bilton 1978 - BC hatchery coho **Gowan and McNeil 1984 - OR hatchery coho** Hartman and Scrivener 1990 - BC wild coho Holtby et al. 1990 - BC wild coho **Mathews and Ishida 1989 - WA and OR hatchery coho** Ward and Slaney 1988 - BC steelhead
Smolt size affects survival at sea: Positive correlation (opinion)	Mathews and Buckley 1976 - WA hatchery coho model
Dissenting opinion: No evidence that eggs from bigger females have higher survival	Holtby and Healey 1986 - BC wild coho
Combining current and delayed compensatory DD would produce overcompensatory DD	Bjorkstedt 2000 - General salmonid model

Geographic applicability

CA is like OR coast (coastal rains dominate, rivers drain directly into ocean), and unlike Columbia River or WA coast	**Anderson & Wilen 1985 - WA to CA wild & hatchery coho**
OR is most sensitive to sea conditions: CA has more upwelling; WA & BC have more littoral production areas	**Nickelson and Lichatowich 1984 - BC to CA mixed coho**

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